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DESERT BIOME

ECOSYSTEM ANALYSIS STUDIES
U.S. INTERNATIONAL BIOLOGICAL PROGRAM

REPORT OF 1972 PROGRESS IN THREE VOLUMES

MAY 1973

Research supported through the US/IBP Desert Biome Program, Grant # GB32139X from the National Science Foundation. The material contained herein does not constitute publication. It is subject to revision and reinterpretation. The authors request that it not be cited without their expressed permission.

VOLUME 1 - CENTRAL OFFICE; MODELLING; AQUATIC STUDIES

VOLUME 2 - METHODOLOGICAL AND VALIDATION STUDIES

VOLUME 3 - TERRESTRIAL PROCESS STUDIES

VOLUME 3

TERRESTRIAL PROCESS STUDIES

VOLUME 3

TERRESTRIAL PROCESS STUDIES

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1972 PROGRESS REPORT

BIOMASS AND NUTRIENTS IN DESERT SHRUB ECOSYSTEMS

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Research Memorandum, RM 73-8

MAY 1973

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ABSTRACT

In the second year of a study to measure distribution of biomass and nutrients in shrub ecosystems as a function of shrub age, season and environmental variables, fifteen shrubs each of mesquite (*Prosopis juliflora*) and palo verde (*Cercidium floridum*) were sampled. Seasonal patterns of change in percentage N of leaves in mesquite and palo verde were observed and appear real. Additional sampling is needed to confirm these changes and to determine if suspected concurrent changes in N of small branches reflecting translocation is real. Nitrogen content of mulch of the overstory shrub appears not to vary spatially under the shrub, but that of understory species does. The understory species may be acting as a bioassay of variable soil N content with distance away from the stem of the shrub.

Although 11 percent of N in the above-ground phytomass of mesquite is contained in the annual plant parts and is therefore subject to seasonal variation, N in the above-ground portion of mesquite is highly correlated with phytomass. The opportunity to extend this relationship and estimate N and C fixed in these ecosystems from mensurational characteristics of the shrubs appears good. Special effort will be devoted to exploration of these relationships during the third year of the project.

INTRODUCTION

A study of seasonal and annual changes in the distribution and balance of biomass and nutrients in mesquite (*Prosopis juliflora*) ecosystems was initiated in 1971 at the Santa Rita Experimental Range. The study was expanded in 1972 to include palo verde (*Cercidium floridum*) at the Santa Rita site, and to sample mesquite on a limited basis at the Jornada Experimental Range in New Mexico. Five shrubs each of the two species were sampled on each of three phenological dates; three shrubs of mesquite were sampled at the Jornada site in August. Twice as many samples of palo verde were collected as we had originally expected to collect. Although the field work was accomplished on schedule and with improved efficiency over the previous year, laboratory work has been delayed because of the increased number of samples for analysis. In 1973, we anticipate that information gained during the first 2 years of the study will permit us to refine our sampling techniques and reduce the laboratory work.

OBJECTIVES

The objectives of this study are to measure the distribution and balance of biomass and nutrients (carbon and nitrogen) in the regime of important desert shrub ecosystems, specifically mesquite (*Prosopis juliflora*) and palo verde (*Cercidium floridum*).

Specific objectives are:

1. To determine the influence of shrub age on distribution of biomass, and on distribution and balance of nutrients in individual shrub ecosystems.
2. To measure seasonal changes in biomass, and in distribution and balance of nutrients in individual shrub ecosystems.
3. To determine the effect of macro-environmental factors (precipitation, temperature, radiation), which vary yearly, on increment of biomass and nutrient distribution.

METHODS

Size data of shrubs (DSCODE A3UKB01) were accumulated by measurements collected three times yearly on five randomly-selected shrubs of each species, representing the population of size classes available. Above-ground biomass of shrubs (DSCODE A3UKB02) was determined through collections made three times yearly on five randomly-selected

shrubs of each species, representing the population of size classes available. Weight was obtained to determine biomass/shrub. Samples were prepared for laboratory analysis.

Collections of root biomass associated with shrubs (DSCODE A3UKB03) were made three times yearly from five randomly-selected shrubs of each species, representing the population of size classes available. Weight was taken to determine biomass/unit volume. Samples were prepared for laboratory analysis.

Collections of understory vegetation of shrubs (DSCODE A3UKB04) were made three times yearly under five randomly-selected shrubs of each species, representing the population of size classes available. Standing dead and live material were separated and weighed to determine weight/unit area, then prepared for laboratory analysis.

Collections of mulch under shrubs (DSCODE A3UKB05) were made three times yearly under five randomly-selected shrubs of each shrub, representing the population of size classes available. Mulch of mesquite and other vegetation was separated and weighed to determine weight/unit area, then prepared for laboratory analysis.

Analyses for total nitrogen by the Kjeldahl method (Bremner, 1965) and for organic carbon by the dry combustion method (Allison, Bollen and Moodie, 1965) using a LECO high-frequency induction furnace, were run on above-ground biomass (DSCODE A3UKB06), understory species (DSCODE A3UKB07), mulch (DSCODE A3UKB08) and soil (DSCODE A3UKB09).

RESULTS AND DISCUSSION

Results of second-year sampling for nutrient content of plant parts of mesquite (Table 1) give us no reason to alter earlier observations (Klemmedson and Smith, 1972) regarding nitrogen content of plant parts and variations as a function of sampling period. Seasonal trends in N content of leaves, current branches, and perhaps branches less than 1 cm diameter, appear to be real and to have biological significance. Bi-weekly sampling was initiated in May to gain more information on the trend of N content in leaves and current branches. The data for leaves of mesquite and palo verde (Figure 1) show a fluctuating pattern for percentage leaf N between the periods of leaf initiation in the spring and the summer rainy period, followed by a steady decline into fall and winter periods. Further analyses are needed to determine if the spring and summer fluctuations are associated with precipitation patterns. The fall decline is likely a combination of translocation and losses by leaching and/or oxidation.

Seasonal differences in N content of larger branches (> 1 cm) and dead wood are difficult to rationalize biologically and must be attributed to sampling variation at

2.3.1.1.-4

Table 1. Percentage nitrogen in plant parts of mesquite and palo verde by seasons

Plant Part	Mesquite				Palo Verde		Significance of Differences
	5-71 ^{††}	9-71	2-72	5-72	2-72	5-72	
	-----%-----						
Flowers	3.67 [†]	----	----	3.16	----	3.35	
Fruit	----	----	----	4.70	----	3.55	
Leaves	3.30	2.83	2.25	3.09	----	3.94	*
Current Branches	2.28	1.98	2.15	1.95	2.56	3.08	*
Branches < 1 cm	1.20	1.54	1.78	1.58	1.61	1.62	
Branches > 1 cm	1.09	1.34	1.14	1.12	.76	1.25	
Dead Wood	.83	1.00	.98	1.15	.90	0.86	*

* Species difference significant at $\alpha = .05$; other species differences were non-significant.

† Except for flowers and fruit, all values are means of five samples.

†† Month and year.

Table 2. Distribution of nitrogen in above-ground phytomass of mesquite

Table 1. Effect of season on the growth of <i>Pinus strobus</i> L.							
Year & Season	Leaves	Flowers	Fruit	Branches			Dead Wood
				Current	<1cm	>1cm	
				-----%			
1971 Spring	17.8	0.3	----	0.1	21.4	38.7	21.1
Fall	6.8	---	----	0.6	21.9	45.6	19.4
1972 Winter	1.0	---	----	1.0	29.5	45.9	22.3
Spring	10.8	0.1	0.4	0.7	13.7	49.4	25.0
Mean	10.6	0.1	<.01	0.6	21.7	44.9	22.0

this time. Paired t-tests show that leaves and current growth of palo verde were significantly higher in the spring of the year than those of mesquite (Table 1). Data in Figure 1 suggest this difference is maintained throughout the year. The significant difference in N content of dead wood for the May 1972 sampling period is highly suspect for reasons given above. Fruit were produced on both mesquite and palo verde this year, yielding high but extremely variable N content between plants.

Data for 20 shrubs show that N in the above-ground phytomass of mesquite is largely tied up in woody tissues. For the average-size mesquite shrub sampled, about 11 percent (approximately 60g) of the N in above-ground phytomass was contained in leaves, flowers and fruit (Table 2). Even so, this is about twice the amount of

N contained in similar plant parts in 50-year-old pole size ponderosa pine (Welch, 1973). The relatively high percentage of N contained in these annual plant parts can be attributed both to the amount of tissue, relative to total phytomass, and to the high percentage of N content of the tissues.

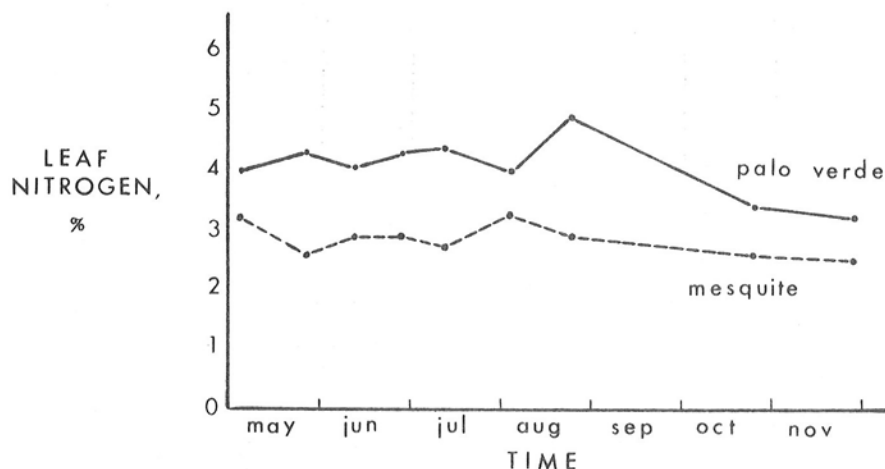


Figure 1. Percentage nitrogen in leaves of mesquite and palo verde as a function of time (DSCODE A3UKB06).

Because of the annual and seasonal differences in percentage N of plant parts which appear to be showing up (Table 1), the percentage distribution of N can be expected to vary also with season. Real trends in distribution of N are suggested for leaves, current branches, and perhaps for branches less than 1 cm diameter (Table 2), even if we account for the fact that these data are not adjusted for differences in shrub size. Because each value in the table is the mean of only five shrubs sampled at random within size class, part of the variation must be attributed to sampling variation.

Despite the fact that concentration of N in plant parts varies from shrub to shrub and at least 11 percent of the N in above-ground phytomass may be subject to seasonal fluctuations, the quantity of N in the phytomass is highly correlated with above-ground phytomass as shown by the regression in Figure 2. This suggests that good estimates of N in the phytomass can be made if the above-ground phytomass is known. A similar regression equation ($Y = -.109 + 0.413 X$, where Y is kilograms of

2.3.1.1.-6

carbon and X is kilograms of phytomass) can be used to estimate the amount of carbon fixed in mesquite shrubs. Since carbon in plant tissues is quite stable, it is not surprising that the correlation coefficient is near 1.0 ($r = .99$). If a regression between some mensurational characteristic of shrubs and their phytomass could be developed with high predictability, much of the tedium of field and laboratory work could be eliminated in determining the quantity of N and C tied up in shrub ecosystems.

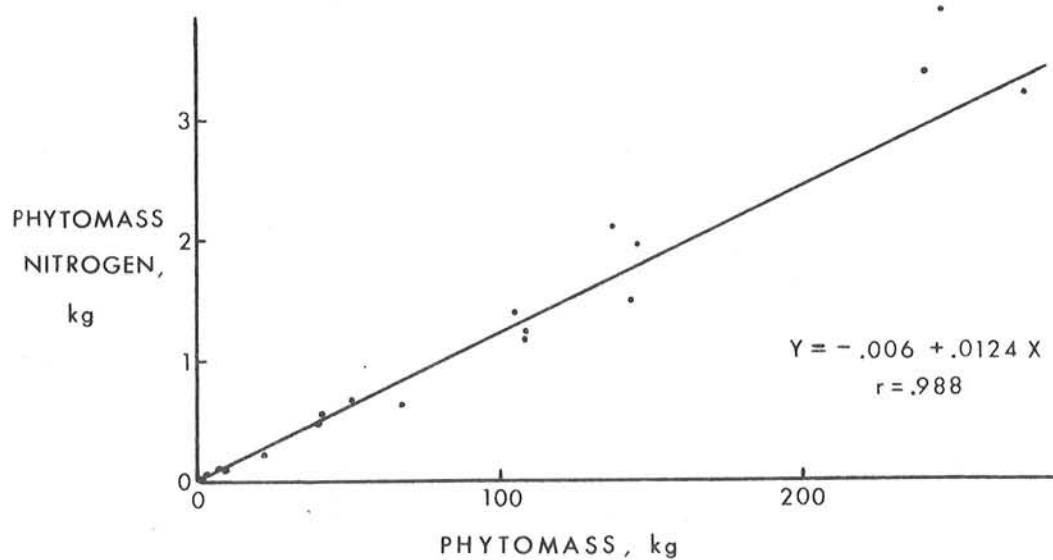


Figure 2. Quantity of nitrogen in the above-ground phytomass of mesquite as a function of phytomass (DSCODE A3UKB06).

The depth function of percentage soil N for the mean of ten mesquite shrubs (Figure 3) is expected from data presented last year showing decreasing amount of N in mulch with distance away from the shrub center (i.e. impact of mulch chemistry should be expressed in the soil). The trend for soil carbon is similar. The influence of canopy position is greatest in the surface 5 cm and decreases with depth. With distance away from the center of the shrub, the decline in percentage N with depth diminishes. The significance of difference between canopy positions, particularly at the 30-60 cm depth, is uncertain. As this pool of data increases, analyses will be performed to determine the effect of shrub size on shape and position of the depth function for each canopy position. An hypothesis for current investigations is that depth function for N and C may be predictable from shrub size and mulch characteristics. If this hypothesis is true, we should be able to greatly simplify soil sampling during 1973.

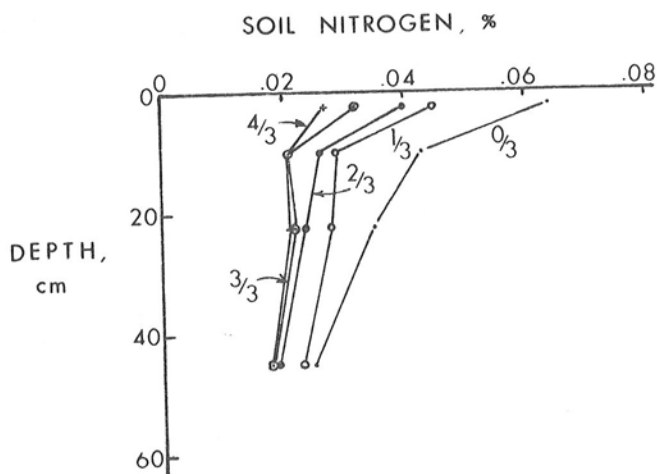


Figure 3. Soil nitrogen as a function of depth and canopy position (i.e. distance from stem to canopy edge). DSCODE A3UKB09.

Table 3. Percentage nitrogen in mulch of mesquite and palo verde ecosystems as a function of species of mulch and canopy position

Species of mulch	Distance from Stem to Canopy Edge			
	1/3	2/3	3/3	4/3
Mesquite	1.61	1.59	1.55	1.58
other spp.	1.31	1.28	1.13	0.87
Palo verde	1.13	1.27	1.22	1.33
other spp.	1.18	1.07	1.05	0.84

Limited data in last year's progress report suggested a possible trend in percentage N of mulch (both for mesquite and other species) as a function of canopy position. Additional data, although not subjected to statistical analysis as yet, suggest that canopy position has no effect on percentage N of mulch from the shrub (either mesquite or palo verde), but that mulch of other species (understory shrubs, herbs and succulents) is higher in nitrogen near the shrub center and declines with distance away from the shrub (Table 3). This effect is apparent for both mesquite and palo verde. It suggests that understory vegetation is acting as a bioassay of soil N conditions under the shrubs, and that the effect is still measurable in the mulch. If so, it confirms the observation of higher soil N under mesquite noted here and elsewhere (Tiedemann and Klemmedson, 1973a) and it's higher availability to plants (Tiedemann and Klemmedson, 1973b). Although species differences have not been tested, the data suggest that mulch associated with mesquite is higher in percentage N than that associated with palo verde; a surprising though unconfirmed result in view of data in Table 1 and Figure 1.

EXPECTATIONS

Work during the calendar year 1973 will proceed with approximately the same sampling objectives as those for the past year. However, we recognize the need to lighten the load of laboratory work which we encountered the past year by adding palo verde to the study. We feel there are good opportunities to reduce the field and laboratory work without sacrificing the intensity of sampling appreciably. There is a good possibility of reducing the soil sampling if depth functions for N and C can be developed with sufficient precision that we can predict with reliability the nutrient content of lower soil layers from the 5-15 cm value. The opportunity for this appears promising. Similar techniques will be examined to refine the determination of biomass. Development of these relations will not only improve the efficiency of this project, but provide methodology for estimating distribution of nutrients and biomass on an areal basis. If these economies in sampling and analysis can be achieved, we stand a chance to include in the 1973 program the chemical analysis of mesquite and palo verde on the Silverbell site and perhaps other species of interest to the Biome project.

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1972 PROGRESS REPORT

SHOOT GROWTH AND LITTER FALL PROCESSES AS THEY BEAR ON
PRIMARY PRODUCTION OF SOME COOL DESERT SHRUBS

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Research Memorandum, RM 73-9

MAY 1973

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A B S T R A C T

Rates of shoot growth and litter fall were qualitatively and quantitatively related to phenological development of *Artemisia tridentata*, *Atriplex confertifolia* and *Eurotia lanata* and climatic patterns in Curlew Valley, Utah. A dry spring and summer caused a truncation of the growth periods and twig dimension increases with most of the populations not completing the reproductive cycle in 1972. Shedding of the large spring leaves was earlier and greater than observed in previous years.

INTRODUCTION

Previous Desert Biome studies by Caldwell and West obtained information on nutrient pools in vegetation and soils (West, 1972) and photosynthesis and transpiration (Caldwell et al., 1972) by major species of cool desert areas. This earlier research suggested that shoot and leaf growth and litter fall patterns of dominants should be better known to explain the primary production, transpiration, and nutrient cycling processes in these ecosystems. Accordingly, phenology and litter production studies were continued from 1971. An attempt to measure stem and twig growth was added during 1972.

OBJECTIVES

To qualitatively and quantitatively interrelate the rates of shoot growth and litter fall with phenological development of *Artemisia tridentata*, *Atriplex confertifolia* and *Eurotia lanata* in Curlew Valley, Utah.

METHODS

Three sites were chosen on the west side of Curlew Valley. These locations all occur within the same square mile (Section 15, T. 13N., R. 11 W.) of the valley bottom with less than 2 m elevation difference between sites (Fig. 1). These sites were chosen because of prior data being available on soil physical and chemical characteristics (Gates et al., 1956; Mitchell et al., 1966; Bjerregaard, 1971), climate, soil moisture, plant phenology (Gasto, 1969) and plant-water relations (Moore, 1971; Love and West, 1972).

Phenology and twig growth were measured on a random set of ten tagged plants in nearly pure stands of each species. On each selected plant a set of four twigs was located in randomly-selected portions of the crown hemisphere. Not only was direction randomized but also height and depth into the crown figured into the possibilities for selection. Phenology was scored by methods developed by West and Wein (1971) (DSCODES A3UW104 and A3UW120). Dimensions were schematically recorded monthly (Fig. 2). Herbarium specimens of twigs in various phenological phases were collected to serve as references for our numerical ratings. Selected photographs of twigs were taken.

Wood increments over past seasons were to be estimated from growth rings, examined from a set of two *Artemisia* and *Atriplex* individuals with well-developed trunks sampled in the same locality of our other studies. An attempt was made to assess the progression of current stem growth by inserting insect mounting pins into the cambium monthly and observing the depth to scar tissue (Wolter, 1971). The irregular form of the stem precluded plans to use vernier band dendrometers (Ferguson, 1964).

Seasonality and amount of litter fall was determined from collections made in nylon mesh enclosures (Fig. 3) following suggestions from Mack (1971) (DSCODE A3UW105).

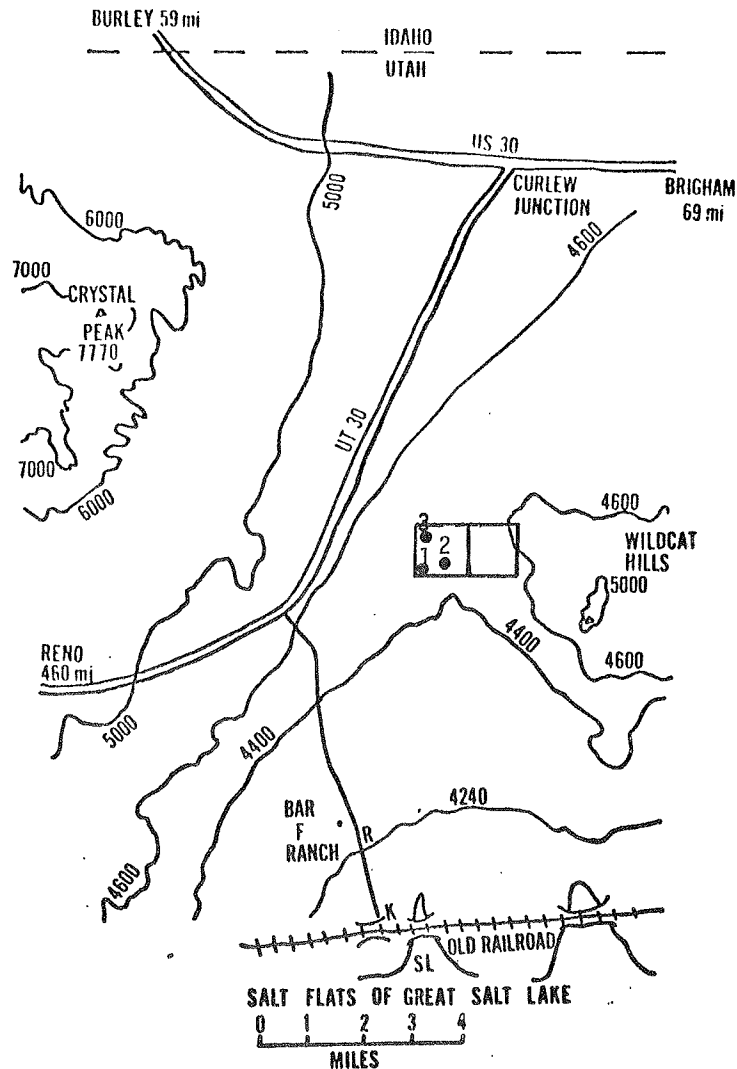


Figure 1. Sketch map of Curlew Valley sampling points. Site #1 - *Atriplex confertifolia*; Site #2 - *Eurotia lanata*; Site #3 - *Artemisia tridentata*.

2.3.1.2.-4

Curlew Valley Shoot Growth Measurement

Species: Artr

Atco

Eula

Date 9-1-72

Plant # 10

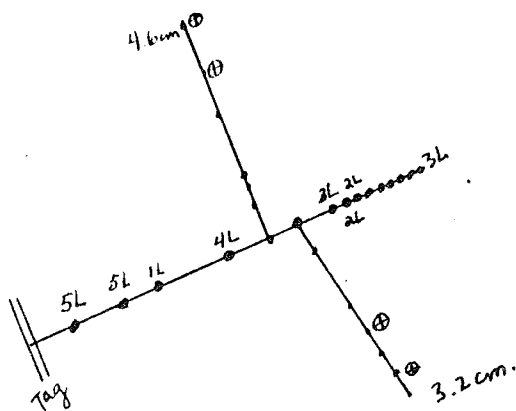
tag:

R

B

W

Y



Lat. spine (s)	
Flower (s)	
Fl. bud (s)	
Fruit	
Surface	
Anomalous dev.	
Shoot length	<u>7.0 cm.</u>
Nodes	<u>15</u>
Leaves	
Rosettes	
Lat. shoot (s)	
Term. bud (s)	
Lat. bud (s)	
Term spine (s)	
Repr. shoots	<u>2</u>

SYMBOL CODE

Node	
Meristem	
Spine	
Bud (vegetative)	
Gall	
Exudate	

Flower bud	
Flower	
Fruit	
Leaf	L preceded by no.
Rosette	R preceded by no.
Dead structure	(over part)

Figure 2. Example of the recording scheme used for quantifying morphological development of the three shrubs. Modified from Wallace and Romney (1972).

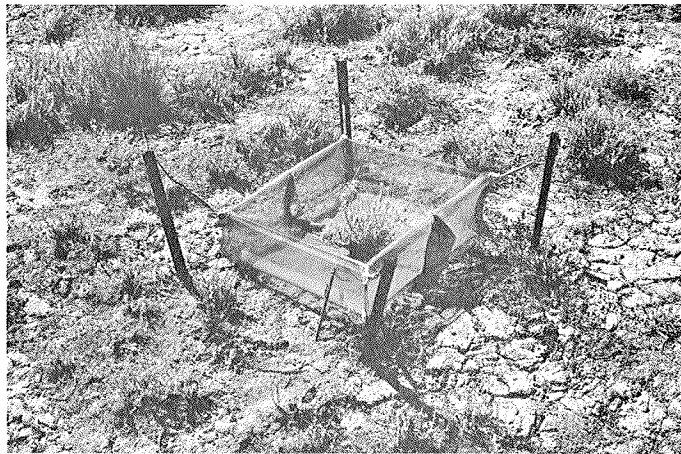


Figure 3. An example of a litter trap around an *Eurotia lanata* plant in Curlew Valley, Utah.

RESULTS

Figure 4 summarizes the phenological patterns for 1972 (DSCODE A3UW104). Table 1 summarizes shoot growth rates (DSCODE A3UW120). Litter production (on a shrub volume basis) is given in Table 2 (DSCODE A3UW105). To get the full response from stem growth rings, we had to wait until well after the end of the growing season to cut down the plants marked with pins. The analysis of growth rings and scar tissue was in progress at the time of report submission. The results will be reported in the 1973 annual report.

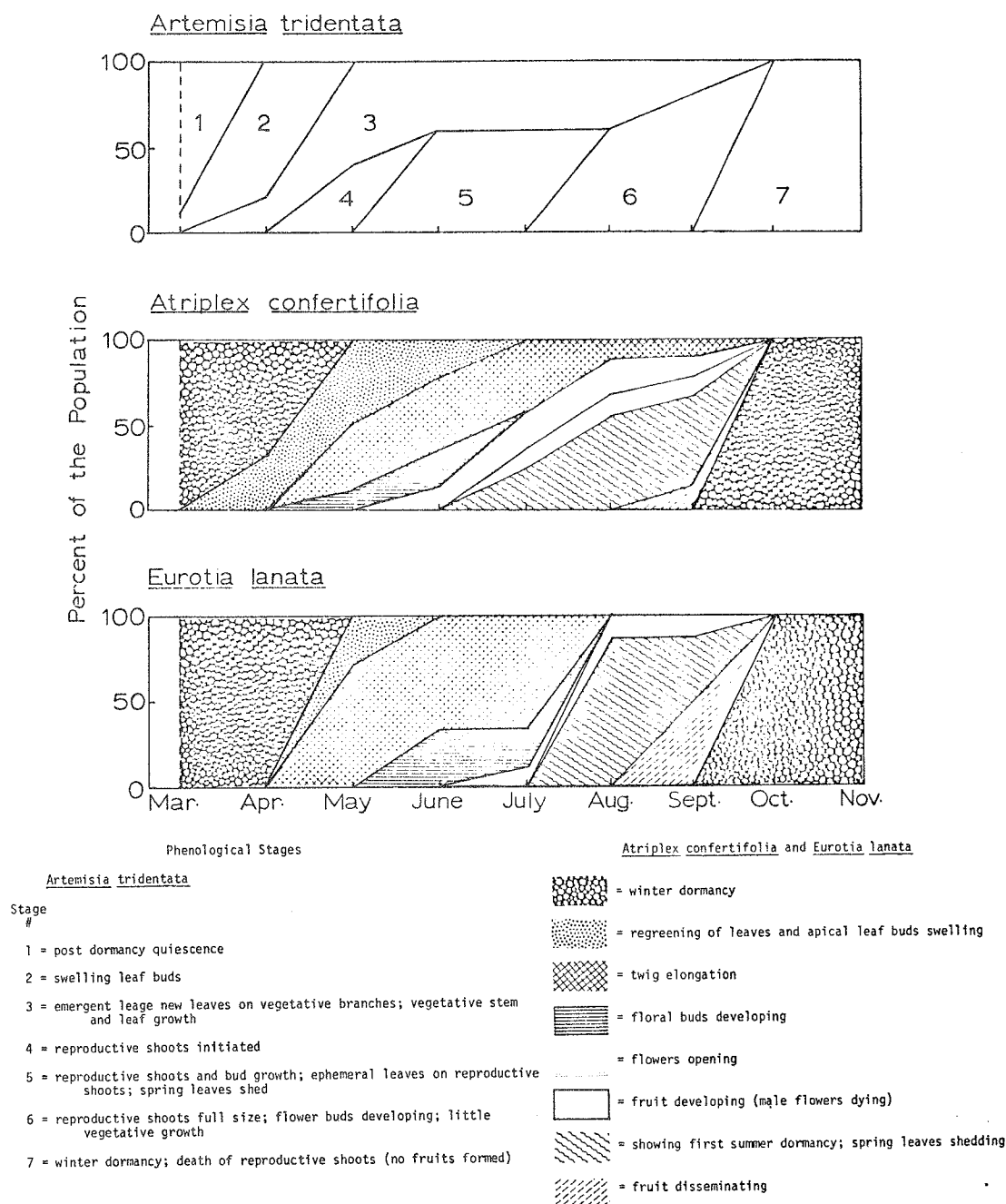


Figure 4. Proportion of Curlew Valley shrub population in a given phenological stage during 1972.

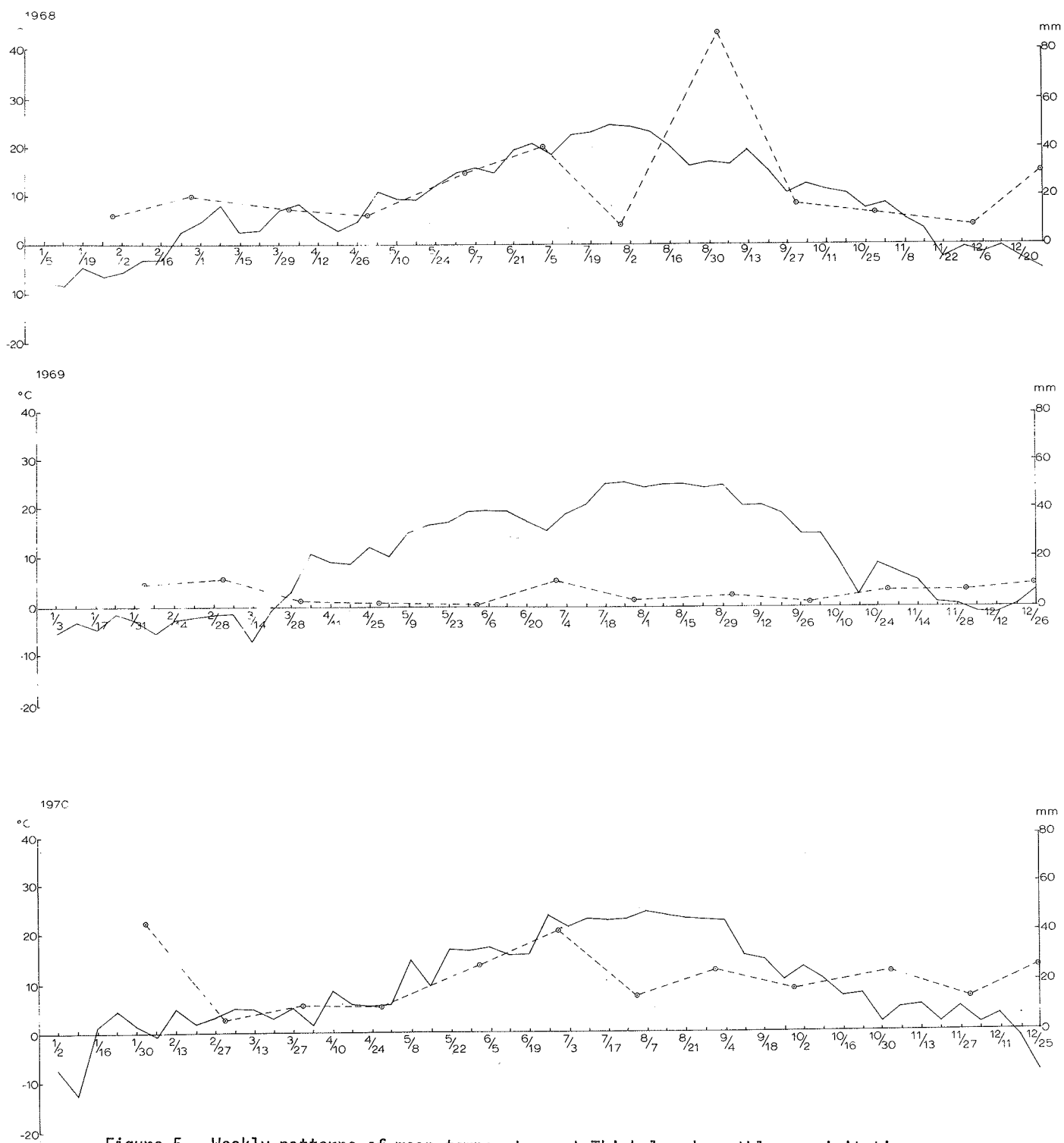


Figure 5. Weekly patterns of mean temperature at Thiokai and monthly precipitation (mean of four storage gauges) in Curlew Valley plots, 1968-1972. Continued on next page.

2.3.1.2.-8

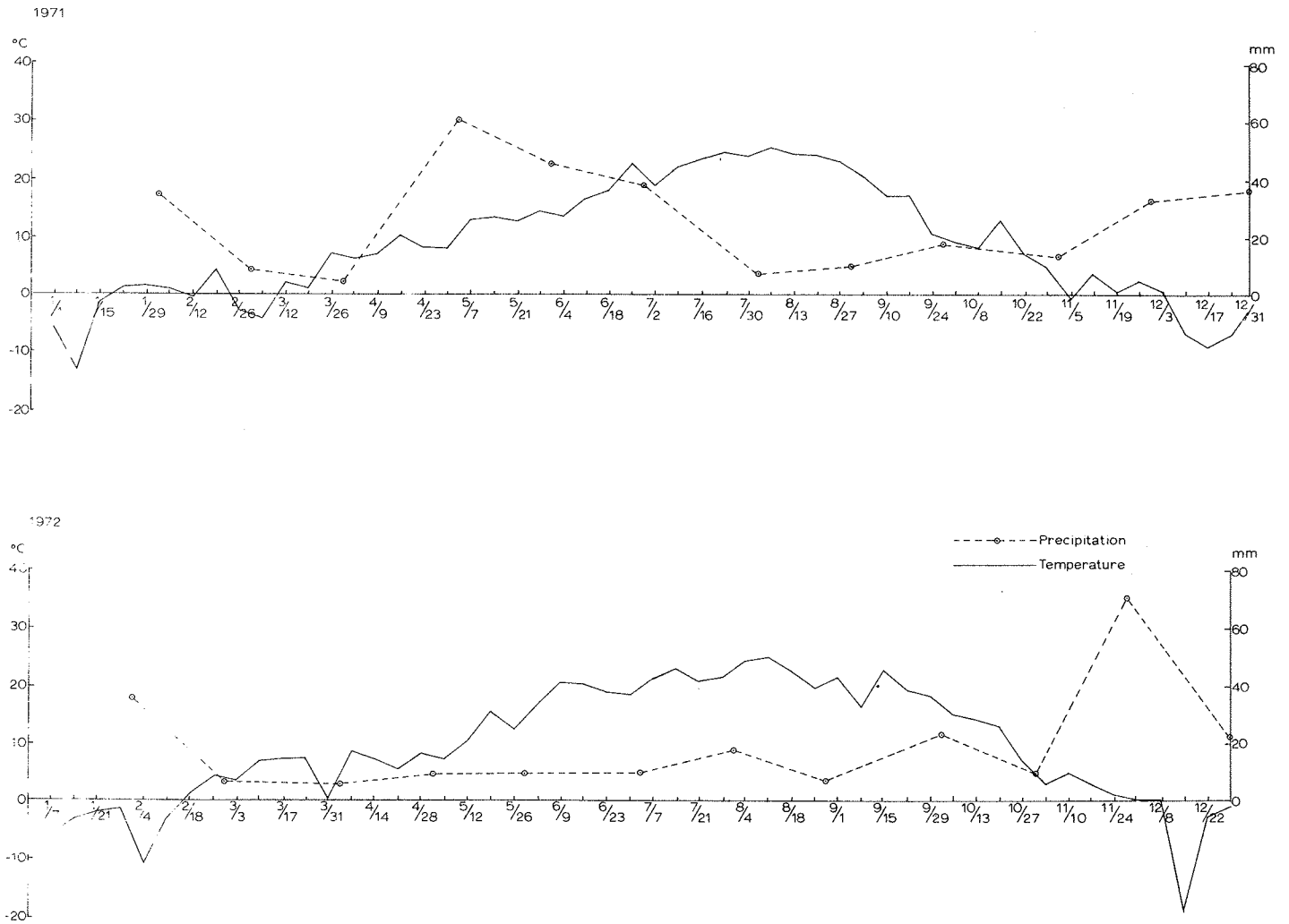


Figure 5. Continued.

Table 1. Shoot growth data, Curlew Valley, 1972 (A3UW120)

	<i>Artemisia tridentata</i>				
	Avg. shoot length (cm)	Avg. # nodes/shoot	Avg. # of live veg. lateral branches/shoot	Avg. # of live repr. lateral branches/shoot	Sample size
Mar.	6.3	9.8	0.4	0.0	36
Apr.	6.4	10.2	0.6	0.0	36
May	8.1	11.9	2.8	0.4	35
June	8.5	13.1	3.2	0.9	33
July	8.6	13.1	4.1	1.0	31
Aug.	8.8	14.3	5.6	1.1	31
Sept.	8.8	17.1	5.8	1.0	29
Oct.	8.7	17.0	5.7	1.0	27
Nov.	8.6	14.2	4.5	0.2	26
<i>Eurotia lanata</i>					
Mar.	8.6	13.1	0.0	0.0	37
Apr.	8.6	13.1	0.0	0.0	37
May	9.5	13.4	0.8	1.7	35
June	9.5	13.4	0.8	1.8	34
July	9.5	13.4	0.8	1.8	34
Aug.	8.7	18.4	1.4	2.5	25
Sept.	7.7	16.8	2.2	2.4	18
Oct.	7.2	16.2	2.0	2.1	16
Nov.	8.3	16.3	1.9	2.3	14
<i>Atriplex confertifolia</i>					
Mar.	7.7	3.4	0.1	0.0	40
Apr.	7.5	3.4	0.2	0.0	39
May	7.9	4.0	0.9	0.3	35
June	7.8	4.6	1.7	0.5	31
July	8.0	6.9	2.1	0.1	29
Aug.	7.8	8.3	2.1	0.1	27
Sept.	7.7	8.1	3.1	0.0	25
Oct.	7.6	6.6	2.75	0.0	24
Nov.	7.6	6.6	2.4	0.0	24

Table 2. Litter production in μg litter/ cm^3 plant volume, based on the means of 10 plants of each species in Curlew Valley during 1972 (A3UW105)

	Leaves	S.D.	Stems	S.D.	Reproductive Material	S.D.	Total	S.D.
<i>Artemisia tridentata</i>								
March	4.33	1.98	1.62	1.57	0.03	0.05	5.98	8.35
April	5.40	1.99	7.17	14.47	0.05	0.09	12.62	14.85
May	24.36	13.60	8.55	2.82	1.28	0.88	34.18	15.72
June	129.22	42.46	14.14	8.96	3.75	3.66	122.23	53.50
July	32.17	16.58	5.84	6.94	4.40	4.62	42.42	17.07
August	13.91	7.52	5.13	5.45	4.34	2.90	23.39	8.92
September	3.30	1.24	2.71	1.16	1.36	1.23	7.37	2.67
October	1.99	0.88	2.53	1.18	0.89	0.88	5.41	2.09
<i>Atriplex confertifolia</i>								
March	46.74	30.35	8.53	10.83	0.18	0.50	55.44	31.00
April	37.32	19.72	9.45	13.96	0.05	0.09	46.82	25.94
May	48.50	28.89	12.29	9.16	14.25	12.54	75.05	32.80
June	119.64	105.08	64.37	85.06	3.12	3.01	187.13	197.26
July	139.62	122.85	8.41	7.44	0.92	1.02	148.95	119.96
August	92.81	58.92	100.76	279.63	1.09	2.63	195.66	281.08
September	18.00	11.87	15.60	20.18	2.87	4.73	36.47	25.02
October	68.89	45.12	8.40	8.06	0.13	0.32	77.42	48.65
<i>Eurotia lanata</i>								
March	39.04	53.06	12.94	19.25	4.94	3.83	56.91	73.09
April	57.73	54.17	58.29	135.06	8.25	14.88	124.27	183.04
May	140.50	231.72	88.48	113.10	4.04	4.64	233.06	338.05
June	728.33	1247.30	587.16	1555.09	1.22	1.65	1316.73	2808.28
July	203.80	86.40	54.77	21.22	0.29	0.43	258.87	73.40
August	302.19	101.35	150.67	71.25	0.79	1.01	453.68	118.43
September	117.95	81.04	473.81	331.29	0.71	0.55	592.00	394.9
October	62.22	73.80	51.45	32.55	1.38	1.69	115.06	93.12

DISCUSSION

All of the processes studied were markedly affected by the prevailing climatic patterns of the year (Fig. 5). A dry spring and summer caused earlier and greater total leaf shedding than has been observed in previous years.

In all three species maximum shoot length was attained in late June to early July. In *Artemisia tridentata* maximum shoot length occurred at the time when flower buds were developing on reproductive shoots. Similarly, *Eurotia lanata* reached its maximum mean shoot length during the period of floral bud development. In contrast, *Atriplex confertifolia* reached its maximum shoot length later during the fruit development stage.

The subsequent reduction of shoot length and total nodes during August for *Atriplex confertifolia* and *Eurotia lanata* and during October for *Artemisia tridentata* is due to breakage of twigs and browsing by rabbits, particularly on *Eurotia*. Considerable evidence of webworm activity was noted during both litter sample and shoot growth observations in 1972. Flowering of all three species was less and seed production was lower than observed previously. Big sagebrush showed very little reproductive activity with few flowers and fruits and much twig and some plant mortality. The site studied is on the xeric limits the species will tolerate in Curlew Valley. The volume of standing dead material in the stand reflects the high mortality the community periodically sustains.

High standard deviation values occurred for data of the stem and floral structure litter of all three species. This is a reflection of the low amount of reproductive activity during the 1972 season. The high standard deviation values for the leaf litter of *Eurotia*, especially during May and June, correspond with the timing of peak rabbit populations in adjoining areas in Curlew Valley (C. Stoddart, personal communication). Rabbit activity was noted inside the *Eurotia* litter traps and it is likely that their movements within the traps would enhance stem breakage and thus litter accumulation.

The unseasonably snowy and cold winter filled the litter traps with snow and ice. The traps could not be cleaned out until March 1 without damage to the traps and plants. A partial thaw in February caused overland flow of water on the frozen surface. This is the first time investigators have observed this phenomenon on these sites. The effectiveness of the snow melt on soil moisture was not as great as was expected (Caldwell, 1973).

2.3.1.2.-12

Graphing of phenological indices (West and Wein, 1971) was also done. However, small sample size coupled with only a small percentage of the plants completing the reproductive cycle gave unreasonable trends to such graphs. Since the phenological index technique is based on the mean phenological stage of all plants on a given date, the values for the 1972 season would have been unrepresentative of either that portion of the population remaining vegetative or the small portion which was reproductive.

All of these idiosyncrasies of the data due to climate causes us to question the extrapolation of these data. Phenology, growth and litter studies will be carried out again in 1973 in hopes of getting a longer set of these data contributing to better averages and determinations of climatic influences. Means for recording the data into computer compatible form have been developed.

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1972 PROGRESS REPORT

PLANT PRODUCTIVITY AND NUTRIENT INTERRELATIONSHIPS OF PERENNIALS
IN THE MOHAVE DESERT

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Research Memorandum, RM 73-10

MAY 1973

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Report Volume 3

Page 2.3.1.3.

PART I

GAS EXCHANGE AND ASSIMILATE DISTRIBUTION
IN MOHAVE DESERT SHRUBS

A B S T R A C T

Gas exchange, assimilate partitioning and fate in several species of desert shrubs were measured as a function of season and environmental variables at the Nevada Test Site in the northern Mohave Desert.

Gas exchange rates were determined using a Siemens null-point gas exchange apparatus (Part I) and assimilate partitioning by incorporation of $^{14}\text{CO}_2$ and subsequent whole shrub excavation (see Parts II, III, IV). Tests were done on plants in Rock Valley under natural field conditions and at Mercury under natural and manipulated conditions.

Species specific differences in gas exchange rates in relation to temperature and moisture regimes were measured. Drought-deciduous species, *Ambrosia dumosa* (Gray) Payne, *Lycium andersonii* Gray and *Lycium pallidum* Miers had higher maximum rates and greater water loss than the evergreen, *Larrea divaricata* (Ses. & Moc. ex DC.) Cov., and summer green, *Krameria parvifolia* Benth., species. Moisture status was the most critical factor determining gas exchange rates and affected temperature optimums and acclimation as the season progressed. Due to a dry spring season, the drought-deciduous species became dormant in late May-early June; the other two species by mid-June exhibited a small positive CO_2 uptake during the morning period.

With adequate moisture, *A. dumosa*, *K. parvifolia*, and *L. divaricata* continued active photosynthesis throughout the summer. *A. dumosa* and *L. divaricata* plants not watered after June 1 did not show any large differences by mid-August in photosynthesis or transpiration compared with watered plants, although there was a greater increase in tissue water potential.

In terms of modelling either photosynthesis or productivity, our data for the past two years indicate a system which is highly responsive to moisture, time of year, and temperature regimes. Desert plant species, with few exceptions, are extremely labile and exhibit large variability and different adaptive strategies.

Abstracts for Parts II, III and IV can be found as follows:

Part II.....	Page 2.3.1.3.-29
Part III.....	Page 2.3.1.3.-34
Part IV.....	Page 2.3.1.3.-42

INTRODUCTION

This project is a continuation of a study started in 1971 of gas exchange rates and assimilate transport in Mohave Desert shrubs. These rates are being determined for relationships to net photosynthesis, productivity, and partitioning and subsequent utilization of assimilate. This study is a combination of two previous studies. We are measuring rates for a second year on undisturbed plants under natural field conditions of moisture, temperature and radiation, and on plants with manipulated conditions of moisture. In 1973 we expect to continue measuring gas exchange rates, but will devote more effort to below-ground processes as affected by above-ground activities.

Information generated in this study will provide material for equations of rate processes in developing models of net photosynthesis and productivity in desert ecosystems and for input in a generalized model of the plant productivity component. Due to the great differences measured in the last two years, we expect a minimum of several years necessary to document changes. Our study is being coordinated with that of M. Caldwell on Great Basin shrubs and with the work on cacti by I. Ting in California and D. Patten in Arizona.

OBJECTIVES

During 1972 our primary objectives of measuring rate changes in various physiological processes were carried out and continued from 1971. During 1972 our specific objectives were:

1. To continue determining rates of net photosynthesis and transpiration water loss of undisturbed plants under field conditions with natural and manipulated conditions throughout the season.
2. To determine assimilate transport and subsequent utilization by desert shrubs on a seasonal basis.
3. To determine nutrient status of the important perennials in relation to season.

In connection with the objective on assimilate transport, additional information was developed on root biomass on a vertical incremental basis and on the relationship of root biomass to total shrub biomass.

Several objectives proposed in 1972 were postponed or deleted due to weather conditions or changes in the experimental design. Studies on annuals were not initiated in 1972 due to late germination and poor growth and survival of the scanty annuals.

2.3.1.3.-4

Only the manipulated effects of water status on gas exchange at Mercury was initiated during 1972, since the number of tests which could be accomplished in the Siemens chamber is limited.

METHODS

Gas exchange determinations were done on five desert shrubs under natural field conditions at Rock Valley, Nevada Test Site. This area is a Desert Biome Validation Site and its characteristics are given in the Rock Valley Validation Site Report (Turner, 1972). Location of the area where plants were tested is 120 m southwest of the weather station on the validation site and abiotic data from both the U.S. Weather Bureau Station and IBP Station I are applicable to the test area (Data Sets A3UTJ01, A3UTJ02, A3UTJ07).

Plant species tested were *Ambrosia dumosa*, *Krameria parvifolia*, *Larrea divaricata*, *Lycium andersonii*, and *Lycium pallidum*. These five species make up 91% of the biomass on the validation site (A3UTJ25). *A. dumosa* and *L. divaricata* form the most widespread plant association in the Mohave Desert and characterize the majority of the Rock Valley vegetation.

Gas exchange was measured using a modified null-point Siemens chamber (Koller, 1970). Use and description of this system are given in the 1971 Progress Report (Bamberg and Wallace, 1972). The system simultaneously measures CO_2 exchange and transpiration of enclosed plants while maintaining constant conditions of temperature, humidity and CO_2 concentration of circulating air in the chamber. The chamber also can be set to approximate ambient conditions. Transpiration is given in $\text{g H}_2\text{O/g dry wt/hr}$ and photosynthesis and respiration in $\text{mg CO}_2/\text{g dry wt/hr}$ (A3UBD01, A3UBD02).

Water status and temperature of soil were measured using thermocouple psychrometers at 15 cm and 30 cm depths (A3UTJ08, A3UTJ09). Radiation was measured in $\text{g cal/cm}^2/\text{min}$ using a Belfast recording pyrliometer. Other measurements at the meteorological station used for this study were precipitation and air temperature (A3UTJ12, A3UTJ06).

Plant water tissue potential was determined after May 1 with a pressure bomb (Scholander et al., 1965; Boyer, 1969). Phenology of the species was recorded at two areas on the validation site (A3UTJ22 - tentative).

In Mercury two series of *A. dumosa* and *L. divaricata* plants were set up in an artificial plot in March, 1971. Plants started from cuttings in the glasshouse were transplanted to an outdoor garden in Mercury in March, 1972. For establishment, all transplants were watered until May 1, at which time the two moisture series were started. One series was left under normal soil moisture conditions after the first week in May. The second series was watered once a week so that soil moisture stayed at a relatively high level throughout the summer. These plants were tested from mid-July through August for gas exchange, temperature acclimation and water use efficiency during the summer season. Radiation and soil and plant tissue water potentials were measured as in Rock Valley.

Computation has been completed on all the 1972 data for the gas exchange rates for individual tests, but at present the analysis in terms of determining correlation and/or regression of the gas exchange rates with the appropriate environmental factors is not complete. Mineral analysis, including nitrogen, of plants has been completed, but was not analyzed in time for inclusion in this report. The results presented here are those available at the time of this report.

RESULTS AND DISCUSSION

ROCK VALLEY (A3UTJ02, A3UTL08, A3UTJ09, A3UTJ12)

Abiotic

Air temperatures in Rock Valley for the first seven months of 1972 are illustrated in Figure 1. Soil moisture and temperature at two depths and precipitation are shown in Figure 2. In contrast to 1971, Rock Valley did not receive an effective rain from January through July. The drying trend is exhibited by soil moisture. Light rains in early June did not have a significant effect on the water status of the soil, nor was there a measureable decrease in plant tissue water potential.

CO₂ exchange (A3UBD01, A3UBD02)

The basic pattern of diel CO₂ exchange of *A. dumosa* is illustrated in Figure 3 as a representative example. Uptake of CO₂ started at a relatively high rate and peaked between 0800 and 1200 hours. The rate of CO₂ uptake then tapered off until dusk. No midday depressions and subsequent late afternoon peaks, as reported by other workers (Strain, 1970; Lange et al., 1969), were observed. Respiration remained low throughout the night. The highest rates of CO₂ loss as respiration occurred in early evening and decreased gradually throughout the night.

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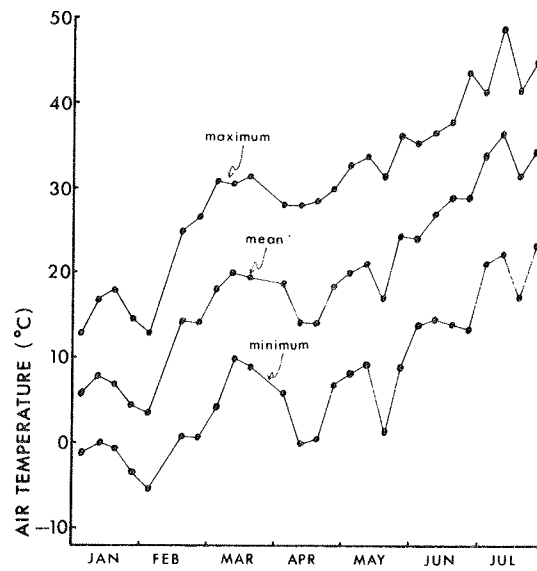


Figure 1. Weekly maximum, minimum, and air temperature in Rock Valley for January - July, 1972. Data from U.S. Weather Bureau Station in Rock Valley.

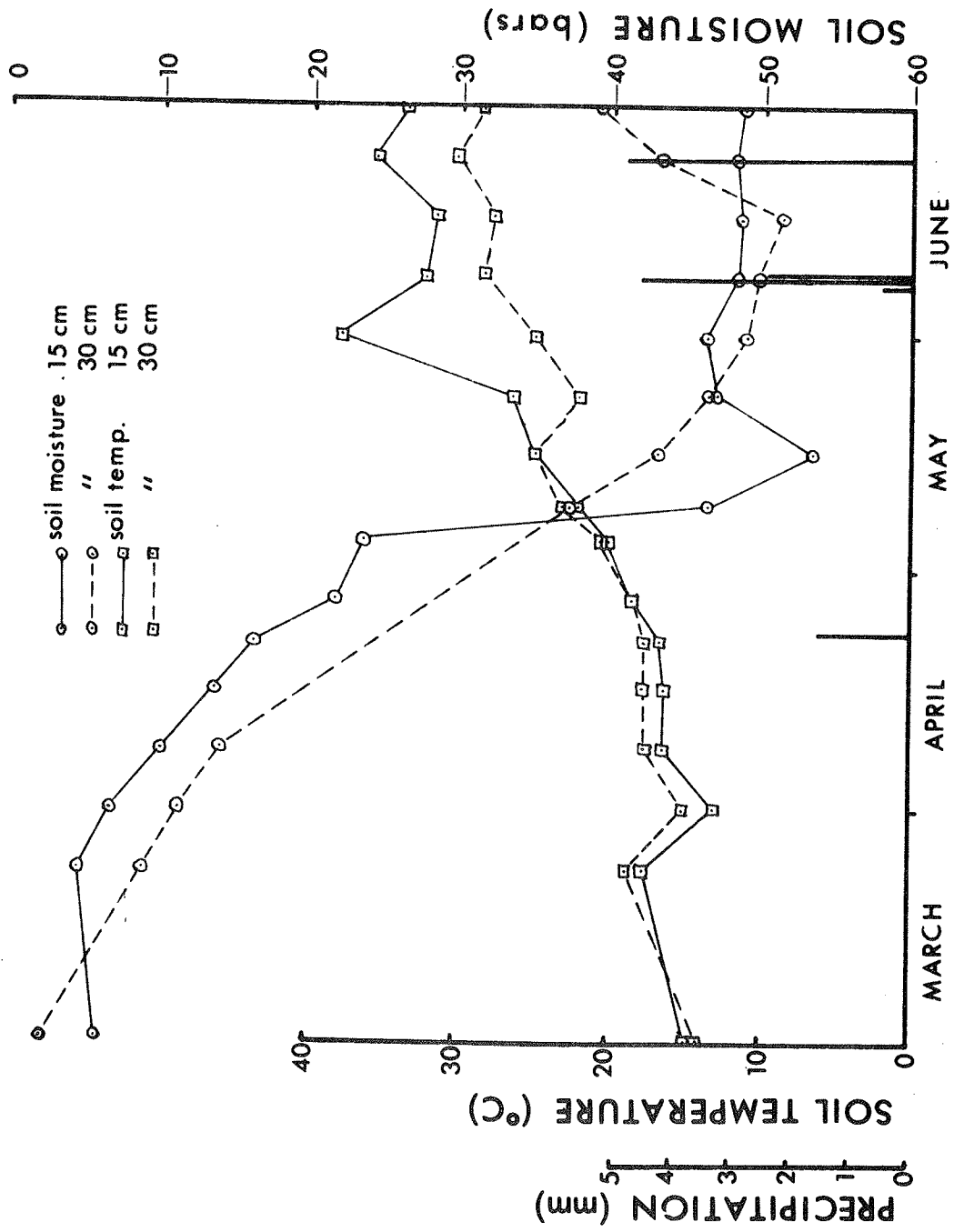


Figure 2. Precipitation and soil moistures and temperatures at 15 cm and 30 cm under shrubs in Rock Valley. Data from Rock Valley IBP Station 1.

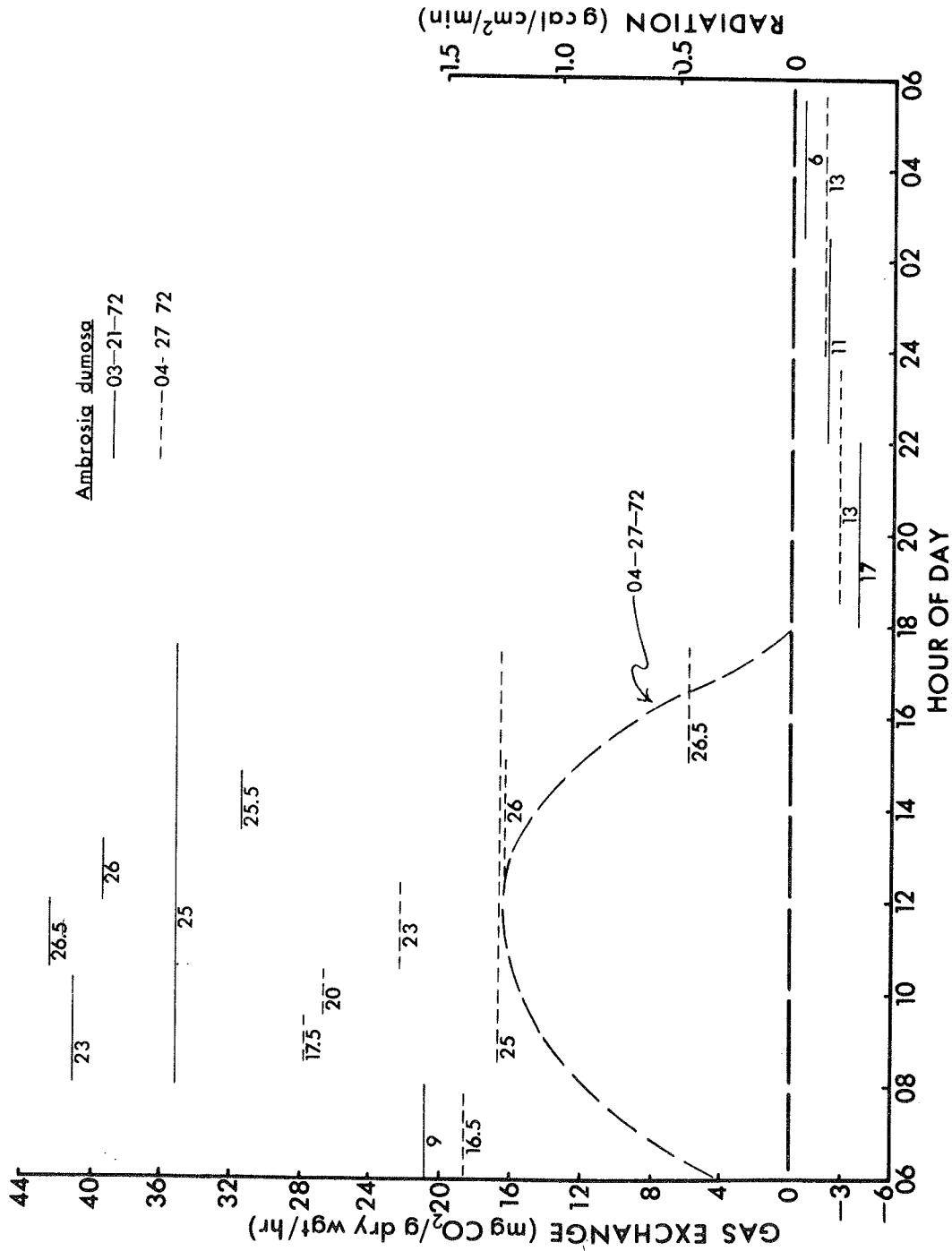


Figure 3. Daily rates of CO₂ exchange for *Ambrosia dumosa* in Rock Valley under ambient conditions. Horizontal lines indicate time period over which rates were determined; numbers represent mean temperature (C) during each interval. Radiation curve is indicated by a dashed line labeled as 04-27-72.

Interspecific differences in net diurnal photosynthesis were noted within the same season (Table 1). Actual periods of time for daily CO₂ uptake or release are given in Table 2. Deciduous plant species (*A. dumosa*, *L. andersonii* and *L. pallidum*) had higher rates early in the season and maintained a higher rate than evergreen species until leaf abscission. Evergreen species under the field conditions of this season never attained high rates and by mid-June had only a small net photosynthesis. We assume no significant photosynthetic activity until rains in mid-August of 1972. Seasonal variation in net diurnal photosynthesis was exhibited by all species (Figures 4-8).

Table 1. Gas exchange rates of desert shrubs at different seasons in the Rock Valley
DSCODE—A3UBD01, BD02

Species		March 15-31	April 1-14	April 15-30	May 1-14	May 15-31	June 1-14	June 15-31
<i>Larrea divaricata</i>	day	10.1*			5.3		1.2	0.4
	night	-2.3			-1.5		-	-
<i>Krameria parvifolia</i>	day		5.7	6.4	3.0	8.9	4.1	1.3
	night		-	-	1.1	-	-0.5	-0.6
<i>Ambrosia dumosa</i>	day	36.2		17.0				
	night	-2.2		-1.6			dormant	
<i>Lycium andersonii</i>	day	44.4	14.5	9.3			dormant	
	night	-3.9	-	-1.6				
<i>Lycium pallidum</i>	day	26.9			3.3		dormant	
	night	-2.3			-1.3			

*mg CO₂/g dry wt/hr

Table 2. Temporal breakdown of gas exchange activities of shrubs in Rock Valley
DSCODE—A3UBD01*

Date	Time (hr)	
	Net Photosynthesis	Night Respiration
3-15-72	11.5	12.5
4-01-72	12	12
4-25-72	13	11
5-02-72	13	11
5-12-72	14	10
6-05-72	14	10

*in mg CO₂/g dry wt/hr uptake or release.

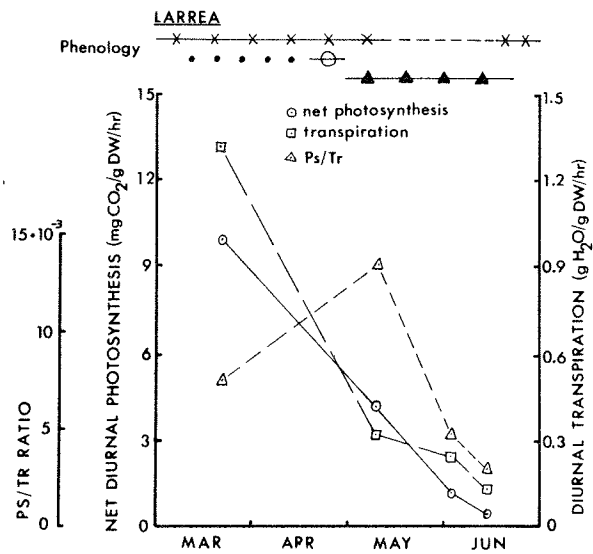


Figure 4. Seasonal changes in diurnal photosynthesis, transpiration and water efficiency use of *Larrea divaricata* in Rock Valley. Phenology symbols:
 • = Bud —○— = Flower —|— = Leaf Fall
 * = Leaf ▲ = Fruit —|— = Dormancy

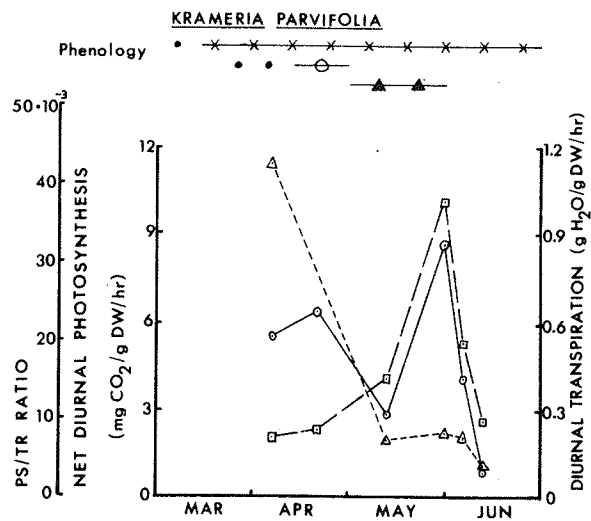


Figure 5. Seasonal changes in diurnal photosynthesis, transpiration and water use efficiency of *Krameria parvifolia* in Rock Valley. Graphic representations are as in Figure 4.

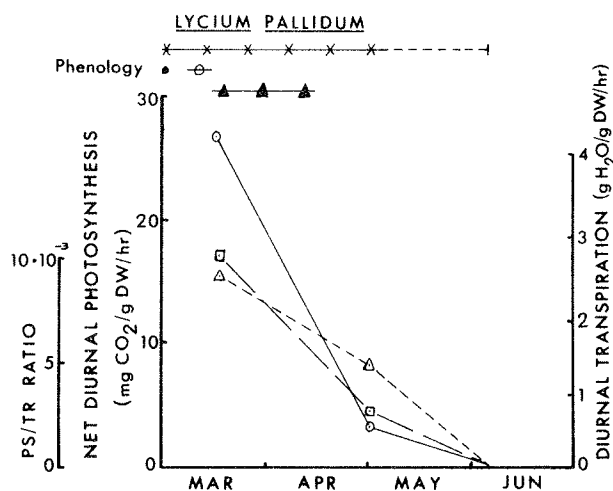


Figure 8. Seasonal changes in diurnal photosynthesis, transpiration, and water use efficiency of *Lycium pallidum* in Rock Valley. Graphic representations are as in Figure 4.

Figure 9 illustrates the effect of temperature on the CO₂ exchange of *L. andersonii* at three times during the spring. The responses of all plants subjected to temperature manipulation at various times during the season are shown in Table 3.

During the study period, soil moisture as well as temperature affected the net photosynthesis of desert shrubs. Fig. 10 illustrates the effect of these factors on the CO₂ exchange of *K. parvifolia*. It exhibits a changing temperature optimum for maximum uptake and thermal compensation and a lowered net CO₂ exchange as soil moisture tensions increase in late season.

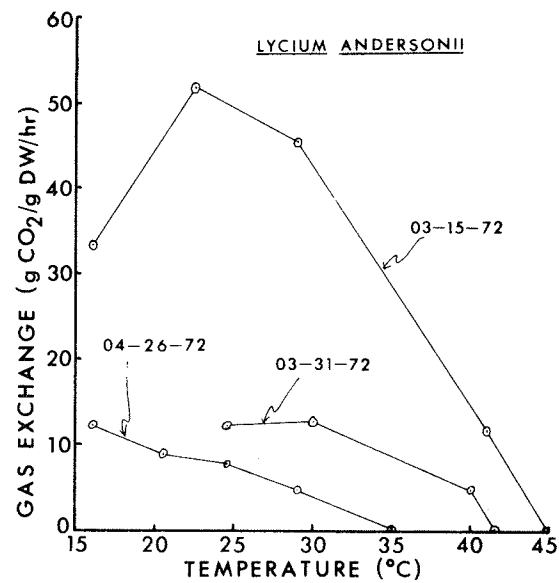


Figure 9. Effect of chamber temperature on daytime gas exchange (CO₂ uptake) of *Lycium andersonii* at different seasons in Rock Valley.

Table 3. Effect of chamber temperature on gas exchange of desert shrubs in Rock Valley, 1972. DSCODE—A3UBD01, BD02

Temperature (°C)		15	20	25	30	35	40	45
Species	Date	mg CO ₂ /g dry wt/hr						
<i>Larrea divaricata</i>	3-21	--	11.0	10.8	10.5	--	3.3	0.0
	5-10	7.7	7.0	5.0	2.6	--	0.0	--
	6-02	--	--	1.9	1.2	0.6	0.0	-1.0
<i>Ambrosia dumosa</i>	3-23	32.3	--	38.8	33.1	--	8.4	--
	4-28	19.2	--	20.6	15.8	5.4	0.5	--
<i>Krameria parvifolia</i>	5-12	--	10.0	5.1	2.7	0.0	-4.5	--
	5-31	--	--	--	8.9	4.0	0.9	-3.2
	6-06	--	3.0	3.1	3.7	3.1	1.8	0.0
	6-15	--	3.6	3.6	2.2	2.0	0.0	--
<i>Lycium andersonii</i>	3-15	34.0	53.2	40.5	39.4	--	10.7	0.0
	3-31	--	--	11.5	11.5	--	4.5	-12.2
	4-26	12.2	9.3	7.9	4.3	0.0	0.0	--
<i>Lycium pallidum</i>	3-17	34.8	33.5	32.8	30.2	--	12.0	--
	5-03	--	--	10.3	3.9	--	0.0	--

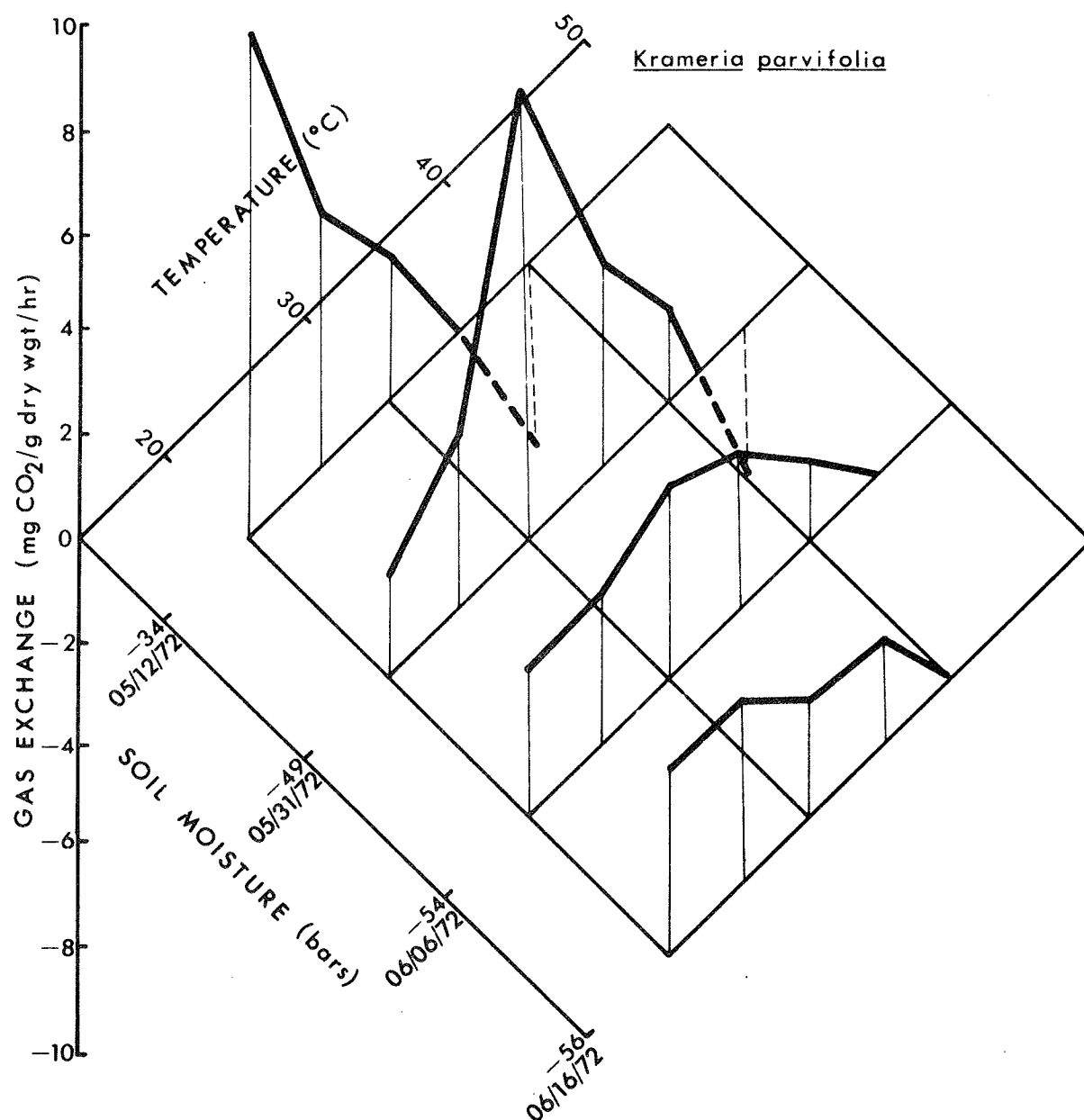


Figure 10. Gas exchange of *Krameria parvifolia* as related to soil moisture and chamber temperature. *Krameria* exhibits a definite shift in optimum CO₂ uptake toward a higher temperature in late spring as long as soil moisture is adequate (less than -50 bars). At higher soil moisture tensions the optimum net CO₂ uptake again shifts to below 25 C.

Water use (A3UBD01, A3UBD02)

Seasonal fluctuations in transpiration and water use efficiency for desert shrubs (Ps/Tr), in relationship to phenology, are shown in Figures 4 - 8. All species except *K. parvifolia* show both a decreasing transpiration rate and water use efficiency as drought increases. *K. parvifolia* is the last plant species to flower and retains leaves throughout the summer. Although seasonal differences in rates are measured, relationships to phenology are not clear in this season when there was a severe late drought (Caldwell et al., 1972).

Of the plants tested, the three deciduous species had linear relationship between temperature and transpiration rate when moisture was adequate. Transpiration increased as temperatures of the chamber were increased to the point where CO₂ uptake ceased. However, both *L. divaricata* and *K. parvifolia* (Table 4) restricted transpiration between 35 C and 45 C and transpired at slower rates than below 30 C or above 45 C. This is an evident adaptation to efficient gas exchange and water use at high summer temperatures.

The drying trend for the first 6 months of 1972 was reflected by the plant tissue water potentials (Table 5). Both *L. divaricata* and *K. parvifolia* exhibited a strong tolerance for high tissue water potentials.

Table 4. Effect of chamber temperature on transpiration rates of desert shrubs in Rock Valley, 1972 DSCODE—A3UBD01, BD02

Temperature	(C)	15	20	25	30	35	40	45
Species	Date	g H ₂ O/g dry wt/hr						
<i>Larrea</i>	3-21	0.0	--	1.4	2.5	--	3.1	2.8
<i>divaricata</i>	5-10	0.0	0.5	0.6	0.6	--	1.0	--
	6-02	--	--	0.2	0.3	0.3	0.3	0.3
<i>Krameria</i>	5-12	--	0.1	1.1	1.5	1.6	1.5	--
<i>parvifolia</i>	5-31	--	--	--	1.1	1.0	0.7	0.5
	6-06	--	0.0	0.3	0.8	1.3	1.0	0.8
	6-15	--	0.0	0.4	0.8	0.8	0.7	--
<i>Lycium</i>	3-15	0.2	5.3	3.7	4.8	--	8.3	9.4
<i>andersonii</i>	4-26	--	--	3.5	2.4	2.7	1.7	--
<i>Lycium</i>	3-17	--	2.2	4.0	5.2	--	6.8	--
<i>pallidum</i>	5-03	--	--	1.1	1.2	--	1.8	--

2.3.1.3.-16

Table 5. Plant tissue water potentials for desert shrubs in Rock Valley and Mercury, 1972 DSCODE— A3UBD01, BD02

Site/Date	<i>Krameria parvifolia</i>	<i>Ambrosia dumosa</i>	<i>Larrea divaricata</i>	<i>Lycium andersonii</i>	<i>Lycium pallidum</i>
Rock Valley	negative bars				
5-01-72	48	39	51	41	44
5-09-72	51	40	54	47	44
5-31-72	63		56		
6-01-72	62	47	63	52	51
6-06-72	65			dormant	dormant
6-12-72	66	dormant	63	dormant	dormant
6-19-72	72	dormant	65	dormant	dormant
Mercury		w ^{1*} un ² w un ²			
7-14-72			48		
7-18-72			42		
7-19-72			43		
7-20-72		35			
7-24-72		27			
7-25-72		43			
7-26-72		43			
8-02-72			57		
8-04-72			35		
8-21-72					

* 1 = watered, 2 = unwatered

MERCURY (A3UBD01)Abiotic

Soil moisture and temperature conditions for watered and unwatered soil underneath shrubs in Mercury Valley are presented in Figures 11-12. Data from the unwatered plot show the effect of a 3 cm rain on August 12, 1972.

CO₂ exchange

Diel CO₂ exchange for watered and unwatered *L. divaricata* and *A. dumosa* plants was determined (Figs. 13 - 14), and daily CO₂ uptake patterns were similar to those found in Rock Valley.

No consistent differences in net diurnal photosynthesis were noted between watered and unwatered plants (Table 6). Small differences in gas exchange rates in the two series of plants are related to the earlier watering regime for plant establishment and the effects of the rain in early June as mentioned above. The effects of this watering

and the natural precipitation were to keep moisture conditions favorable for both *L. divaricata* and *A. dumosa*, as both soil potential and tissue water potential measurements indicate. Plants were under only slight moisture stress by mid-August when a 3 cm rain again lowered soil moisture potentials (Table 5). The results of the temperature compensation experiments on watered and unwatered plants are listed in Table 7. In general, *A. dumosa* exhibited higher rates of CO_2 uptake than did *L. divaricata*.

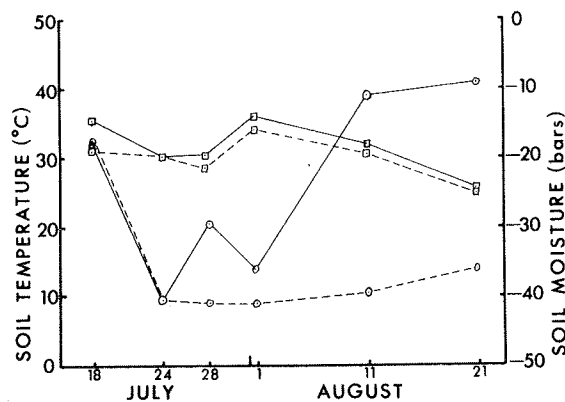


Figure 11. Soil temperature and moisture at 15 cm and 30 cm under shrubs in artificial watered plots in Mercury for July and August, 1972. Graphic representations as in Figure 2.

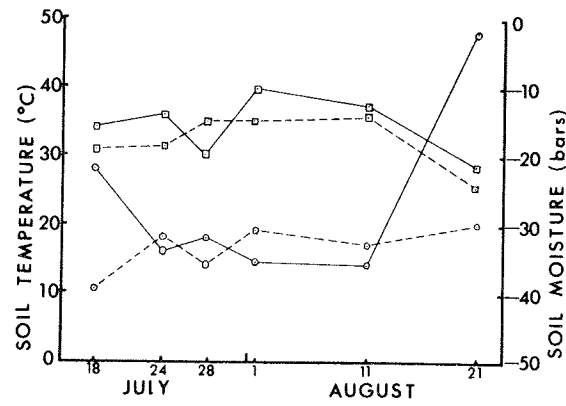


Figure 12. Soil temperature and moisture at 15 cm and 30 cm under shrubs in naturally watered plots in Mercury for July and August, 1972. Graphic representations as in Figure 2.

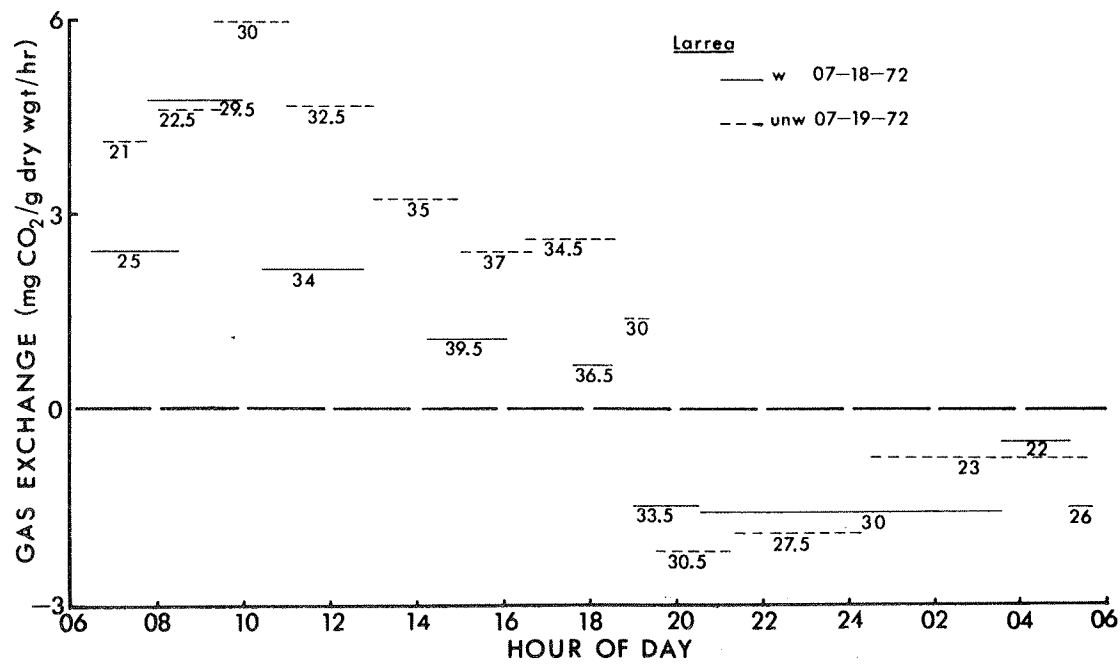


Figure 12. Daily rates of CO₂ exchange for *Larrea divaricata* in Mercury under ambient conditions of light and temperature. Graphic representations are as in Figure 3; w = watered, unw = unwatered.

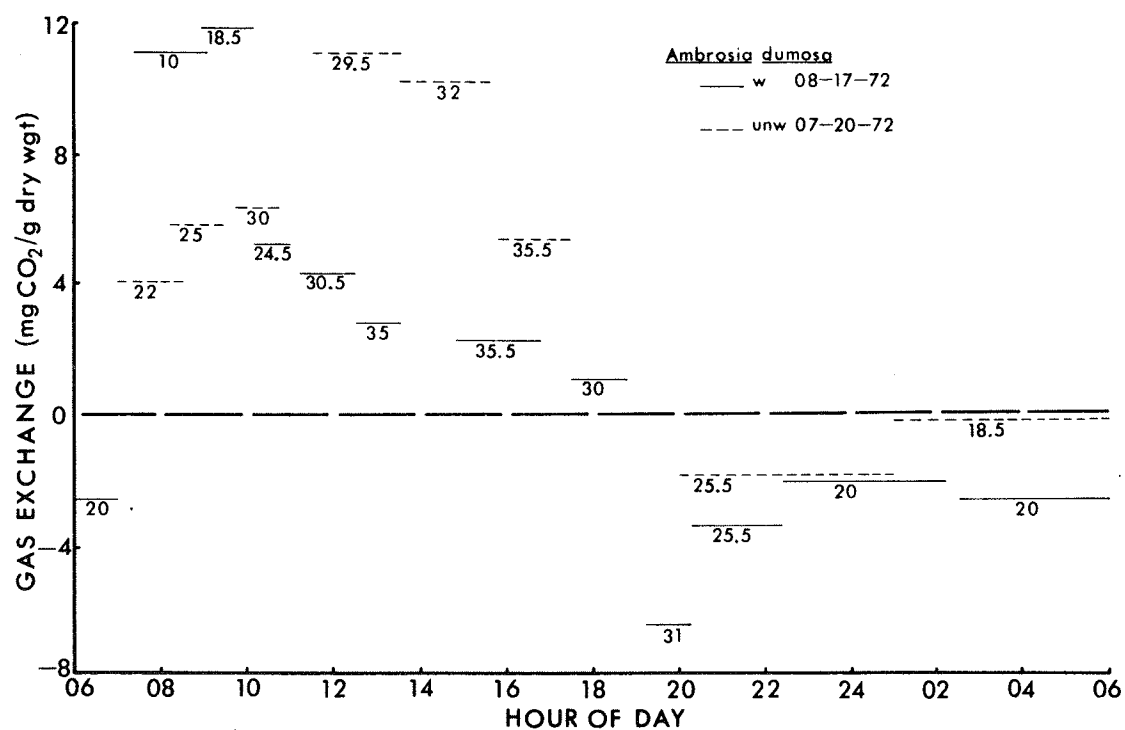


Figure 14. Daily rates of CO₂ exchange for *Ambrosia dumosa* in Mercury under ambient conditions of light and temperature. Graphic representations are as in Figures 3 and 13.

Table 6. Photosynthesis, transpiration and Ps/Tr ratios for *Larrea* and *Ambrosia* from watered and unwatered plots in Mercury, 1972 DSCODE—A3UBD01

Species/Date	Photosynthesis mg CO ₂ /g dry wt/hr		Transpiration g H ₂ O/g dry wt/hr		Ps/Tr	
	w ^{1*}	unw ²	w	unw	w	unw
<i>Larrea</i>						
<i>divaricata</i>						
7-17-72	2.0		1.5		1.3	
7-18-72	2.3		1.5		1.5	
7-19-72		3.9		1.9		2.1
7-25-72		5.0		1.9		2.6
7-27-72	4.6		1.2		3.8	
8-04-72		1.5		0.7		2.2
8-08-72		5.8		1.5		3.9
8-16-72	4.9		3.0		1.6	
8-21-72	6.7		2.9		2.3	
8-22-72	7.6		4.4		1.7	
<i>Ambrosia</i>						
<i>dumosa</i>						
7-20-72		9.6		4.2		2.3
7-24-72	11.2		5.8		1.9	
8-03-72		2.3		0.8		2.8
8-09-72		8.0		6.9		1.2
8-17-72	4.3		3.7		1.2	
8-23-72	4.6		4.0		1.1	

*1 = watered, 2 = unwatered

Water use

Table 6 lists transpiration and Ps/Tr values for watered and unwatered plants. Differences may be due to individual variation and do not seem to be related to the treatments, since moisture stress did not develop. Table 5 shows the plant tissue water potentials of both watered and unwatered plants. Fluctuations in tissue water potentials seem to follow changes in soil moisture.

A. dumosa and *L. divaricata* in the plots at Mercury again showed the difference in transpiration between a drought-deciduous and an evergreen species when both are not under water stress at high summer temperatures (Fig. 15). *L. divaricata* had the same transpiration depression in the temperature range of 35 C to 45 C whereas *A. dumosa* had a linear relationship and rates of 4 to 11 g H₂O/g dry wt/hr transpired compared to 2 to 3 g H₂O for *L. divaricata* at temperatures above 45 C.

Table 7. Effect of chamber temperature on gas exchange of *Larrea* and *Ambrosia* from watered and unwatered plots in Mercury, 1972 DSCODE—A3UBD01

Temperature (C)		10	20	25	30	35	40	45	50
Species/ water status	Date	mg CO ₂ /g dry wt/hr							
<i>Larrea divaricata</i>									
watered	7-18	--	--	--	5.0	2.3	1.1	--	--
	8-16	6.8	6.1	--	5.1	4.7	2.2	0.0	-1.7
	8-22	--	10.5	10.6	9.1	5.1	2.8	0.3	--
unwatered	7-25	--	--	8.1	7.0	3.2	0.4	-0.7	--
	8-04	--	--	2.9	2.0	1.3	0.5	0.1	--
	8-08	--	--	6.0	6.0	5.1	4.2	3.3	2.4
<i>Ambrosia dumosa</i>									
watered	7-24	--	--	--	13.0	9.7	9.4	--	--
	8-17	11.8	12.5	5.6	4.6	3.0	0.1	--	--
	8-23	--	6.4	6.0	6.0	6.2	4.0	1.8	--
unwatered	7-21	--	4.3	6.2	6.7	4.6	1.9	0.0	--
	8-03	--	3.0	2.7	2.0	-1.3	--	--	--
	8-10	--	--	7.7	7.9	8.0	7.2	6.7	--

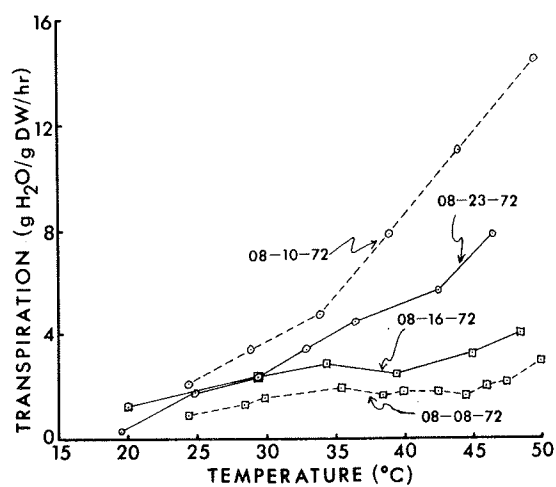


Figure 15. Effect of chamber temperature on transpiration of *Ambrosia* and *Larrea* in Mercury. Graphic representations: o—o = *A. dumosa* watered; o--o = *A. dumosa* unwatered; □—□ = *L. divaricata* watered; □--□ = *L. divaricata* unwatered.

Photosynthesis

Seasonal: Photosynthetic rates for the five shrub species exhibit seasonal differences which are characteristic for each species. The deciduous species, *A. dumosa*, *L. andersonii* and *L. pallidum*, which shed leaves in response to summer drought and winter cold, have high rates of net photosynthesis of up to 52 mg CO₂ fixed per g dry weight per hr in the morning, and a daily average of 40 mg CO₂/g dry wt/hr in early spring and decreasing until leaves are shed later in the season. *K. parvifolia* begins at a low rate in early spring and reaches its maximum rate in late spring or early summer. Since leaves are retained on *K. parvifolia* throughout the summer, presumably this species responds to moisture at any time from late spring until leaf fall in late October (Ackerman and Bamberg, 1972). *L. divaricata* and *K. parvifolia* had lower overall CO₂ uptake rates (only 10.1 mg CO₂/g dry wt/hr for *L. divaricata* and 8.9 mg CO₂ measured for *K. parvifolia*) than the three drought-deciduous species, but retained the ability to fix CO₂ longer at much higher soil moisture tensions through the early summer. These lower rates for leaf-retaining species may be anatomically related to their drought resistance in terms of diffusive resistance (El-Sharkawy and Hesketh, 1964).

In the watered plots at Mercury, *A. dumosa* retained leaves and both *A. dumosa* and *L. divaricata* photosynthesized throughout the whole summer. A comparison of *A. dumosa* and *L. divaricata* in the watered and unwatered plots at Mercury shows that under high temperatures of mid to late summer both species had low rates of up to 11.2 and 5.8 mg CO₂ fixed per hr, respectively, although earlier in the year at Rock Valley *A. dumosa* had rates of almost four times that of *L. divaricata*. *L. divaricata* had similar rates in the spring at Rock Valley and in the summer at Mercury.

Daily cycle of gas exchange: Gas exchange rates in all species climb during the early morning to high values between 8:00 and 9:00 and reach a maximum between 10:00 and 12:00. The rates then slowly decrease during the afternoon. These rates early in the season approximate the curve of incoming radiation over the day and net positive CO₂ uptake is dependent on direct sunlight, i.e., starting as soon as the sunlight hits the leaves and ceasing when the sun sets (Cunningham and Strain, 1969). At no time was a midday depression measured in either of the series tested at Rock Valley or Mercury. In Rock Valley, *L. divaricata* and *K. parvifolia* had, by mid-June, positive CO₂ uptake in the morning, decreasing to near zero in early afternoon as air temperature rose, but no second period of uptake in the late afternoon.

At Mercury, under both artificially watered and "natural" moisture conditions, *A. dumosa* and *L. divaricata* maintained the same daily cycle in the summer with the maximum rate shifted to early morning due to high midday temperatures of 40 C to 42 C. The rates and timing of the daily cycles are dependent on temperatures, moisture status, and acclimation as discussed in the next sections (Adams and Strain, 1968; Strain, 1969).

Effects of moisture and temperature: Moisture is the most critical factor affecting photosynthetic and transpiration rates in these desert shrubs. Three species, *A. dumosa*, *L. andersonii* and *L. pallidum*, have high photosynthetic rates in spring when there is adequate moisture and rates decline as both soil water potential and tissue water potentials increase. Activity ceases and leaves are shed when tissue water potentials approach -50 bars in the two *Lycium* species and at -55 bars in *A. dumosa*. In 1972 these values were reached in mid-May, and in 1971 not until the first of July.

The other two species, *K. parvifolia* and *L. divaricata*, retain their leaves throughout the summer and also have net photosynthesis at higher plant tissue potentials. In 1972 *K. parvifolia* had a small positive CO₂ uptake at -72 bars and *L. divaricata* at -65 bars, under field conditions. At soil moisture potentials above -40 bars, *L. divaricata* and *K. parvifolia* maintain a tissue water potential -10 to -15 bars higher than the other three species. In Mercury, even on the plots with adequate soil moisture of less than -10 bars, *L. divaricata* had plant tissue potentials of not less than -35 bars. Again, these high tissue potentials, even when soil moisture is high, are probably an adaptive response to high temperature; many such adaptive features of arid plants have been described or inferred in the literature (Bjorkman et al., 1972; Cunningham and Strain, 1969; Harrison et al., 1971; Wallace and Romney, 1972).

Effects of temperature on photosynthesis under natural conditions are more difficult to assess. In 1972 by mid-March, temperatures of 10 C to 30 C were favorable for CO₂ uptake. Plants responded to the combined effects of temperature and moisture as the season progressed. In 1972 a drying cycle and gradually increasing temperatures stopped plant activity in Rock Valley by mid-June, when maximum temperatures were around 35 C and soil moisture tensions exceeded -65 bars. In contrast, during May and June, 1971, with temperatures not exceeding 32 C and soil moisture of around -30 bars, plants continued active CO₂ uptake until early July.

With adequate moisture both *L. divaricata* and *A. dumosa* continued active CO₂ uptake with air temperatures approaching 49 C in July 1972. In the manipulated moisture plots at Mercury, as previously mentioned, the attempts to develop moisture stress in plants in the unwatered plot were interrupted by an early June rain of 2.1 cm. This rain provided adequate moisture for both *L. divaricata* and *A. dumosa* throughout the period of June, July and early August, so that tissue water potentials were increasing but there was no measurable effect on gas exchange. These results indicate that for moisture stress to affect gas exchange in these two plant species in the summer, a longer period of drought is needed.

Temperature has a direct effect on respiration rates during the dark periods. There was a high rate of respiration immediately after sunset and in the early evening hours, which gradually decreased in all tests during the night as temperatures cooled. We assume this decreasing respiration rate is temperature-dependent although the magnitude may also be somewhat controlled by a circadian rhythm.

Temperature acclimation: Measurements of the optimum temperatures for maximum photosynthesis have not yet revealed any consistent results. In most of the tests so far, all species except *K. parvifolia* show declining rates as temperatures increase from 15 C to 40 C. *K. parvifolia* showed a slight increase in temperature optimum as the daily temperatures increased in late spring.

In contrast to the temperature optima, upper thermal compensation points showed two trends related to moisture. If moisture was adequate, i.e., less than -40 bars, plants continued to acclimatize to higher temperatures with the upper limit depending on the species and the previous temperature regime. *L. divaricata* still showed a small net CO₂ uptake at 50 C (the limit of our control) when maximum temperatures the previous two weeks were 40 C to 50 C. If moisture tensions increase, then all species except *K. parvifolia* show decreasing upper thermal compensation points. *K. parvifolia* was able to acclimatize to higher temperatures even though plant tissue potentials were increasing. The three drought-deciduous species lose their leaves as previously discussed, but also have been observed to abscise some leaves in hot, dry winds even if soil moisture is adequate (Wallace and Romney, 1972). Lower thermal compensation could not be determined in summer since the heat loads prevented taking the chamber temperature below 10 C. Relatively high rates of CO₂ uptake were observed at low temperatures (10 C) even in late summer (Table 7). Plants are rarely subjected to daytime temperatures below 15 C from April through October. Further tests earlier in the season will help determine if lower thermal compensation points are seasonally different.

Water use

Transpiration: Transpiration rates show the same seasonal and daily trends for the different species as the photosynthetic rates discussed above. One difference noted was that the transpiration rate sometimes did not decline in the afternoon as did the photosynthesis rate, but remained at a fairly constant rate until sunset. There was no transpiration after sunset in the spring season; however, in summer with high night temperatures of 25 C and above, there was transpiration at 10 to 50% that of daytime rates. Below temperatures of about 15 C, plants transpire at very low rates during the day and not at all at night.

After a rain of 2 cm or more, plants respond within 3 days to a week by either a flush of new leaves or an increased CO_2 uptake. Our observations at Mercury indicate that the length of time necessary for desert plants to exhibit signs of water stress may be over 2 months after a substantial rain and subsequent lowering of transpiration and photosynthesis, even under severe summer conditions, and that even newly established plants are able to withstand high temperature. The length of time a rain is effective depends on the amount and season. In spring and fall this is up to 5 to 6 months and in summer for perhaps 2 to 3 months.

Water use efficiency: In 1972 water use efficiency (Ps/Tr) decreased in all species as the soil became drier. The reverse of this situation occurred in 1972 when water use efficiency increased in early summer after a May 2 rain of 2 cm.

Water use efficiency responds to plant moisture status and temperature both during the day and seasonally. Preliminary analysis of the Ps/Tr of each species shows that the relationship was linear at temperatures of 23 C to 35 C, and was flattened below 23 C so than below 20 C little transpiration occurred and Ps/Tr increased. Above 35 C the curve steepens and plants become less efficient, and above 40 C efficiency becomes negative in some tests in that transpiration still occurs but net CO_2 is given off. In the summer *L. divaricata* and *A. dumosa* acclimatized to higher temperatures and at 45 C to 50 C still were able to have positive CO_2 uptake, although efficiencies were low. Late in the spring and in the summer the Ps/Tr was lower and decreased rapidly with rising temperatures.

When under water stress, all of the species tested were less efficient in water use at all temperatures except *K. parvifolia* which had the highest water efficiency value at any temperature. We expect to develop regression equations for Ps/Tr for each species for a particular water status and temperature range.

Plant tissue water potential: Plant tissue water potentials as measured with a pressure bomb give a good comparative index of plant water status (Scholander et al., 1965). In the plant species tested at similar soil moisture conditions, a difference of -10 to -15 bars was observed, as previously mentioned. The relationship of tissue potentials to soil moisture potentials cannot yet be determined except in a general way. Studies of the effects of plant tissue water stress on photosynthesis rates on a diurnal and seasonal basis were initiated in 1972, but again only preliminary results were obtained. Most of these results are discussed in detail in previous sections.

Phenology and acclimation: There was a lack of clear-cut phenology phases which could be related to changes in gas exchange rates. During 1972 at Rock Valley the

2.3.1.3.-26

spring and summer season was notable for a lack of effective precipitation from early January through the middle of August. Although soil moisture was excellent early in the season following a rain of 5.3 cm in December, 1971, the effects of a late season dry period obscured phenophases in that several species produced a few flowers and fruit, and plants went dormant a month and a half earlier than in 1971. Decreasing moisture and increasing temperatures are overriding factors for gas exchange rates and in part determine phenology of the test species. While the dry season was mainly responsible for the low net photosynthesis in late spring and early summer, the presence of fruit on the plants tested may lower the net amount of CO_2 taken up. The green fruit of *L. andersonii* exhibited respiration rates of between 1 and 3 mg CO_2 /g dry wt/hr at temperatures of 20 to 35 C.

In general, additional moisture during the growth period from February through October results in an increase in photosynthesis and transpiration. If the rain is of sufficient amount, renewed growth, flowering, and fruiting occur. With such an extremely labile system, phenology, as such, is not an important consideration for gas exchange in those species listed, although Caldwell et al. (1972) found a closer relationship in Great Basin plant species.

Precipitation for the period of August 13 to November 18, 1972, totaled 10 cm in Rock Valley. Although gas exchange was not measured during this period, all of the five plant species responded with new leaves and growth for this fall period. The response of *K. parvifolia* has been minimal and *L. pallidum* had only a few leaves except in drainage areas.

Acclimation to heat and low moisture was not evident for any plant species in transpiration rates, although acclimation does occur in photosynthesis rates throughout the season. *K. parvifolia* and *L. divaricata* show some acclimation of photosynthesis to moisture stress; however, at the same time moisture stress is increasing, temperatures are also rising. *L. divaricata* and *A. dumosa* in watered plots at Mercury acclimated to high temperatures in the upper thermal compensation points, but not in optima for photosynthetic rates. There was considerable variation between the plants of any one species in the response of both photosynthesis and transpiration to tests in which a series of increasing temperature was set.

Modelling

Various models have been proposed for photosynthesis or productivity and most productivity models incorporate photosynthesis (Duncan et al., 1967; Miller, 1972).

Photosynthesis models are generally based on single leaf or canopy determinations for energy budgets, leaf temperatures, radiation, wind, and diffusive resistance. Most photosynthesis models treat moisture status as a constant rather than a variable and do not deal adequately with either mesophyll resistance or biochemical resistance to CO_2 diffusion, or rather again treat them as a constant value (Hall, 1971). Helms (1972) treats the effects of radiation, temperature, and CO_2 concentration effects on photosynthesis.

Our results indicate that for modelling either photosynthesis or productivity on a daily or seasonal basis in deserts, one should deal with water deficit effects on resistances in the leaf, and the combined effects of moisture and temperature on acclimation during the season. Brittain (1972) in a preliminary model does consider plant water potential and phenology, in addition to other factors, as important in photosynthesis for plants with noncrassulacean acid metabolism. Other environmental stresses used in models which effect photosynthesis, such as radiation and wind, were not sufficiently tested to determine their effects on our species. Although these conditions may be extreme in deserts, plants have adapted to them (Bjorkman, 1972).

Several adaptive strategies are apparent from the five species tested and indicate the need of several alternate schemes for photosynthesis models. These strategies are:

1. *L. divaricata* -- evergreen with low photosynthetic rates and ability to depress transpiration loss during moisture and temperature stress; will photosynthesize during any favorable period.
2. *K. parvifolia* -- summer green, low photosynthetic rates and also can depress photosynthetic and transpiration rates and can withstand higher temperature and moisture stress in summer; winter-deciduous.
3. *A. dumosa* -- drought-deciduous with high photosynthetic and transpiration rates during favorable conditions. Some ability to withstand temperature stress and will retain leaves in summer with sufficient moisture; winter-deciduous.
4. *Lycium* spp. -- drought-deciduous with higher photosynthetic and transpiration rates for short periods during favorable conditions in spring or fall. Slight ability to withstand temperature and moisture stress with leaf abscission in summer; winter-deciduous.

In measuring rates in the field, all the environmental factors vary simultaneously so that a series of multiple regression equations may best express actual conditions. Attempts should be made using equations for n^{th} dimensional hyperspace, such as multiple regression or principal component analysis. Plotting rates as points on a two or even three dimensional graph may account for, at most, 50 to 75% of the variation observed.

2.3.1.3.-28

Productivity models of desert ecosystems will need to reflect the great variability in environmental factors, particularly moisture, and the facultative response of plants to them. Threshold values of factors for various physiological processes leading to new growth, flowering, and fruiting need to be determined.

PART II

ROOT AND STEM RELATIONSHIPS AMONG TEN
SPECIES OF NORTHERN MOHAVE DESERT PLANTS

ABSTRACT

Root and stem weights were obtained from field samples of ten species of perennial plants in the northern Mohave Desert. The specific purpose was to develop methods for determining below-ground biomass in connection with a general study on assimilate distribution. Root and stem weights for all species were highly correlated and linear regression in most cases adequately expressed the relationship between root weight and stem weight. Root weight for the total of all plants considered was about 45% of the sum of stem and root weights. There were species differences. The proportion that was root was generally independent of whether the plant was large or small. It was concluded that root biomass can be estimated from stem weights for a population of some species, at least within a possible error of ± 10 to 20%.

INTRODUCTION

For many reasons it is necessary to know the amount of standing biomass of perennial plants for below ground as well as above ground. This need was the motivating force for a study of the distribution of root systems of several species of perennial desert plants. Some data of this nature are available in the literature for some desert plant species (Jones and Hodgkinson, 1970). It is, of course, recognized that shoot-root ratios of plants do vary with environmental conditions (Harris, 1914). Conventional methods for measurement of root biomass are poorly adapted to desert conditions because of the sparse and irregular nature of vegetation in deserts such as the northern Mohave. If small cores of samples were taken to obtain root samples, some 80 to 90% of them would contain no roots under the conditions which prevail in the Mohave Desert. Those samples having roots would vary several-fold. Instead, individual plants were excavated to determine root-shoot relationships.

OBJECTIVES

(See Part I, page 2.3.1.3.-3)

METHODS

The sampling location was the Rock Valley area of the Nevada Test Site. The species were *Atriplex canescens* (Pursh) Nutt., *Atriplex confertifolia* (Torr. and Frem.) Wats., *Ambrosia dumosa*, *Larrea divaricata*, *Lycium andersonii*, *Lycium pallidum*, *Grayia spinosa* (Hook) Moq., *Krameria parvifolia*, *Ephedra nevadensis* Wats., and *Acamptopappus shockleyi* Gray.

The dry weights of stems and roots of 113 individual plants were determined. The soil was carefully excavated for each plant and often 1 to 3 m³ of soil was removed. Excavation of such plants involved movement of soil often for one or more m in each direction from the base of the plant (Wallace and Romney, 1972). The soil was not screened to remove fine roots, but sufficient soil was removed with each plant to obtain the large majority of the root system. We have estimated that no more than 15% of the root system was missed, and this mostly because of very fine roots. Plants were selected which had a minimum of interference from adjoining shrubs. This, of course, would probably give some bias when results were extrapolated to a unit area of desert.

Calculations were made with these data to give correlations, standard deviations, and linear regressions.

RESULTS AND DISCUSSION

The data (Table 8) indicate that standing biomass of roots may be reasonably estimated from stem-weight measurements. Standard deviations for root/root + stem varied between 20 to 30% of the mean (coefficient of variation). Variability is understandable because of pruning of stems which occurs by wind and animal action, because of die-back of stems, of die-back of roots, of age of plants, of differential water availability due to microterrain, and because of a host of other factors. The standard errors for root/root + stem were generally between 5 to 10% of the means. With these statistics, standing-root biomass for a single plant cannot be estimated from weight of stems with 95% confidence within ± 40 to 70% (twice the coefficient of variation), but the estimates for a population with 95% confidence as a whole can be within 10 to 20% (twice the standard error). The values for weights of root x stem were highly positively correlated.

If one were looking for the estimate of root weight from the stem weight within one standard deviation of the real value with a 95% percent confidence level for a population, only four root/root + stem ratios need to be taken (Snedecor, 1946); 16 would be needed for within one-half standard deviation at the same level of precision. Since the standard deviations of the root/root + stem of plants were around 25%, it would appear that a 16-plant sample per species would express the root biomass under field conditions to a precision of 10 to 15%. Obtaining the samples, however, involves considerable careful effort.

Table 8. Root-stem relationship for ten different perennial plant species collected in the field at the Nevada Test Site, northern Mohave Desert DSCODE—AU3BD04-5

Species	N	Mean		Root X stem	Root* X root+ stem	Root** root + stem	Root+ root+ stem (mean)	Stan- dard devi- ation of mean	Stan- dard error of mean	Root+ root + stem	Linear regression††	
		g	g								Root (g)	+ b stem (g)†‡
<i>A. confertifolia</i>	14	42.9	115.7	.989	-.181	27.1	27.7	9.5	2.54	29.9	R=(0.29 stem + 9.3)	1.15
<i>A. dumosa</i>	25	99.0	98.2	.926	.498	50.2	46.3	9.5	1.90	53.6	R=(1.15 stem - 13.95)	1.15
<i>A. canescens</i>	11	71.3	121.9	.903	-.300	36.9	41.3	7.9	2.36	40.2	R=(.42 stem + 20.3)	1.15
<i>L. divaricata</i>	13	316.6	293.8	.981	.238	51.9	47.7	12.3	3.40	55.3	R=(1.374 stem - 87.1)	1.15
<i>L. pallidum</i>	10	182.7	128.5	.973	.241	58.8	55.9	15.4	4.87	62.2	R=(1.465 stem - 5.3)	1.15
<i>G. spinosa</i>	5	226.4	372.8	.943	-.083	37.9	39.8	11.3	5.05	41.7	R=(0.60 stem + 2.38)	1.15
<i>L. andersonii</i>	10	182.6	251.4	.959	.468	42.1	39.3	10.3	3.26	45.5	R=(.818 stem - 23.0)	1.15
<i>K. parvifolia</i>	6	112.2	163.4	.722	.120	40.7	42.9	9.5	3.87	44.1	R=(.349 stem + 55.2)	1.15
<i>E. nevadensis</i>	11	73.2	102.0	.891	.647	41.8	37.6	11.6	3.49	45.5	R=(0.85 stem - 26.2)	1.15
<i>A. shockleyi</i>	8	13.0	26.2	.948	-.409	33.2	36.9	8.9	2.16	36.4	R=(0.45 stem + 1.23)	1.15
All species	113						41.6	12.6	1.22			

*Non-significance means that a normal curve may be followed

**Weighed mean or mean of the total root and total stem for all samples by species. LSD values for this column were 7.0 (.05), 9.2 (.01)

†Corrected root/root + stem assuming that 15% of roots not recovered

††The 1.15 factor corrects for roots not recovered

PART III

USE OF ^{14}C TO ESTIMATE ASSIMILATE TRANSPORT
AND BELOW GROUND PRIMARY REPRODUCTIVITY
AMONG EIGHT SPECIES OF PERENNIAL
MOHAVE DESERT PLANTS

A B S T R A C T

The distribution of photosynthate subsequent to production in leaves or stems gives an estimation of how plants respond to seasonal factors in their production.

In this study in 1972, photosynthate was labeled with ^{14}C for 24 plants representing eight species. Results showed that after 127 days the mean percentage of ^{14}C in roots as compared with the estimate of that originally fixed was 11.8; the percentage in stems was 43.8. The ratio of root/root + stem for ^{14}C was 0.212 and only half the ratio for actual weights of field plants. The correlation coefficient for ^{14}C in roots x root/root + stem (ratio of dry weights) was +0.84. Small stems were the major storage organ for the ^{14}C . Shoots of *A. dumosa* plants were exposed to ^{14}C in 1971 and the distribution of ^{14}C in roots, stems, and leaves was measured at one week, two months, and five months. Only about 12% of the photosynthate was stored in the root. Much of that stored in stems was available for new leaf growth.

Root growth of eight perennial desert plants grown in the glasshouse was followed as plants increased in size. The mean percent of whole plant that was root for the eight species was 17.7%. The mean proportion of the increase in plant weights that went below ground for the eight species was 19.5%.

INTRODUCTION

The distribution of primary productivity among leaves, stems, and roots is an important process and can be related to the amount of standing biomass below ground as well as above ground. The need to know also how assimilate transport related to root biomass was the motivation for a study of the development of root systems of eight species of perennial desert plants. Data of this nature are available in the literature for some desert plant species (Jones and Hodgkinson, 1970). It is, of course, recognized that shoot-root ratios of plants do vary with environmental conditions (Harris, 1914).

OBJECTIVES

(See Part I, page 2.3.1.3.-3)

METHODS

On March 21, 1972, and March 27, 1972, 24 plant specimens (*A. dumosa*, *A. confertifolia*, *L. pallidum*, *L. andersonii*, *L. divaricata*, *A. canescens*, *E. nevadensis*, and *Eurotia lanata* (Pursh) Moq.) were labeled in the field as in 1971. Ten mc of ^{14}C NaHCO_3 was present in 120 ml solution and 5 ml was used for each plant. The ^{14}C was released inside the plastic bag by pouring HCl into the NaHCO_3 . After 126 to 127 days the plants were excavated and separated as before. At this time most of the leaves had abscised on most of the species.

On June 11, 1971, about 900 hr, four *A. dumosa* plants in the northern Mohave Desert were covered with plastic bags and 125 μC $^{14}\text{CO}_2$ were released into each bag. Two hr later the bags were removed and leaf and stem samples were taken from each for determination, by Q-gas counting, the amount of ^{14}C fixed. The number of leaves on the samples collected was counted as well as those remaining on the plant, so that a reasonably accurate assessment of the total ^{14}C fixed by the plants could be made. Plants were excavated after 1 week, 2 months, and 5 months. Total ^{14}C present in small roots, large roots, small stems, large stems, and leaves was determined.

Eight species of desert plants were propagated in the glasshouse, some by seedlings and others by cuttings, and planted individually into containers of Yolo loam soil (3.7 kg). Nitrogen fertilizer (50 ppm N as NH_4NO_3 monthly on dry weight of soil basis) was added and soil moisture was kept at around one-third bar during the study. The species employed were *A. canescens*, cuttings; *A. confertifolia*, cuttings; *A.*

hymenelytra, cuttings; *E. nevadensis*, cuttings; *A. dumosa*, seedlings; *L. divaricata*, seedlings; *L. andersonii*, cuttings; *L. pallidum*, seedlings.

After about 2 months, a sampling procedure was started in which plants were separated into leaves, stems, and roots at approximately 2-week intervals to give a series of plants of different and increasing sizes.

RESULTS AND DISCUSSION

In the glasshouse study on roots, the percentage increase in dry root weight compared with the percentage increase in total weight as plants increased in size, indicated a mean percentage of new growth going below ground of 19.5% (Table 9). Highest value was for *L. pallidum* (33.7%) and lowest was for *A. confertifolia* (4.7%). In a companion field study with eight species (Part II), highest root/root + stem was for *L. pallidum* (62.2%) and lowest was for *A. confertifolia* (29.9%). Correlation coefficient between the ratios in Table 9 and the root/root + stem for the field (Part II) was +0.98.

In the 1971 ^{14}C -fixation study the plants fixed about 4% of the ^{14}C supplied. Between the time of fixation and sampling dates, little of the ^{14}C seemed to have been lost to respiration in that the recovery after 2 months was around 90% of that originally fixed (Table 10). A most interesting aspect of the data was the relatively low levels transferred to the roots (9.4% at 1 week, 12.3% at 2 months, 10.0% at 5 months). This is in contrast to the 80% found for a grass by Dohleman (1968). The leaves of *A. dumosa* seemed to serve as a storage site for a period of time, but the major storage site was twigs and stems. *A. dumosa* is a deciduous plant so that any photosynthate remaining in leaves is lost to the plant at the time of leaf abscission. Stored reserves in the stems become mobilized and are used in early development of new growth when environmental conditions become favorable. In the case of *A. dumosa*, this is largely a matter of adequate soil moisture.

The transport of about 10% of the photosynthate below ground is somewhat less than the 26.7% of new growth of the glasshouse plants being compartmented in roots, and the 23.2% of roots relative to whole plant for field plants.

In the 5-month sample, 56% of the estimated $^{14}\text{CO}_2$ fixed was still present in the plant. In addition to respiration loss and loss from abscised leaves, there are losses due to flowering and fruiting and possibly also to herbivores. A portion of the 56% was present in new leaves which had grown in response to a late summer rain. At this

2.3.1.3.-38

point the root/root + stem for the ^{14}C was 20.7%, which is considerably less than the value for weights of field plants (53.6% in Part II). This indicates that biomass losses from stems (animal, weather) are greater than losses from roots.

The 1972 data for ^{14}C verify the trend indicated by *A. dumosa* in the 1971 study (Table 11). In comparison with the estimated amount of ^{14}C originally fixed, the mean ^{14}C in roots for the eight species was 11.8%. It ranged from a low of 3.9% with *A. confertifolia* to a high of 22.3% for *L. pallidum*. These are the identical species with low and high transport values for the glasshouse study (Table 9) and for the field study (Part II). The correlation coefficients for the root/root + stem values for ^{14}C and the ratios of weights for field plants (Part II) was +0.84. But again the ^{14}C values are much below the weight values. The hypothesis mentioned above for *A. dumosa* must be applicable for all the species studied; i.e., in the field biomass loss is greater for stems than for roots so that the measured ratio is greater than the ratio of new photosynthate distributed between stems and roots.

The transfer to roots of ^{14}C was especially low in those species which retained a large proportion of leaves at time of sampling. This was pronounced for *A. confertifolia*, *A. canescens*, *E. lanata*, and *L. divaricata*. The means for roots for these four species compared with the other four were 7.1% and 16.5%, respectively. Perhaps the latter is the more accurate value for distribution of photosynthate below ground, and perhaps a longer time would be needed for an evaluation of root transport for the species. The fact remains, however, that seed and leaves of *A. confertifolia* constitute a large use and loss of photosynthate.

From the various studies made it seems that only 10 to 20% (sometimes less) of the annual photosynthesis productivity goes into the root systems. Considering, however, that there are losses to respiration, herbivores, leaf abscission, wind, flowering, and fruiting, the estimates may be realistic. Small stems (twigs) may constitute the major storage sites for carbon in these desert plants. 1971 and 1972 were years of low productivity and this may affect the proportion of photosynthate being transported and stored in various plant organs and that lost through reproductive structures.

Table 9. Root, stem, leaf relationships for the plants grown in the glasshouse DSCODE—A3UBD03

Species	No. of plants	Root	Stem	Leaf	Mean increase dry wt in roots*	Root g	Stem g	Root/ root + Stem**	C.V. [†]	Root + stem (field data) ^{††}
		% distribution			% in root % in whole plant		g		%	%
<i>A. dumosa</i>	9	20.5	44.4	35.1	26.4	5.33	10.43	33.8 ± 3.01	26.7	53.6
<i>E. nevadensis</i>	10	14.5	85.5	-	13.2	1.03	6.08	14.5 ± 0.68	14.8	45.5
<i>A. hymenelytra</i>	6	19.3	27.7	53.0	19.5	4.52	6.47	41.1 ± 2.57	15.3	-
<i>A. confertifolia</i>	8	4.3	30.9	64.8	4.7	1.19	8.59	12.2 ± 1.66	38.4	29.9
<i>A. canescens</i>	7	12.0	41.8	46.2	12.7	3.15	11.77	21.1 ± 2.01	25.2	40.2
<i>L. pallidum</i>	9	26.3	59.3	14.4	33.7	5.74	12.91	30.8 ± 1.96	19.1	62.2
<i>L. andersonii</i>	7	21.9	73.0	5.1	20.9	6.56	19.20	25.5 ± 2.72	28.2	45.5
<i>L. divaricata</i>	7	23.5	39.6	36.9	25.0	4.78	8.07	37.2 ± 2.94	20.9	55.3
Means		17.7			19.5					

*Calculated by using the smallest plant as the base.

**±standard error of mean

†C.V. is coefficient of variation of $\frac{\text{root}}{\text{root} + \text{stem}}$.

††Ref (Part II)

2.3.1.3.-40

Table 10. Distribution of ^{14}C label of photosynthate in plant parts of *A. dumosa*, 1971, DSCODE—A3UBD03

cpm fixed (2 hr)* per plant	1 week 2,600,000	2 months 2,400,000	5 months 2,700,000
% remaining	98	90	56
g dry wt/plant			
Leaves	18.77	9.54	3.96**
Small stem	37.87	12.16	19.43
Large stem	27.99	42.97	25.12
Large roots	36.72	46.82	27.09
Small roots	6.33	8.02	6.38
% Distribution at sampling times of ^{14}C \pm remaining in plant			
Leaves	57.0	22.2 \pm 7.31	13.5**
Small stem	25.8	35.4 \pm 8.37	43.3
Large stem	7.8	28.8 \pm 14.31	25.3
Large roots	8.5	10.4 \pm 1.77	15.6
Small roots	1.1	3.2 \pm 0.15	2.3
Total	100.2	100.0	100.0
% of original fixed ^{14}C in stems and roots at sampling times			
Small stem	25.3	31.9 \pm 7.5	24.2
Large stem	7.6	25.9 \pm 12.9	14.2
Large roots	8.3	9.4 \pm 1.6	8.7
Small roots	1.1	2.9 \pm 0.14	1.3
Total roots	9.4	12.3	10.0
^{14}C in stems/ ^{14}C in roots (ratio)			
	3.50	4.90	3.84
^{14}C root/root + stem, %			
	22.2	17.5	20.7

\pm is a standard deviation.

*cpm fixed at 50 mg counting wt.

**Original leaves had abscised and a new flush of leaves had grown in response to late summer rain, but some of these leaves had abscised also.

PART IV

VERTICAL ROOT PROFILES OF PERENNIAL PLANT SPECIES FROM THE ROCK VALLEY AREA OF THE NORTHERN MOHAVE DESERT

A B S T R A C T

The root systems of 48 perennial plants representing nine species from the Rock Valley area of the northern Mohave Desert were excavated by 10 cm vertical increments to determine distribution by depth. The depth of penetration of all species was relatively small and obviously limited by depth of penetration of precipitation (about 10 cm annual mean) and presence of caliche layers. There were species differences, however, in distribution of roots. Even though a sizeable proportion of the root systems was in the first 10 cm of soil, this portion consisted largely of multiple woody tap roots with relatively few small roots. From 50 to 80% of the total root systems was in the first 20 cm. In most cases the majority of small roots were between 10 and 30 cm in depth.

INTRODUCTION

A complete understanding of the role of soil processes in desert ecosystems requires that the distribution of plant roots in soil profiles be known. The purpose of the present investigation was to obtain some information needed in this regard. Studies of rooting habits of desert plants in the western USA have led to conclusions that the plants are generally not deeply rooted, unless they are in places where rain water accumulates (Cannon, 1870; Dittmer, 1964; Markle, 1917; Waterman, 1923). These workers recognized that depth of rooting was often limited by caliche layers near the soil surface or unfavorable soil chemistry or soil physical properties. None of the workers reported quantitative information on the amounts of roots at different depths. Consequently, the distribution with depth of roots of several major perennial plants in the Rock Valley area of the northern Mohave Desert was studied.

OBJECTIVES

(See Part I, Page)

METHODS

Root systems of 48 individual plants representing nine species were excavated during the spring and summer of 1972. The species were: *A. canescens* (6), *A. shockleyi* (3), *A. confertifolia* (7), *L. divaricata* (3), *E. nevadensis* (7), *L. andersonii* (5), *L. pallidum* (6), *K. parvifolia* (3), *A. dumosa* (8). The numbers in parentheses refer to the number of plants excavated for each species. These collections were made in connection with another study which involved the shoot-root relationship of perennial desert plants (Part II).

The excavations were made by hand shovel, and roots were separated by 10 cm depth increments. Individual roots were followed as far as possible and often 1 to 2 m³ of soil was removed in the excavation of a single root system. Roots were separated into those larger or smaller than 2 mm diameter. All roots were washed and dry weights determined.

RESULTS AND DISCUSSION

The mean weight of root systems together with percentage distribution by depth with standard errors for each increment are given in Table 12.

In general, most of the root systems were in the first 50 cm of soil, or shallower in some species. Means for the nine species showed 39% in the first 10 cm, 70% in the first 20 cm, and 95% in the first 40 cm. This shallow depth of rooting is related to the sparsity of precipitation with an annual mean of about 10 cm (Beatley, 1967; Wallace et al., 1972), and the presence of a caliche layer at 40 to 50 cm. Phenology over a 4-year period of the species concerned has been reported (Wallace et al., 1972), as has behavior of winter annuals in the area (Beatley, 1967).

The portion of the root system in the first 10 cm of soil, even though relatively large, was mostly in the form of multiple tap roots. Evidence for this was the small proportion of fine roots compared to total roots in this zone (mean was 3.2% for eight of the nine species compared with 8.7% for the second 10 cm). Most of the small roots were in the 10 to 30 cm zone. It can be expected that high temperatures of the soil surface together with the fact that soil surfaces are drier than lower horizons are responsible for this behavior. These two factors would account for the absence of small roots in the first 10 cm of soil.

There were species differences in root distribution. *A. shockleyi* and *K. parvifolia* were more shallow-rooted than other species. Over 85% of the root systems for these two species were in the first 20 cm. Less than 50% of the root system was in the first 20 cm with *A. canescens*. Lower stems of *K. parvifolia* were usually covered with about 10 cm of blow sand because of the catchment nature of the shrub, so that roots actually were not as close to the surface as indicated. *L. andersonii* roots were more uniformly distributed throughout the root zone than most other species although *L. pallidum* was somewhat similar. The two species which remain photosynthetically active longer in the season than others (*L. divaricata* and *K. parvifolia*) were not too much unlike other plants except for the shallow nature of *K. parvifolia*, mentioned above. *K. parvifolia* had a greater proportion of small roots than did other species.

Table 12. Distribution by depth of roots from 9 perennial plant species collected from Rock Valley; values are % of total root system DSCODE—A3UBD06

Depth cm	<i>A. shockleyi</i> (3)	<i>L. divaricata</i> (3)	<i>L. andersonii</i> (5)	<i>L. pallidum</i> (6)	<i>E. nevadensis</i> (7)
Large roots (above 2 mm)					
0-10	45.7± 9.4	22.4± 0.8	25.9± 5.4	27.5± 4.5	38.4± 5.3
10-20	25.3± 7.5	25.4± 1.0	15.5± 3.6	28.3± 4.8	19.7± 3.6
20-30	5.2± 2.9	12.6± 1.9	15.1± 2.6	9.8± 2.0	11.2± 2.0
30-40	0.8± 0.8	7.0± 1.6	9.2± 2.0	5.4± 0.4	5.2± 1.8
40-50	0.0	3.1± 2.2	8.7± 3.8	3.5± 1.6	1.0± 0.4
Over 50	0.0	0.0	0.0	0.0	0.0
Small roots (2 mm or less)					
0-10	5.9± 1.6	2.1± 0.7	2.2± 0.8	2.9± 1.1	1.6± 1.0
10-20	8.5± 6.1	8.3± 2.6	8.3± 2.0	10.5± 3.4	5.7± 1.1
20-30	7.1± 6.4	7.2± 1.7	7.3± 1.7	6.5± 2.5	10.6± 3.3
30-40	1.5± 1.5	4.1± 1.5	4.6± 1.2	3.2± 0.9	5.4± 2.2
40-50	0.0	2.9± 1.8	3.1± 0.7	2.6± 1.1	1.1± 0.5
Over 50	0.0	0.0	0.0	0.0	0.0
Total %	23.0	24.6	25.5	25.7	24.4
All roots					
0-10	51.6± 9.8	29.6± 0.5	28.1± 5.2	30.4± 5.0	40.0± 5.9
10-20	33.3± 1.6	33.7± 3.1	23.9± 5.5	38.7± 5.1	25.4± 4.4
20-30	12.3± 9.1	19.8± 2.3	22.4± 3.3	16.3± 2.6	21.9± 4.1
30-40	2.3± 2.3	10.9± 1.8	13.8± 2.6	8.6± 1.0	10.6± 3.4
40-50	0.0	6.0± 4.0	11.8± 4.2	6.0± 2.6	2.0± 1.0
Over 50	0.0	0.0	0.0	0.0	0.0
Total wt(g)	20.7	225.1	269.5	222.8	86.9

± is standard error of mean . Number in parenthesis is number of plants

	<i>A. dumosa</i> (8)	<i>K. parvifolia</i> (8)	<i>A. canescens</i> (6)	<i>A. confertifolia</i> (7)
Large roots (above 2 mm)				
0-10	35.8± 2.4	39.9± 3.3	29.8± 5.0	39.7± 6.1
10-20	25.7± 2.2	20.1± 5.2	14.9± 2.2	16.1± 1.5
20-30	10.4± 1.7	2.1± 2.1	10.6± 2.5	6.7± 1.5
30-40	4.0± 1.6	2.0± 2.0	4.9± 1.8	2.8± 0.6
40-50	1.7± 1.2	0.0	6.0± 2.0	1.4± 0.6
Over 50	0.0	0.0	1.4± 1.4	1.2± 1.2
Small roots (2 mm or less)				
0-10	2.3± 0.7	16.3± 7.7	3.4± 1.1	6.1± 1.1
10-20	9.9± 1.9	14.3± 3.3	10.7± 2.6	10.0± 3.0
20-30	6.4± 1.6	2.9± 2.9	8.4± 1.7	7.4± 1.6
30-40	4.4± 0.8	2.5± 2.5	4.9± 1.4	5.8± 1.5
40-50	1.4± 0.9	0.0	4.5± 1.2	2.4± 0.9
Over 50	0.0	0.0	1.1± 0.7	0.6± 0.6
Total %	24.4	36.0	33.0	32.1

Table 12 continued on next page.

Table 12. (Continued)

	<i>A. dumosa</i> (8)	<i>K. parvifolia</i> (8)	<i>A. canescens</i> (6)	<i>A. confertifolia</i> (7)
All roots				
0-10	38.0± 2.6	56.2± 8.4	33.8± 6.1	45.7± 6.6
10-20	33.6± 3.1	34.3± 2.5	24.9± 2.8	26.1± 3.6
20-30	16.8± 2.7	5.0± 5.0	18.5± 3.4	14.1± 2.7
30-40	8.5± 2.0	4.5± 4.5	9.8± 1.7	8.5± 1.7
40-50	3.1± 2.1	0.0	10.5± 2.8	3.7± 1.4
Over 50	0.0	0.0	2.5± 2.0	1.8± 1.8
Total wt (g)	113.2	129.9	86.8	76.1

± is standard error of mean.

Number in parenthesis is number of plants.

EXPECTATIONS

During 1973 we will continue analyzing 1972 data for developing multiple regression equations of environmental factors which will account for the variation in rates measured. An analysis of nutrient status of species made in connection with this study will be completed. Parts of this study will be continued or expanded as follows:

Gas exchange

We will continue and expand the gas exchange measurements in 1973 to include simultaneous measurements of several environmental factors. An automatic data acquisition will be added to the system.

Assimilate distribution

Whole shrub labeling and sampling will be continued with a possibility of extending time between labeling and sampling up to a year.

Diffusive resistance

For determining leaf diffusive resistance, we will measure leaf temperatures and plot leaf area of each sample photogrammetrically. Each leaf sample will then be freeze-dried for later biochemical analysis in the laboratory.

Plant water status

A complete series of moisture status determinations will be made on all species for diurnal and seasonal patterns and relationship to gas exchange in the plant and to external soil moisture conditions.

Nutrient distribution

Data available will be processed to show distribution among plant parts and relationships to phenological events.

Respiration

We will attempt to determine photorespiration and the relationship of dark respiration to diurnal rhythms and nocturnal temperatures.

ACKNOWLEDGEMENTS

We wish to thank Bernardo G. Maza of the Laboratory of Nuclear Medicine and Radiation Biology for programming the computer analysis of Siemens output. Harold Mork helped set up and operate the Siemens apparatus at the Nevada Test Site. Dr. Jong Whan Cha helped with the root studies.

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1970 PROGRESS REPORT

Productivity and Water Stress in Cacti

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April 1971

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PROGRESS REPORTS ON PROCESS STUDIES (2.3)

Productivity and Water Stress in Cacti (2.3.1)

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Abstract

The objectives of this study are to determine the biomass contribution of cacti to the Sonoran Desert ecosystem and the productivity rates and water flux that influence this biomass. Harvesting and sampling of cacti and other perennials have shown the significant contribution of cacti to the ecosystem. Growth rates are shown to respond to rainfall and temperature regimes. Cacti are shown to be major recyclers of nutrients. Carbon dioxide exchange measurements of cacti are being used to pinpoint the environmental conditions and times of best growth.

Objectives

The basic objectives of this study were to determine the productivity of cacti (especially a prickly pear and cholla species) under different environmental conditions including variable moisture stress conditions. In order to achieve these objectives, secondary objectives were established during 1970. These included determination of (1) the relative importance of cacti in a typical Sonoran Desert community, (2) actual environmental conditions that influence cacti productivity and moisture stress, (3) total biomass of selected species of cacti in a limited study area as well as dry weight ratios between plant parts for future estimation of biomass, (4) growth rates of plants, especially stem parts in cacti, in relation to time and environmental factors, and (5) differential CO₂ exchange through time as a measurement of short term productivity rates. It was not intended when establishing these secondary objectives that results would be obtained during 1970 to completely satisfy all the primary objectives.

Methods

A few cactus plants have been studied in South Mountain Park south of Phoenix, Arizona; however, most work has been carried out at a study site in Utery Mountain Regional Park northeast of Mesa, Arizona at 2,200 ft. elevation. An 100 x 100 m plot has been set aside for permanent study while actual harvesting of plants has been done outside of the plot.

Vegetation Analysis

In order to determine the contribution of cacti to the vegetation of the study area, fifty 5 x 5 meter quadrats within the 100 x 100 m plot were sampled for total perennial vegetation. Density, frequency, and aerial cover were determined for each species. These were converted to relative figures and summed to give an importance value for each species in the stand.

Environmental Conditions

Soil moisture and air and soil temperature are being measured at the Utery study site. Soil moisture is being measured both gravimetrically and by Colman blocks at 10 cm and 30 cm depths at four locations. Both air and soil temperatures are being measured with Sixes type maximum-minimum thermometers. Two thermometers on stands measure air temperatures 30 cm above the soil surface and four thermometers in metal containers measure soil temperatures 10 cm in the soil. These are read periodically and only the maximum and minimum temperatures are recorded. Precipitation data used is an average of data from three U. S. Weather Bureau Stations located within a ten mile radius of the study site.

Biomass Determinations

One hundred prickly pear cactus (Opuntia engelmannii) pads were harvested to determine the relationship between pad dimensions and dry weight. Length times width of each pad is best for estimating pad dry weight. One hundred prickly pear fruits were harvested to obtain an average dry weight per fruit. Eight total prickly pear plants were harvested to determine dry weight relationships between pads (photosynthetic stems), stems (with corky tissue), fruits, and roots. These plants ranged in size from 20 pads per plant to 110 pads per plant. All of these data have been used in estimating the total biomass for prickly pear cacti within the study area. Similar data are being collected for staghorn cholla (Opuntia acanthocarpa).

Productivity and Water Stress in Cacti - continued

Growth Rates

Selected pads from prickly pear plants have been measured periodically as to length, width and thickness. These data can be used to determine the gradual increase and fluctuations in biomass relative to time and environment.

Carbon dioxide exchange and water loss. Carbon dioxide exchange patterns of prickly pear cactus are being measured with a Beckman 215R infrared gas analyzer. Laboratory studies are under controlled light and temperature regimes whereas field studies are under conditions as similar as possible to the existing environmental situation. Whole plants are used when they are small but excised parts of larger plants, shown to vary little from intact plants (Patten and Dinger, 1969), are used for most experiments. Water loss by the plants is being measured by differential psychrometry between inflow and outflow air streams from the plant chamber.

Findings

Vegetational Composition

Bur sage (Franseria deltoidea) is the dominant species in the study area (Table 1). The cholla cacti (Opuntia acanthocarpa, O. leptocaulis, and O. fulgida) are the dominant cacti while prickly pear (O. engelmannii) appears to contribute little to the community as expressed by Importance Value (Table 1). Palo Verde (Cercidium spp.) and ironwood (Olneya tesota) were not sampled because no wash intersected the sampled area; however, they were present in the desert area surrounding the study site.

Table 1. Importance Values (I. V.) of the perennial species sampled at the Usery Mountain study site.

<u>Species</u>	<u>I. V.</u>
<u>Franseria deltoidea</u>	145.1
<u>Larrea divaricata</u>	37.3
<u>Opuntia acanthocarpa</u>	30.9
<u>O. leptocaulis</u>	20.0
<u>O. fulgida</u>	16.0
<u>Mammillaria microcarpa</u>	12.9
<u>Simmondsia chinensis</u>	11.2
<u>Echinocereus engelmannii</u>	8.0
<u>Ferocactus acanthoides</u>	5.6
<u>Brickellia coulteri</u>	4.1
<u>Cereus giganteus</u>	4.1
<u>Opuntia engelmannii</u>	2.6
<u>Lycium</u> sp.	2.2

Environment

Temperatures, soil moisture, and precipitation from June into November 1970 are presented in Figure 1. Soil moisture responds directly to precipitation with shallower soil wetting up faster and to a greater extent than the deeper soils. Although most of the soil moisture measurements were taken shortly after a rain (24 hours), the maximum water content measured was six percent. Air and soil temperatures show fluctuations through the summer and then a gradual drop toward winter. Although data from December 1970 are not in Figure 1, minimum air temperatures during December have dropped below freezing.

Biomass Measurements

Using dry weight measurements of totally harvested prickly pear plants and calculated estimates from other plants it was possible to develop a biomass ratio between pad dry weight and stem dry weight (Fig. 2). The curve established by these ratios can be used for estimating total dry weight of a plant when knowing only the number of pads on the plant and relative dimensions of representative pads.

Total biomass of the prickly pear cactus plants and of the various plant parts is presented in Table 2. These data are based on estimates of (1) dry weight of the pads determined on a curve relating pad dry weight to length times width calculations similar to the relationship shown in the mid-year report for pad dry weight compared to length x width x thickness; (2) ratios of pad dry weights to stem dry weights (Fig. 2); and (3) average fruit dry weight. As one might expect, the pads make up more than half of the total dry weight of the plants but, unexpectedly, the fruit, which are shed each year, make up more than ten percent of the total dry weight. The estimate for total dry weight of prickly pear cactus at the study site of 83 kg/ha is much more accurate than the 75 kg/ha reported at mid-year (1970). Similar data are not complete for the cholla cactus being studied.

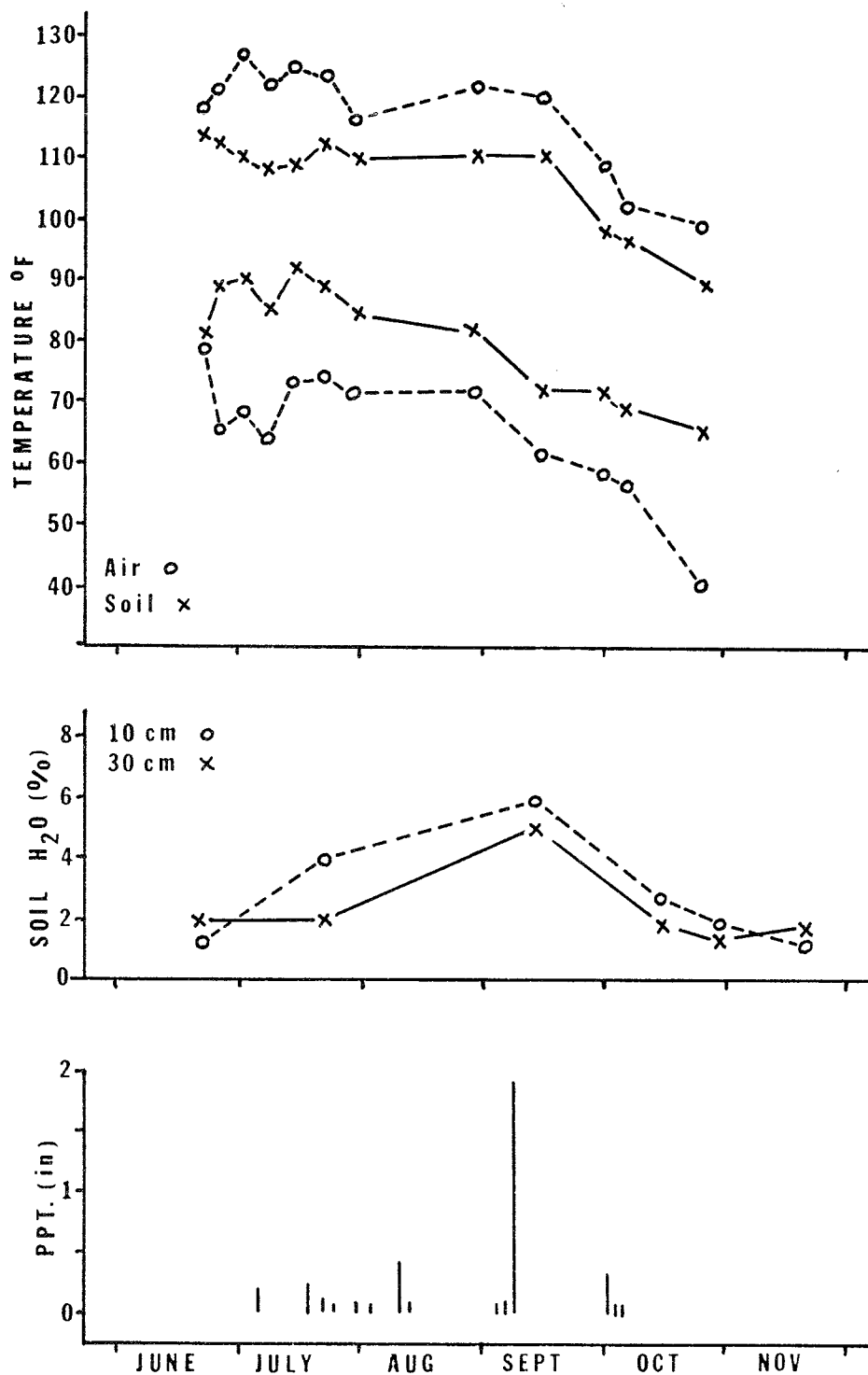


Fig. 1. Average air and soil temperatures (max. and min.), soil moisture, and precipitation data from the Usery Mtn. Park site.

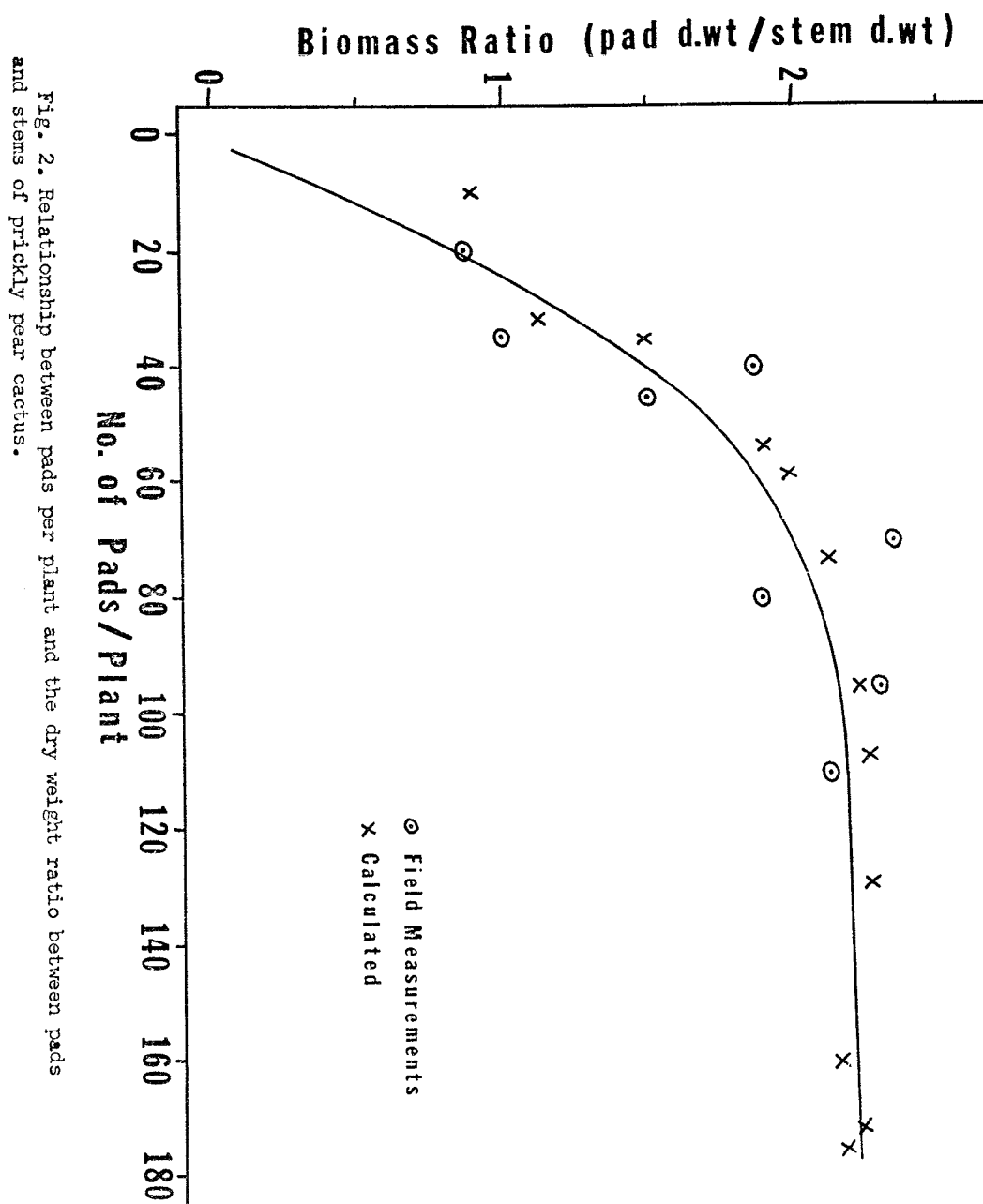


Fig. 2. Relationship between pads per plant and the dry weight ratio between pads and stems of prickly pear cactus.

Productivity and Water Stress in Cacti - continued

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Table 2. Biomass relationships of prickly pear cactus in a 100 x 100 m study plot in the Usery Mountains, Arizona

Plant No.	Number of pads	Number of fruits	pads	Biomass (gm)			Total
				stem	roots	fruits	
1	161	320	5320	2450	400	2330	10,482
2	175	103	2312	1050	140	725	4,227
3	35	9	1171	780	100	63	2,114
4	107	215	3886	1710	220	1500	7,316
5	129	180	5101	2230	319	1260	8,910
6	106	30	4201	1861	238	210	6,510
7	58	2	1840	920	115	14	2,869
8	40	12	1367	910	100	84	2,461
9	31	39	1007	890	81	273	2,251
10	28	2	609	550	45	14	1,218
11	177	150	7505	3350	400	1050	12,305
12	54	19	1365	720	85	143	2,313
13	36	7	1407	755	112	49	2,323
14	10	2	280	310	35	14	639
15	78	46	2095	980	125	322	3,522
16	95	57	4576	2050	284	400	7,310
17	9	2	288	330	27	14	659
18	73	29	3755	1770	245	203	5,973

Totals	1402	1224	48,067	23,616	3,071	8,668	83,422
--------	------	------	--------	--------	-------	-------	--------

Pads	= 57.6% of total biomass
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Stem	= 28.3% of total biomass
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Roots	= 3.7% of total biomass
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Fruits	= 10.4% of total biomass
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Productivity and Water Stress in Cacti - continued

Growth Rates

Periodic measurements of dimensions of selected prickly pear pads show the growth to be a series of surges rather than a single development of new pads in the spring (Fig. 3). Some of the growth follows rainy periods but other surges appear to occur during periods of some available moisture and optimum temperatures. The dimensional increases of length times width are maintained following a growth surge, whereas, thickness measurements fluctuate in relation to available moisture following rain storms. The growth surges shown in Figure 3 were measured after the initial rapid development of the new pad. The beginning part of the curves is probably the end of the development stage.

Carbon Dioxide Exchange and Water Loss

Early measurements of prickly pear cactus CO₂ exchange were inaccurate due to problems with the plant chamber. Field measurements made in December show little or no CO₂ exchange from the plants during the day at air temperatures of 57°F (14°C). Laboratory studies are beginning to show CO₂ exchange patterns similar to those we have previously measured in other cacti under controlled conditions. Not enough data have been accumulated yet to yield any significant results comparable to the biomass measurements.

Discussion

The cacti make up a significant part of the Sonoran Desert vegetation at 2,200 ft elevation. The biomass of the cacti probably contributes more to the total biomass of area than do the biomass of shrubs or annual plants. Prickly pear cactus with a low I.V. of 2.6 still contributed 83 kg/ha in biomass. The cholla undoubtedly will contribute more. A comparison of biomass of cacti compared to that of the woody shrubs should be made.

Shrubs have always been considered important in terms of nutrient recycling due to leaf and twig fall, whereas the cacti have been considered as biomass that is tied up and not recycled except when the plant dies. To the contrary, ten percent of the biomass of prickly pear cactus is recycled annually in the form of fruits that are either eaten by rodents and other animals or disintegrate after falling. This percentage of recycling is probably considerably more than that from leaf and litter fall of woody plants.

Growth of the prickly pear cactus comes in surges. The greatest surge occurs in spring when new pads and fruits are formed. This new growth is greater than ten percent of the total dry weight of the plant because this amount is contributed just by the new fruits and not the new pads. Periodically during the summer, especially following rains, and again in the fall there are smaller surges of growth in the pads. Pad thickness fluctuates widely during this time but since the fluctuation is due in part to water uptake it might be disregarded. However, increased water content is concomitant with an increase in polysaccharides thus the fluctuation in thickness is also a growth response. As the pad thickens the increase in soluble carbohydrates accumulates in the pad and, as the pad becomes thinner the carbohydrates are probably translocated to another location. We should continue to consider all dimensions as significant in terms of growth patterns.

Carbon dioxide and water flux measurements will help to more accurately determine the periods of growth surges. These measurements will also tell what environmental regimes are best suited for growth and which tend to put the cactus in a semidormant state. The ultimate of tying together environment, growth, and water relations of the cacti can only come after a few years of gathering data through fluctuating environmental conditions.

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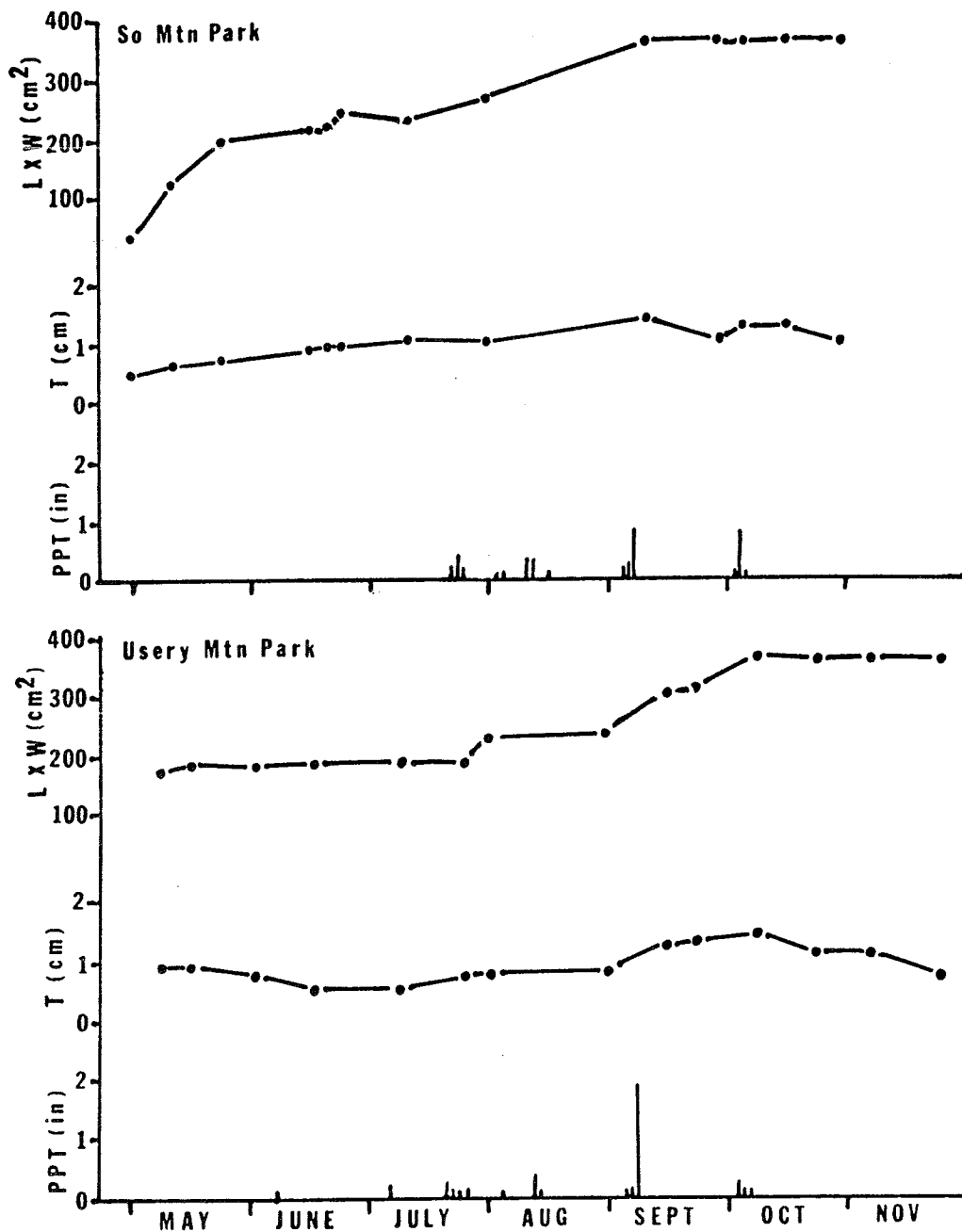


Fig. 3. Growth rates of prickly pear cactus expressed as an average of length times width (L x W) and thickness (T) measurements of pads from cacti at South Mtn. Park and Usery Mtn. Park compared to precipitation (Ppt.)

1972 PROGRESS REPORT

GAS EXCHANGE AND PRODUCTIVITY FOR *Opuntia* spp.

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Research Memorandum, RM 73-12

MAY 1973

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It is subject to revision and reinterpretation. The authors
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Report Volume 3

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A B S T R A C T

Annual rates of primary production have decreased for the cholla cacti, *O. acanthocarpa* and *O. bigelovii*. Such results appear to be directly related to a nineteen-month period of very arid conditions at Deep Canyon.

During periods of dry, arid conditions stomata remain closed throughout the 24-hour day. Cuticular resistances exceed 600 sec/cm for the three *Opuntia* species, such that $^{14}\text{CO}_2$ uptake cannot be measured. The day/night fluctuation in stem tissue acidity is low and quite predictable.

Following periods of precipitation the physiological activity of the *Opuntia* species increases significantly. Stomata open during the night and stem diffusion resistances can decrease to 5 to 10 sec/cm. Exogenous CO_2 assimilation is enhanced and increases progressively following precipitation. This response is directly related to decreasing stomatal and mesophyll resistances to CO_2 uptake. Rates of dark gross CO_2 assimilation increase to 1 to 2 mg $\text{CO}_2/\text{dm}^2/\text{hr}$, with near ambient concentrations of CO_2 . The response to elevated concentrations of CO_2 is linear up to 800 $\mu\text{l/l}$, and approaches 15 to 20 mg $\text{CO}_2/\text{dm}^2/\text{hr}$ in some situations. The large variation in the rates of gross exogenous CO_2 assimilation is probably related to the variation in the mesophyll resistance. The level of maximum stem tissue acidity increases concomitantly.

Stem tissue respiration rates range from 0.35 to 0.60 mg $\text{O}_2/\text{g}/\text{dry wt}/\text{hr}$. Such values are higher than the rates of exogenous CO_2 assimilation yet measured in stems of *O. basilaris*. These findings indicate the *Opuntia* plants may commonly be in a state of negative carbon balance, which would be very significant if the intact stem were not so impervious. The regulation of stomatal opening and the enhancement of CO_2 assimilation are key factors to the success of the *Opuntia* species in desert environments.

I N T R O D U C T I O N

The genus *Opuntia* is well represented in the deserts of the western hemisphere. There are approximately 300 species extending from Canada to the tip of South America. Many of them appear as dominants in the vegetation complexes of the desert regions. The three species reported on here, *O. acanthocarpa*, *O. basilaris* and *O. bigelovii*, are particularly conspicuous components of the vegetation in the Sonoran and Colorado deserts of the southwestern United States and northern Mexico. Perhaps the most distinctive feature of the genus is its succulent habit. This feature is common to the whole family Cactaceae, to which *Opuntia* belongs. It is also an important characteristic of many other desert species belonging to other plant families in other warm deserts of the world. Together, such succulents often comprise a very substantial part of the vegetation responsible for the primary production of desert ecosystems. There is considerable evidence in the literature to suggest that the succulent habit is correlated with a unique type of carbon metabolism. This study, along with the Desert Biome work of Duncan Patten at Arizona State University, Tempe, investigates the characteristics of gas exchange and primary production of the more conspicuous *Opuntia* members.

Through our observations with *Opuntia* during 1971, it became apparent that once exogenous CO_2 was initially incorporated it may be endogenously recycled within the intact succulent stem. This finding was based upon: 1) a persistent day/night fluctuation in stem tissue acidity, 2) stomatal closure during the hours of daylight, 3) an insignificant incorporation of $^{14}\text{CO}_2$ during periods of stomatal closure, and 4) restriction of night stomatal opening to periods of more optimal environmental conditions. Though additional data were lacking it was assumed that the cacti's reserve of endogenous carbon was retained by a highly impervious *Opuntia* stem. Preliminary results during the winter months of 1971 indicated maximum rates of exogenous CO_2 assimilation could occur at low air temperatures, and suggested a seasonal adaptation to the milder periods of the year.

During 1972 our continuing observations with *Opuntia* from Deep Canyon, California, supported many of the preliminary results obtained throughout the previous year. Additional data were gathered which further confirmed the highly impervious nature of the intact *Opuntia* stem. Each of the three *Opuntia* species demonstrates high rates of stem tissue respiration, which further suggests a rapid recycling of endogenous carbon. Exogenous CO_2 assimilation was enhanced following precipitation, the effect increasing progressively with time following rainfall and/or irrigation. The increase in maximum stem tissue acidity, which has been measured throughout the different seasons

of the year, suggests that the *Opuntia* plant retains the capacity for maximum physiological activity throughout the entire year. Long periods of reduced physiological activity may be quickly replaced by intervals of maximum activity. This type of dynamic response may be a key factor of the success of *Opuntia* species to desert environments.

During the coming year the responses of the three *Opuntia* species to environmental parameters will be investigated further. Additional emphasis will center around the two cholla cacti-- *O. acanthocarpa* and *O. bigelovii*. The significance of such periods of maximum physiological activity will be evaluated in terms of the annual carbon balance. A predictive model for estimating productivity has been initiated by Hyrum Johnson.

OBJECTIVES

1. To determine the relationship among water status, temperature, gaseous exchange, and vegetative growth of *Opuntia* species under field conditions.
2. Use the data obtained in developing a predictive model for estimating productivity for periods encompassing the range of environmental conditions to which the species is naturally subjected but for which observations will have not been made.
3. To gain further insight into fundamental functions which help to determine the success of succulents in arid environments. In this respect the genus *Opuntia* represents one of the most successful plant taxa in the Western Hemisphere.

METHODS

Biomass (DSCODE A3UTM10)

Number of stems per plant obtained by direct counting. Fresh weights obtained by weighing stems of various sizes. Dry weights obtained by weighing stems of various sizes, which have been oven-dried for 48 hr at 90 C. Whole plants of various sizes weighed in the field to establish a size vs. field weight correlation. Standing crop biomass estimated by correlating the whole plant size to whole plant weight estimated. Conducted at both study sites.

Productivity (DSCODE A3UTM11)

Length of stems obtained by direct measuring. Changes in linear dimensions due to growth obtained by periodic remeasurements of marked stems. Changes in stem weight due to growth estimated from length vs. weight correlations.

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CO₂ assimilation (DSCODE A3UTM20)

CO₂ assimilation by methods of Austin and Longden (1967), and Shimshi (1969). Analyses of CO₂ assimilation are performed in the field at various periods throughout the entire day, and are repeated with different concentrations of CO₂. Half-maximum CO₂ concentration obtained for the rate of CO₂ assimilations at half the maximum CO₂ assimilation rate (Gates et al., 1969).

Total acid number (DSCODE A3UTM21)

Total acid number determined by modified method of Sideris, Young and Chun (1948). Stem tissue sections are harvested in the field at various time periods throughout the entire day and are stored under dry ice. Approximately 5 g fresh weight of tissue are homogenized in distilled water, and titrated to pH 6.4 with 0.01 NaOH to determine total titratable acidity - TAN. The pH of the homogenate is read directly from a pH meter prior to titrations.

Gas diffusion resistance and transpiration (DSCODE A3UTM30)

Gas diffusion resistance measured by methods of Ting, Thompson and Dugger (1967), with a van Bavel-type diffusion resistance hygrometer. Diffusion resistance determined in the field from transit time of a 0.2 to 0.3 reading on the microamp scale resistance hygrometer. Calibration of the diffusion resistance hygrometer by method using discs which lose water vapor at a known, constant diffusion resistance. Calibrated in both the field and laboratory.

Tissue temperature by direct measuring with thermocouple, or thermister. Air temperature by direct measuring with thermocouple or thermister. Relative humidity by direct measuring with a portable, electric hygrometer.

Water status estimates (DSCODE A3UTM40)

Thermocouple psychrometer probes are inserted into the stem and allowed to equilibrate, or sections of tissue are equilibrated in a small thermocouple psychrometer chamber. The water potential of the tissue can then be directly measured with a thermocouple psychrometer (Wescor, Inc.). Sampling conducted in both the field and laboratory.

Respiration (DSCODE A3UTM50)

O₂ consumption determined manometrically with slices of stem tissue. Laboratory work only.

Soil water status (DSCODE A3UTM60)

Soil psychrometer probes are placed at different soil depths and allowed to equilibrate. Soil water potential determined directly using a thermocouple psychrometer (Wescor, Inc.).

RESULTS

Productivity (DSCODE A3UTM11)

During the period from December, 1971, to November, 1972, growth measurements were taken on 54 individual plants -- 18 plants of each of the three *Opuntia* species. The total number of individual stems sampled was 333. The data accumulated for this year are presented below, with the corresponding data from last year included for comparison.

Growth was estimated from changes in length of individual stems. During the year we have noticed that the size of the stem can change quickly, in response to precipitation, and such changes are not necessarily the result of net primary production. To minimize such errors we have estimated the growth over an 11-month period. A summary of the growth patterns observed in the three *Opuntia* species is presented in Table 1. Some interesting patterns have developed during the year 1972. Stems sampled on plants of *O. acanthocarpa* were shifted in their growth patterns, as a larger percentage of stems showed a net loss of dry matter. It appears that a corresponding decrease in the percentage of stems showing a net gain of dry matter has also occurred. Unlike *O. acanthocarpa*, stems of *O. basilaris* appear to have shifted in the opposite direction showing a percentage increase in stems with net gain of dry matter. The most significant shifts in stem growth patterns have occurred at the lower elevation study site, i.e., site 01. Such patterns may be the result of an increased amount of precipitation occurring during the year at this location.

Table 1. Summary of the growth patterns in the stems of the *Opuntia* species with data of 1971 included for comparison (DSCODE A3UTM11)

Species	Site	% stems increasing in weight		% stems with no net growth		% stems decreasing in weight	
		1971	1972	1971	1972	1971	1972
<i>O. acanthocarpa</i>	01	52	21	44	50	4	29
	02	39	49	55	44	6	7
<i>O. basilaris</i>	01	17	68	30	20	53	12
	02	50	55	36	29	14	16
<i>O. bigelovii</i>	01	48	48	34	26	18	26
	02	70	71	26	13	4	16

Primary productivity estimates, generated from the data of Table 1, are presented in Table 2. The results suggest that net primary production for two of the three species has decreased during the year 1972. Primary productivity for *O. basilaris* appears stable

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at site 02, the upper elevation study site, and has increased at site 01. *O. acanthocarpa* and *O. bigelovii* show a marked decrease in net primary production at both study sites. Our data for 1971 may, however, be an overestimation of the annual primary production as the sampling during that year was restricted to a 7-month period. The 1971 values presented were adjusted to estimate the annual primary production by dividing the observed growth changed by 7/12. This adjustment may account for the apparent differences in the primary productivity estimates. Environmental conditions at Deep Canyon during the last half of the year of 1972 would have suggested that primary productivity would at least be comparable to the values obtained during 1971.

Table 2. Primary productivity estimates for the *Opuntia* species with data for 1971 included for comparison (DSCODE A3UTM11)

Species	kg/ ha/ yr			
	Site 01		Site 02	
	1971	1972	1971	1972
<i>O. acanthocarpa</i>	36.8	9.8	50.0	22.6
<i>O. basilaris</i>	-2.8	7.0	2.3	2.1
<i>O. bigelovii</i>	32.8	18.1	68.7	21.8

The magnitude of the net primary production contributed by the three *Opuntia* species to the desert ecosystem is well below the mean value of primary productivity for a desert scrub ecosystem (Whittaker, 1970). Whittaker's data suggest our estimates are within the range of net primary production expected in such habitats.

CO₂ assimilation (DSCODE A3UTM20)

Exogenous CO₂ assimilation has been measurable in the field following periods of precipitation and/or irrigation. During these periods total diffusion resistances are generally lower and ¹⁴CO₂ can be incorporated by the stem tissue. Under sustained desert conditions diffusion resistances are typically high, i.e., 300 sec/cm, or higher. Little if any ¹⁴CO₂ is incorporated during such periods (Table 3). This type of response is detectable at any time of the year when stomata remain closed throughout the 24-hour day. Based upon such samplings we have established a level of CO₂ incorporation, i.e., 0.10 mg CO₂/dm²/hr, which may represent ¹⁴CO₂ adsorbed to the cuticle and not incorporated by the stem tissue. CO₂ assimilation rates above this minimum level of activity are most likely due to ¹⁴CO₂ uptake through stomata.

Table 3. Uptake of $^{14}\text{CO}_2$ by stems of *O. basilaris* which have diffusional resistances greater than 2300 sec/cm (DSCODE A3UTM20)

Condition	CO_2 $\mu\text{l/l}$	Radioactivity cpm/ sample ¹	CO_2 Assimilation Rate $\text{mg CO}_2/\text{dm}^2/\text{hr}$	n
Light	68	147	-	3
"	240	200	.04	3
"	287	243	.05	3
"	801	174	.01	3
Dark	240	36	.00	3
"	264	93	.02	4
"	296	30	.00	2
"	600	200	.03	4

¹ = mean of n observations

Following precipitation stomata respond by opening during the night, although daytime closure continues to occur. Data collected during June, 1972, which are typical for this type of response, also suggest the mesophyll resistance to CO_2 transfer and carboxylation (r'_m) decreases following precipitation (Table 4).

Table 4. Effect of precipitation on CO_2 assimilation, stomatal diffusion resistance (r'_s) and the mesophyll resistance (r'_m) in stems of *O. basilaris* (DSCODE A3UTM20)

*Day	**Number of Rate Obser.		Dark CO_2 Assimila- tion Rate		r'_s		r'_m
	Rate <.1	Rate >.1	(mg $\text{CO}_2/\text{dm}^2/\text{hr}$)		(sec/cm)		(sec/cm)
			Mean	Max	Min	Max	Min
0	15	0	<.1	.07	10	300	200
2	9	9	.54	1.43	8	31	147
6	1	8	.56	1.51	8	18	17

*Day 0 corresponds to June 20, 1972.

** Number of observations when rate of assimilation was (1) greater than 0.1 and (2) less than 0.1. Determined with CO_2 concentrations 240, 287 and 296 $\mu\text{l/l}$ CO_2 .

Precipitation during Day 0 and Day 2 totalled 1 cm at the study site. During the night of Day 0 stomatal diffusion resistances (r'_s) were high in most stems sampled and dark CO_2 assimilation was insignificant. By Day 2 stomatal resistances had dropped markedly, with the maximum observed resistance approximately 31 sec/cm. Exogenous CO_2

2.3.1.5.-8

assimilation had increased, due to a decreased r'_s and r'_m in the stems sampled. By the night of Day 6 most of the stems were fixing exogenous CO_2 . Stomatal resistances were comparable to those of Day 2, though the mesophyll resistance had decreased further. Most plants of *O. basilaris* continued to show night-time stomatal opening for the next two weeks, but within one month gas exchange was restricted to the early morning hours prior to sunrise.

The effect of elevated concentrations of CO_2 on gross CO_2 assimilation has been investigated further during 1972. The results of our earlier work in 1971 suggested that the response showed a linear relationship up to 1000 $\mu\text{l/l}$. Data accumulated this year support this earlier work, as we have not yet been able to saturate the assimilatory mechanism with respect to CO_2 . Additional data are forthcoming with concentrations of CO_2 higher than 1000 $\mu\text{l/l}$.

The maximum observed rates of gross CO_2 assimilation with elevated concentrations of CO_2 have increased markedly (Table 5). During 1971 the maximum observed rates were approximately 4 $\text{mg CO}_2/\text{dm}^2/\text{hr}$ with 1050 $\mu\text{l/l}$ CO_2 . The enhanced response may be due in part to lower stomatal resistances. However, in all the samples included in Table 5, stomatal diffusion resistances to CO_2 , r'_s , were approximately similar -- ranging from 4 to 11 sec/cm . Significant variation of the mesophyll resistance, r'_m , probably accounts for the range of response in Table 5. Preliminary results, as those of August 10, 1972, indicate the mesophyll resistance varies across the surface of individual stems. An understanding of the magnitude of this variation and the environmental parameters influencing the r'_m component are fundamental to any interpretation of the net CO_2 assimilation in *Opuntia* spp. This is a major area of our research interest at the present time.

Total acid number -- TAN (DSCODE A3UTM21)

The magnitude of the day/night fluctuation in the total titratable acidity is directly related to environmental conditions. As such, we are able to estimate the existing level of metabolic activity by random samplings of acidity in stems of *Opuntia* species.

Under dry, arid conditions in the desert, stomata remain closed throughout the 24-hour day. Exogenous CO_2 is not incorporated, and it is likely that the amount of endogenous CO_2 diffusing out of the stem is very low. Metabolic events involving CO_2 , i.e., acidification, deacidification, photosynthesis, and respiration, which are occurring during periods of stomatal closure, must be solely dependent upon the recycling of an endogenous supply of CO_2 . Such biochemical transformations are undoubtedly affected by stem tissue temperature and internal water status, though the endogenous supply

of CO_2 probably remains relatively static. During such periods the day/night fluctuation in acidity is reduced and quite predictable. Typical values for the three species of *Opuntia* are listed in Table 6.

Table 5. Response of gross CO_2 assimilation rates¹ in stems of *O. basilaris* to various concentrations of CO_2 , with corresponding values of the stomatal (r'_s) and mesophyll (r'_m) resistances to CO_2 uptake included for comparison (DSCODE A3UTM20)

Day	CO_2 concentration ($\mu\text{l/l}$)			r'_s (sec/cm)	r'_m sec/cm)
	287	296	801		
June 21, 1972	.43		3.15	11	158
June 22, 1972	1.35		21.11	5.5	19
June 23, 1972			12.27	4	38
"			3.35	4	150
July 27, 1972			19.44	8	18
"		.35	7.45	7	60
"		1.27	20.73	6.5	17
June 30, 1972		.24	5.43	9.5	81
July 28, 1972		2.98	10.34	11	36
"		.58	8.90	11	44
August 10, 1972*			24.17	8	13
"			20.07	8	17
"			14.50	8	26
August 10, 1972**		1.97		6.5	87
"		1.28		6.5	138
"		.19		6.5	968

¹ in units of $\text{mg CO}_2/\text{dm}^2/\text{hr}$

* stem no. 1, 3 measurements on same stem

** stem no. 2, 3 measurements on same stem

Table 6. Magnitudes of the day/night acid fluctuation in stem tissue of the *Opuntia* species: typical values for dry, arid environmental conditions (DSCODE A3UTM21)

Species	Total Titratable Acidity ($\mu\text{eq/g}$ fresh wt tissue)	
	Day Minimum	Night Maximum
<i>O. acanthocarpa</i>	10	30
<i>O. basilaris</i>	10	35
<i>O. bigelovii</i>	15	35

2.3.1.5.-10

Following precipitation and/or irrigation the magnitude of the day/night fluctuation in acidity increases markedly (see Figures 1-3). During more optimal environmental conditions the level of acid metabolism in the *Opuntia* species approaches the levels commonly found in other CAM plants (Kluge and Osmond, 1972). Increased acidification has been recorded at various time periods throughout the year -- from periods of natural winter rains to periods of artificial summer irrigations. Physiological responses may vary during the year, though an enhancement of acidification persists.

During the summer months at Deep Canyon precipitation is generally lacking and most rainfalls occurring at that time are small. High night-time temperatures probably accelerate metabolic transformations of CO_2 . Absorption of water from precipitation enhances the internal water status, which can further accelerate assimilatory pathways in *Opuntia* (Kausch, 1965). Stomata respond by opening, though high night-time temperatures probably limit stomata from attaining maximum apertures. Exogenous CO_2 can be assimilated, resulting in enhanced levels of acidity.

During the winter months at Deep Canyon precipitation is more frequent and provides the major amount of precipitation for the year. During these periods enhanced levels of acidity have also been recorded. Lower night-time temperatures may reduce the rate of metabolic transformations of CO_2 , though low night-time temperatures also favor stomata opening (Shreve, 1916; Nishida, 1963; Ting et al., 1967). Maximal stomatal apertures, occurring for longer time periods, may sufficiently compensate for lower night-time temperatures, so that acidification is again enhanced by the assimilation of exogenous CO_2 .

Following precipitation the day/night fluctuation of acidity increases progressively (Figure 4). During the night immediately following a summer rainfall, Day 0, the level of acid fluctuation is low. By the night of Day 1 stem tissue acidity had increased by 45%, while within three days following the precipitation (Day 3) the level of maximum acidity had increased 200% above the maximum level of Day 0. Such responses are directly related to changes in stomatal diffusion resistances (see Figure 5, DSCODE A3UTM30), as well as enhanced rates of CO_2 assimilation (see Table 4, DSCODE A3UTM20).

Radioactive $^{14}\text{CO}_2$ is mainly incorporated into malic acid as revealed during dark $^{14}\text{CO}_2$ feeding experiments in the field with stems of *O. basilaris*. Little ^{14}C is detected in other organic acids. Lipid fractions and neutral fractions show no incorporation of ^{14}C during one-hour incubations in the dark. Preliminary results of initial labeling experiments indicate significant labeling of the amino acid fraction --

most likely due to incorporation of ^{14}C into aspartic acid and/or glutamic acid. Such results are similar to earlier work conducted in our lab with *O. echinocarpa* (Ting and Dugger, 1966). The data further support a crassulacean-type acid metabolism in stems of *O. basilaris*.

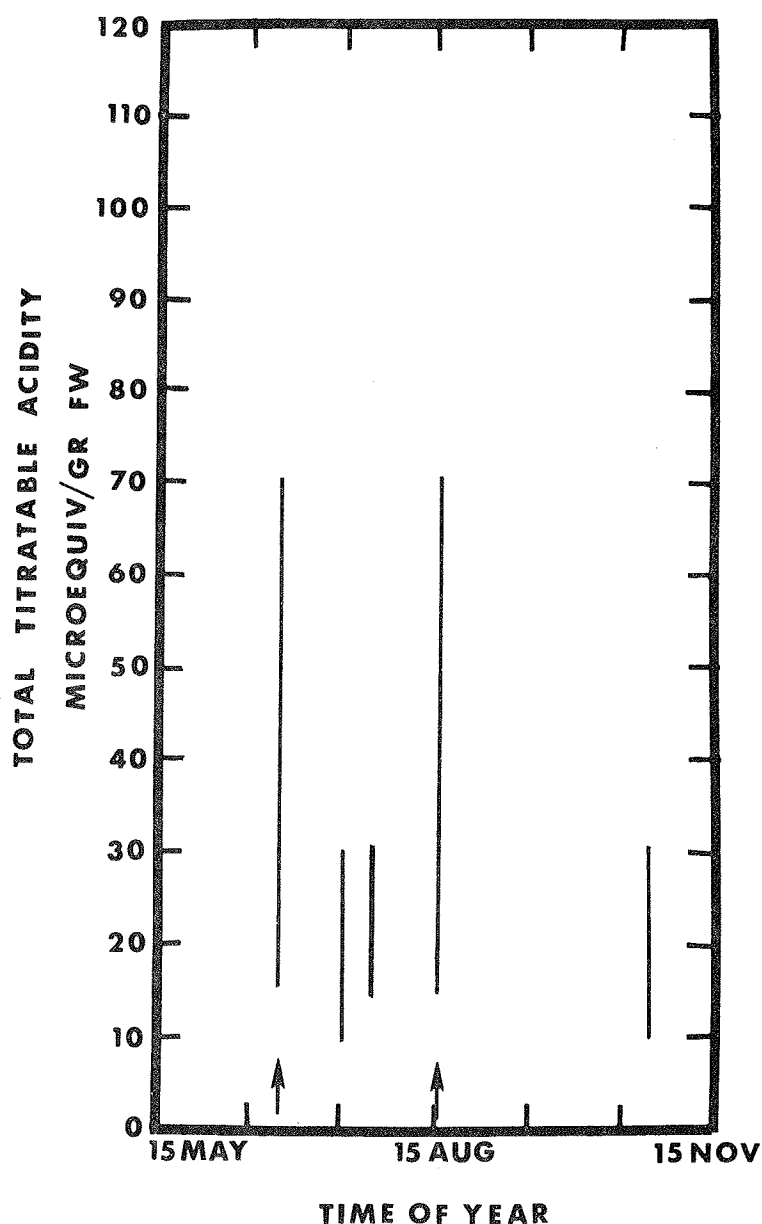


Figure 1. Magnitude of the day/night fluctuation in stem tissue acidity for stems of *O. acanthocarpa*. Arrows indicate irrigation and/or precipitation. (DSCODE A3UTM21)

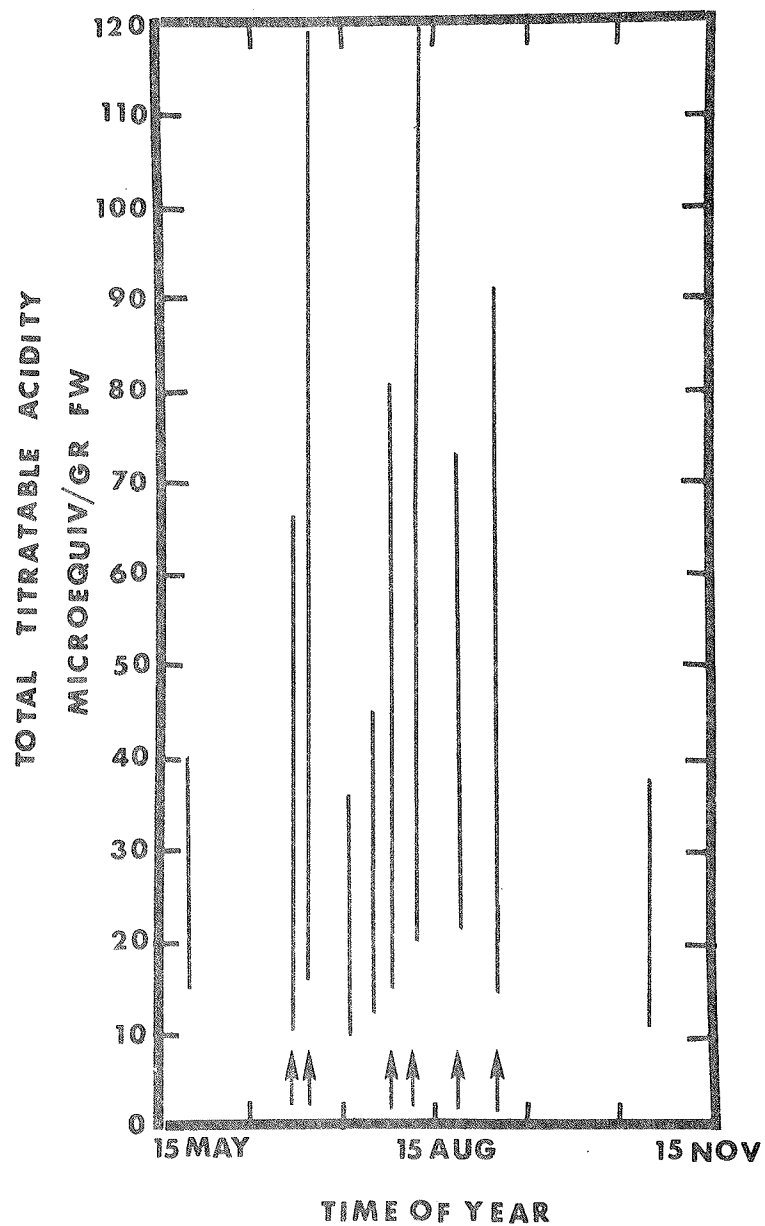


Figure 2. Magnitude of the day/night fluctuation in stem tissue for stems of *O. basilaris*. Arrows indicate irrigation and/or precipitation. (DSCODE A3UTM21)

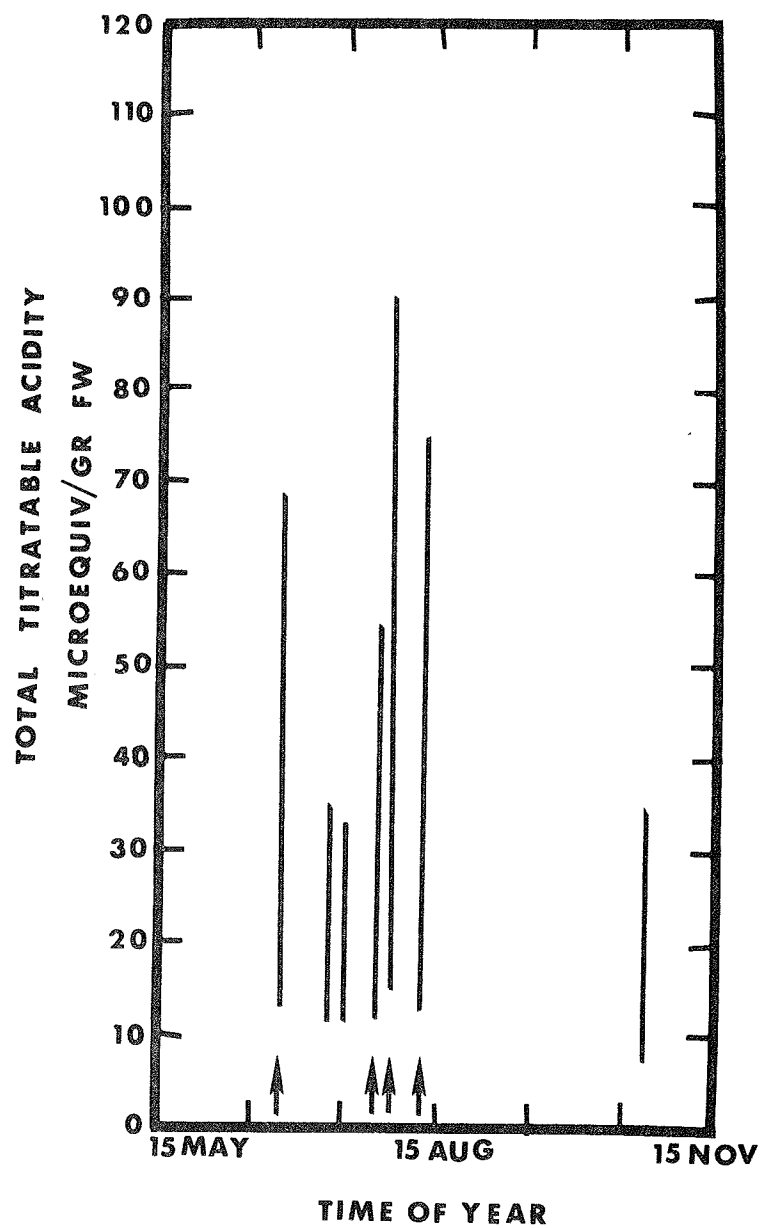


Figure 3. Magnitude of the day/night fluctuation in stem tissue acidity for stems of *O. bigelovii*. Arrows indicate irrigation and/or precipitation. (DSCODE A3UTM21)

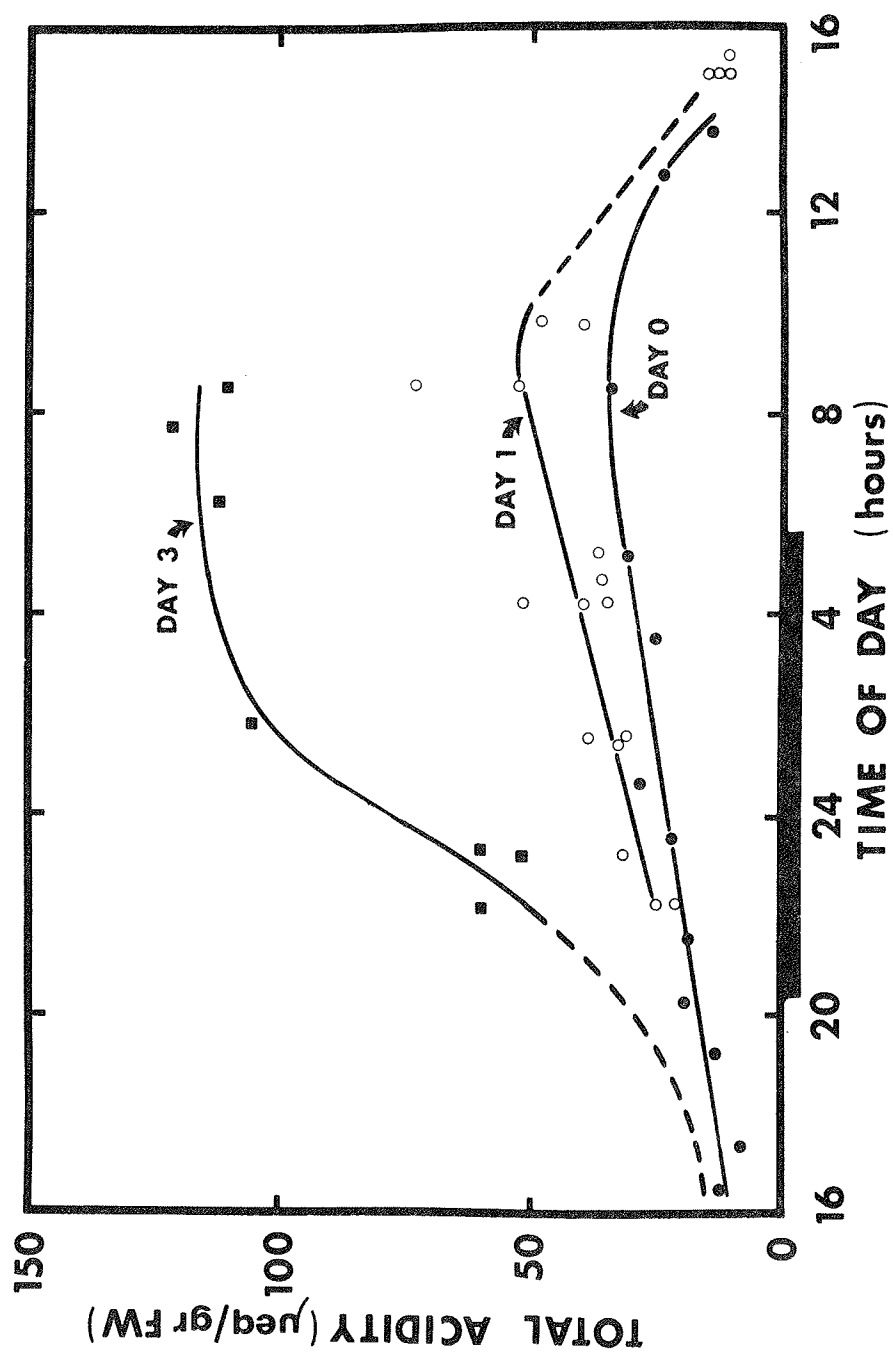


Figure 4. Shifts in the day/night fluctuation of stem tissue acidity following precipitation. Day 0 corresponds to June 20, 1972. Stems of *O. basilaris*. (DSCODE A3UTM21)

Determinations of accurate acid fluctuations are complicated by spatial variations in the total titratable acidity across the stem surface. Samples taken simultaneously along the periphery of single stems can vary up to 15%. Stem tissue sections have to be taken from the same approximate location on different stems to minimize such errors. Additionally, reduction of the tissue sample to 1 g fresh wt or less also appears to minimize such sampling errors.

Gas diffusion resistances (DSCODE A3UTM30)

Stomata are critical pathways of gas exchange and are indirectly controlled by environmental conditions. Following extended periods of dry, arid conditions stomata fail to open following small summer precipitations. Stomatal opening may occur in some instances, but is restricted to the hours preceding dawn. During such periods stomatal closure is rapid following the first direct sunlight. Following periods of more frequent precipitations and/or irrigations, stomata open early in the night and may remain open for several hours. Stomatal closure again occurs following the first direct sunlight, though some stems may be transpiring up until midday. This variation in response is directly related to the internal water status of the *Opuntia* stem.

Following precipitation, the stomatal diffusion resistance decreases progressively (see Figure 5). During the day immediately preceding a summer precipitation, Day 0, stomata remained closed throughout the 24-hour day. Gas diffusion resistances exceeded 200 sec/cm in all of the stems sampled. However, by Day 1, the first day following precipitation, stomata opened during the night and closed rapidly following sunrise. By Day 3 stomata were open widely, earlier in the night, and minimum diffusion resistances were lower than those measured during Day 1. Stomata closed at approximately the same time of the morning, again restricting transpirational water vapor loss during the day. Within two weeks most of the stems sampled were only transpiring during the hours preceding dawn, and within one month stomata were remaining closed throughout the 24-hour day.

During 1972, minimum diffusion resistances measured in the field were lower than the values measured during 1971. Following large amounts of precipitation and/or irrigation minimum resistances were commonly between 5 and 10 sec/cm. Such values are two to three times lower than the minimum stomatal resistances measured the previous year. Aubert (1971) has measured stomatal diffusion resistances approaching 6 sec/cm in pineapple, another CAM plant. Such low values are still higher than the corresponding resistances often measured in nonsucculent, mesophytic plants, e.g., corn and tobacco.

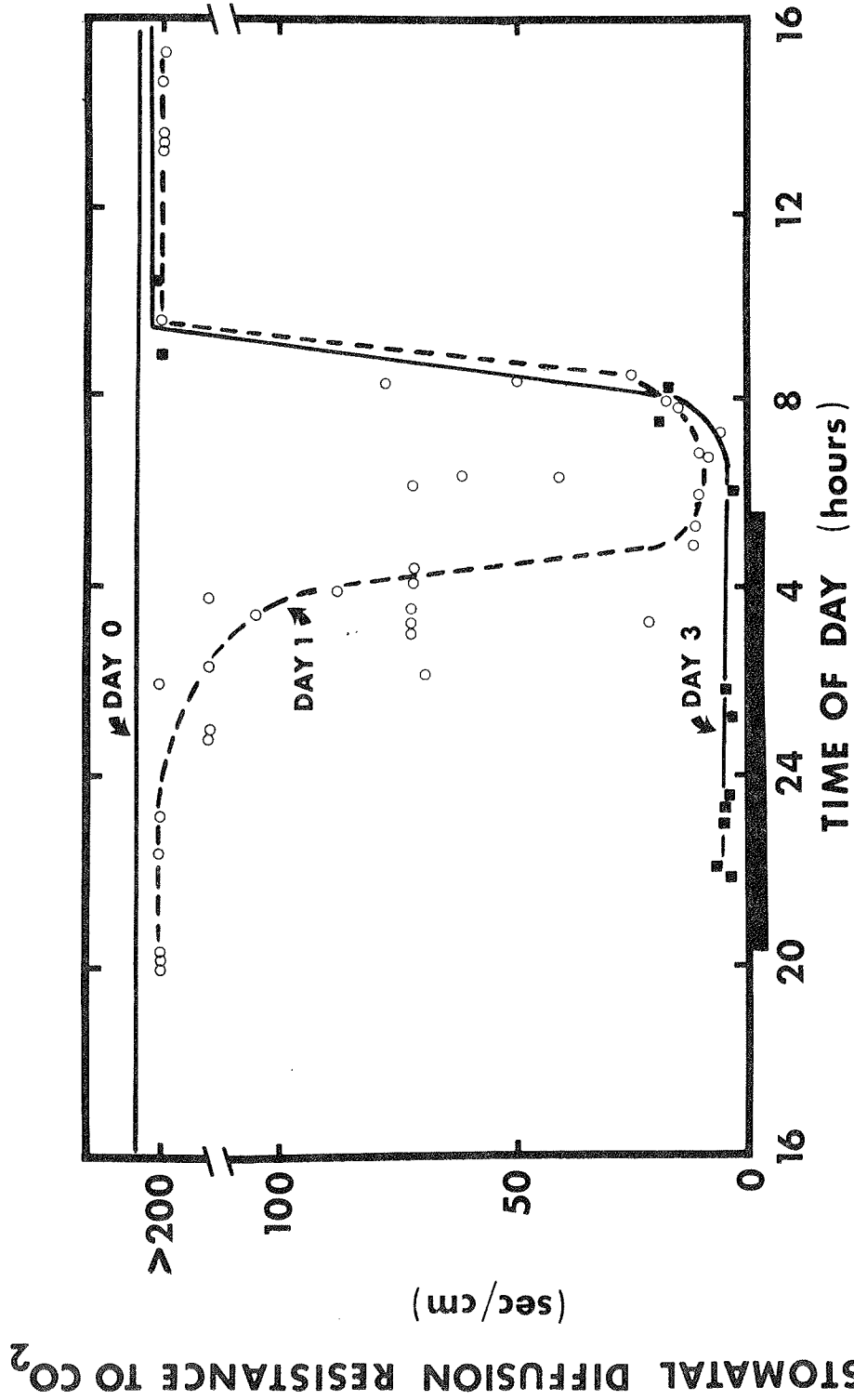


Figure 5. Shifts in the stomatal diffusion resistance in stems of *O. baselaris* following precipitation. Day 0 corresponds to June 20, 1972. (DSCODE A3UTM30)

Cuticular resistances are high in the three *Opuntia* species, such that transpiration can be viewed solely in terms of stomatal diffusion resistances. Cuticular resistances to water loss were determined gravimetrically with severed stems of *Opuntia*. Typical results are presented in Table 7. The magnitude of these resistance values indicates that the amount of water vapor and CO₂ diffusing out of the *Opuntia* stem must be very low, as long as stomata remain closed.

Water status estimates (DSCODE A3UTM40)

Stem tissue water potential has been found to vary across the surface of individual stems, with the more negative readings being found along the lateral edges. The water potential also appears to vary in tissue sections taken at different depths from the epidermis, with the more negative readings being found in the chlorophyll-containing layer of subepidermal cells. Water potential estimates are generally higher in tissue sections taken from the pith of stems of *O. basilaris*.

Following extended periods of dry, arid conditions gas exchange is not induced by precipitations of short duration and/or small amounts of rainfall. However, in areas where water may accumulate some plants may be found transpiring -- possibly due to an increased amount of water, which could be absorbed from the soil. Following irrigations and/or larger precipitations, gas exchange is first detectable in the smaller size plants of *O. basilaris*, although all sizes of plants eventually respond to the available water. These findings suggest the length of the pathway for water transport inside the plant may influence the response time to precipitation. During periods of active gas exchange stem tissue water potentials have ranged between -2 to -7 bars, for subepidermal tissue sections from *O. basilaris*. During periods when gas exchange is not detectable, the stem tissue water potential is lower and approaches -12 to -16 bars of negative pressure.

Table 7. Cuticular diffusion resistances (r_c) of stems of the *Opuntia* species; mean values of n stems sampled (DSCODE A3UTM30)

Species	r_c (sec/cm)	n
<i>O. acanthocarpa</i>	624	16
<i>O. basilaris</i>	619	21
<i>O. bigelovii</i>	1022	17

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The data at present suggest a threshold level of stem tissue water potential, i.e., -7 bars, may be required to attain stomatal opening in *O. basilaris*. With water potentials in this range or higher, environmental factors, e.g., light and temperature, regulate stomatal opening. With water potentials below this range environmental factors have little control over stomatal action. This hypothesis is not unlike our findings of 1971, when stem tissue water potentials were generally always lower than -7 bars of negative pressure.

Respiration (DSCODE A3UTM50)

Some results of our respiration experiments with *Opuntia* stem tissue are presented in Table 8. These data are from stem tissues with maximum water potentials and thus may indicate the magnitude of maximum stem tissue respiration. In all cases the rates of respiration exceed the measured rates of exogenous CO₂ assimilation with near ambient concentrations of CO₂. Such data further underscore the significance of stomatal closure and a highly impervious cuticle in *Opuntia* species, which enhances retention of endogenous gases. If stomata were open during the day, when respiration predominates over net CO₂ consumption, the net carbon balance would be significantly more negative. Warburg and Austruc in the 1880's were perhaps the first investigators to suggest that the *Opuntia* stem itself acts as a compartment for internally contained gases (cited in Richards, 1915).

The rates of respiration presented here are within the range of respiration rates found by other workers with *Opuntia*. Comparative values are presented in Table 9.

Table 8. Respiration rates of the *Opuntia* species; mean values of n samples (DSCODE A3UTM50)

Species	n	Respiration Rate			
		Rate ₁	Rate ₂	Rate ₃	Rate ₄
<i>O. acanthocarpa</i>	4	15.8	11.5	.48	.35
<i>O. basilaris</i>	4	5.6	5.9	.43	.40
<i>O. bigelovii</i>	3	15.4	11.3	.83	.60

Rate₁ mg CO₂ produced/ dm²/ hr

Rate₂ mg O₂ consumed/ dm²/ hr

Rate₃ mg CO₂ produced/ g dry wt tissue/hr

Rate₄ mg O₂ consumed/ g dry wt tissue/hr

Experimental conditions: dark, 30 C, pH 6, direct method of Warburg manometry.

Table 9. Comparative respiration rates of other *Opuntia* species (DSCODE A3UTM50)

Species	Tissue	Respiration Rate	Reference
<i>O. versicolor</i>	stem, young	1 - 2 mg CO ₂ / g dry wt/ hr	Richards
"	stem, mature	.7 - .9 mg CO ₂ / g dry wt/ hr	"
<i>O. phaeacantha</i>	stem	.1 - .8 mg CO ₂ / g dry wt/ hr	Spoehr
<i>O. echinocarpa</i>	stem	.07 mg O ₂ / g fresh wt/ hr	Ting (1966)
"	root	.4 mg O ₂ / g fresh wt/ hr	"

Soil water status (DSCODE A3UTM60)

The collection of soil water data and soil temperature data is being continued. Gas exchange in *Opuntia* species appears to be indirectly related to soil water potential, and is more closely associated with stem tissue water potential. Soil parameters may prove to be of secondary importance in establishing our predictive model of gas exchange.

DISCUSSION

The decrease in net primary production for *O. acanthocarpa* and *O. bigelovii* may be due to sampling errors and/or environmental conditions at the study sites. Initially, many elongating, first-year stems were chosen on both of these species to monitor the maximum rates of productivity and translocation. During this second year of data collection these stems have decreased appreciably in rates of elongation. Such stems may characteristically show rapid elongation rates during the first year and grow more slowly during subsequent years. Monthly precipitation at both study sites has been below normal since January, 1971. Prior to August, 1972, the monthly precipitation for this period totalled 4.4 cm at the lower elevation study site. The total precipitation during this 19-month interval is well below the annual average precipitation of 9.8 cm for the same study site. Since August, 1972, an average of 6.8 cm of precipitation has occurred at this study site. These recent rainfalls have substantially improved growing conditions at Deep Canyon, and the 1973 primary productivity estimates may reflect these more optimal environmental conditions.

The non-autotrophic CO₂ metabolism of the *Opuntia* species and its associated array of physiological characteristics are well adapted to arid environments. During periods of water shortage, endogenous gases are retained via stomatal closure and cuticular resistances exceeding 600 sec/cm. High rates of stem tissue respiration occur in the

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three *Opuntia* spp., which rapidly recycle endogenous carbon, oxygen and water, and provide a continual synthesis of chemical energy. Though levels of dark acidification, photodeacidification and photosynthesis are reduced, the impervious stem acts as a compartment for such compounds. The effect is a relatively stable net carbon balance, which probably is slightly negative.

Following precipitation the physiological activity increases dynamically, provided sufficient soil water is absorbed to raise the stem tissue water potential to the range of -7 bars. Stomata respond by opening in the night, permitting assimilation of exogenous CO₂. Initially, the net carbon balance is probably still negative with stomata open. The major resistance to net CO₂ uptake, the mesophyll resistance, decreases several fold following such precipitations. Active net assimilation of CO₂ probably follows this decrease in the mesophyll resistance, so that sufficient CO₂ can be fixed into the temporary organic acid storage pool, yielding a net positive carbon balance during the subsequent light period. The overall effect is reflected in the larger magnitudes of the day/night acid fluctuations, which have been measured throughout the year. Stomatal opening is restricted to continually decreasing time intervals after precipitation, and may be directly related to the lowering of the stem tissue water potential. During periods when stomata are closed throughout the 24-hour day the magnitude of the acid fluctuation is reduced and the net carbon balance is probably slightly negative.

EXPECTATIONS

During the coming year the following data will be collected:

Productivity -- DSCODE A3UTM11

1. Periodic remeasurements of growth changes occurring in the *Opuntia* species

CO₂ assimilation -- DSCODE A3UTM20

1. Determine minimum mesophyll resistances observed in the field
2. Determine maximum CO₂ assimilation rates observed in the field
3. Establish the half-maximum CO₂ concentration, in relation to the expected mesophyll and stomatal resistances

Total acid number (TAN) -- DSCODE A3UTM21

1. Distinguish CO₂ liberated from deacidification from respiratory CO₂
2. Evaluate the significance of recycling of CO₂ to acid fluctuation

Gas diffusion resistances -- DSCODE A3UTM30

1. Establish a relationship for length of time following precipitation and expected minimum stomatal diffusion resistances

Water status estimates -- DSCODE A3UTM40

1. Continue examination of the relationship between stem tissue water potential and stomatal and mesophyll resistances
2. Determine the error due to the sampling technique

Respiration -- DSCODE A3UTM50

1. Establish the relationship between temperature and respiration rate
2. Establish the relationship between stem tissue water potential and respiration rate
3. Estimate the significance of respiratory activity to internal recycling of CO₂

ACKNOWLEDGEMENTS

We gratefully acknowledge the assistance of Mr. Gil Brum, who contributed to the collection of field data from Deep Canyon and assisted with the final preparation of this report.

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1972 PROGRESS REPORT

GAS EXCHANGE, TRANSLOCATION AND ROOT GROWTH OF COLD
DESERT PLANTS

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Research Memorandum, RM 73-13

MAY 1973

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Report Volume 3

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A B S T R A C T

Photosynthesis, transpiration and dark respiration were measured in the field for *Artemisia tridentata* in relation to plant water status and phenology, and microenvironmental parameters. Photosynthetic capacity changed during the course of the growing season in absolute magnitude and in response to leaf temperatures. Curtailment of photosynthesis in the afternoon hours later in the summer were largely attributable to increases in leaf resistance.

Preliminary gas exchange measurements of *Gutierrezia sarothrae* and *Agropyron spicatum* are also reported.

Soil-root observation chambers with inclined plexiglass observation panes were installed in Curlew Valley. Root growth of *Atriplex confertifolia* was observed throughout the summer months extending as late as October. Root growth was observed in soil of water potentials in the range of -70 to -80 atm.

Annual ring counting was used to reconstruct growth patterns of the root and shoot system of *Artemisia tridentata*.

Pulse labeling with $^{14}\text{CO}_2$ was assessed as a technique for determination of root growth rates in undisturbed field conditions. This was only moderately successful in the field for these Great Basin shrub species.

Soil cores were removed in the field, and the soil was returned free of all root material. These cores will be removed in 1973 to determine root regrowth rates as an index of root productivity.

Radioactive carbon was used under field conditions to develop techniques for assessing translocation and root productivity of Great Basin shrub species. A quantitative counting technique involving an in-vial combustion procedure and scintillation counting was applied in these preliminary studies.

Translocation patterns in these shrubs correlated well with shoot growth patterns. Root productivity will be assessed in 1973 based on specific activity changes in the living root systems of plants labeled in 1972.

INTRODUCTION

This process study of 1972 was in part a continuation of plant gas exchange studies of 1970 and 1971. Gas exchange of Great Basin plants in relation to relevant environmental parameters is being extensively studied to provide data for the primary productivity modeling effort of the Desert Biome. At the same time there is need to relate shoot gas exchange of these plants to growth and productivity in a quantitative manner. Although gas exchange results from this study are correlative with shoot growth and phenological data of Dr. Neil West and studies at Curlew Valley Validation Site, underground plant productivity has yet to be assessed even in gross magnitude. For this reason, substantial effort in 1972 has been devoted to work on root growth and translocation of Great Basin plants.

This report includes analysis of gas exchange data collected in 1971 for *Artemisia tridentata* with interpretive discussion of these results in light of the Biome modelling effort. In addition, this report also contains preliminary results of gas exchange data collected for *Gutierrezia sarothrae* and *Agropyron spicatum* collected in 1972. Development of techniques for the study of translocation and root growth of these species and preliminary data for these processes collected in 1972 are also related in this report.

OBJECTIVES

General goals of this project were: To relate plant gas exchange rates to plant water status, plant phenology and to relevant environmental parameters in order to construct models of primary productivity and water use. The second major goal was the development of techniques for the study of translocation and root growth in the field for these Great Basin species.

During 1972 our specific objectives were:

1. To reduce and analyze gas exchange data collected during 1971 for *Artemisia tridentata*.
2. To carry out gas exchange determination for *Gutierrezia sarothrae* and preliminary determinations for *Agropyron spicatum* and to initiate analysis of these data.
3. To develop techniques for studying translocation of photoassimilates in these species in the field.
4. To develop techniques for the evaluation of timing of root growth activity in the field.
5. To develop techniques for the assessment of underground productivity of these species in the field.

METHODS

Gas exchange determinations for *Artemisia tridentata* during 1971 were carried out in Cache Valley near Logan, Utah. During 1972 similar measurements were made on *Gutierrezia sarothrae* and to a limited extent on *Agropyron spicatum*. Instrumentation and methodology employed in these studies were described in detail in the 1970 progress report of the Desert Biome.

A brief summary of these methods follows:

Photosynthesis, dark respiration, and transpiration of *Artemisia tridentata*, *Gutierrezia sarothrae* and *Agropyron spicatum* were measured in the field in relation to pertinent micro-meteorological parameters. The shoots of individual plants in the field were enclosed in Siemens gas exchange chambers for photosynthesis, respiration and transpiration measurements following monitored ambient conditions (data set A3UCB43, A3UCB44, A3UCB97, and A3UCB98), and when the chambers were programmed for constant environmental conditions while varying one factor such as irradiation or temperature independently (data set A3UCB41, A3UCB87, A3UCB88).

Pertinent microenvironmental parameters, plant water stress and phenology, and leaf area and weights are also logged under the above appropriate DSCODES. Air temperatures were measured by resistance thermometers, leaf temperatures with fine wire thermocouples, humidity by lithium chloride sensors calibrated against a Cambridge dewpoint hygrometer, total short wave irradiation with an Eppley pyranometer. In 1972 quantum sensors were used inside each chamber to determine total quantum flux between 400 and 700 nm (Biggs et al., 1971). Plant water stress was measured with a Scholander pressure bomb, and leaf area with a photoelectric planimeter (Caldwell and Moore, 1971). In 1972, preliminary attempts were also made to estimate photorespiration of *Gutierrezia sarothrae*. This was carried out by comparisons of net photosynthetic rates in 2.0% oxygen atmosphere with rates in a normal oxygen atmosphere. The difference in net photosynthetic activity between low and normal oxygen concentrations is used as an index of photorespiration.

To obtain an atmosphere of 2.0% oxygen, bottles of compressed nitrogen, oxygen and CO₂ in nitrogen were mixed with a gas mixing pump to simulate the artificial atmosphere. Water vapor concentrations, temperature and irradiation were held constant for these comparative determinations of net photosynthetic rates in low and normal oxygen concentrations.

To determine the timing of root growth in the field, six soil root observation chambers were installed in Curlew Valley, two each in communities of *Atriplex confertifolia*, *Eurotia lanata* and *Artemisia tridentata*. Each contained a large plexiglass observation window inclined at a slight angle (see Diagram 1). Excavations for the observation chambers were carried out as carefully as possible to effect a minimal disturbance to the existing root-

2.3.1.6.-4

soil system. Thermocouple psychrometers similar to those used in 1970 were installed immediately next to the observation pane and then also 50 cm distant in the undisturbed soil profile. These were used for total soil water potential determination. Thermocouples were also placed in these locations for determinations of soil temperatures. These soil observation chambers are being used to observe the timing of root growth activity during the season.

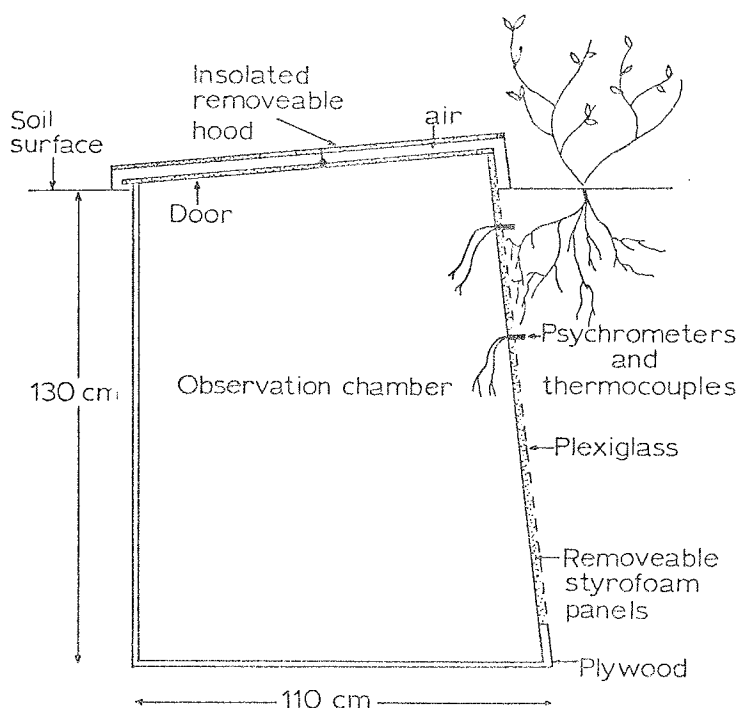


Diagram 1. Diagram of soil-root observation chambers.

To assess the temporal growth patterns of *Artemisia tridentata* for older under-ground parts, annual rings of various roots were counted and compared to the pattern of shoot growth. This was carried out on five *Artemisia* plants excavated and brought into the laboratory. Unfortunately this technique was only possible for *Artemisia tridentata*, since secondary growth in *Eurotia lanata* and *Atriplex confertifolia* is anomalous in nature and does not lend itself to counting of annual rings.

To determine root growth rates of individual roots in an undisturbed soil environment, a pulse labeling technique was attempted. This technique was described by Wardlaw (1969) for grass roots. This technique involved the administration of $^{14}\text{CO}_2$ to leaves of the plant for two short periods of time with an intervening interval of at least several weeks between

the pulses of $^{14}\text{CO}_2$. This technique was applied to several plants in the laboratory and also in a few field trials. Labeling was carried out by evolving $^{14}\text{CO}_2$ from labeled bicarbonate and exposing shoots of the plant to approximately 0.3 mc for one hr in a plastic cuvette. The plant was then excavated after a few days or several weeks using a water stream to carefully remove the root system, keeping it as intact as possible. Autoradiography was used to determine the qualitative distribution of labeled carbon in the root system.

Attempts to assess underground productivity had been directed towards two techniques. A technique described to Milner and Hughes (1968) for grassland systems was initiated this year. This technique consists of removing a soil core in the field and then removing the root material from this soil core and replacing the soil. Several such cores were excavated and replaced in communities of *Artemisia tridentata*, *Atriplex confertifolia*, and *Eurotia lanata*. In some cases a nylon sack was used when the soil was replaced; in other cores the soil was simply replaced and carefully marked for recoring in 1973. In all situations, a careful attempt was made to replace increments of soil at the same depths from which they were removed. All of these cores will be again removed in 1973 to assess invasion by new root material as an index of root productivity.

Use of radioactive carbon was tested as a medium for analyzing translocation of photo-assimilates and root productivity. Labeling was carried out by exposing the plants to $^{14}\text{CO}_2$ (0.1 mc per plant) in a plexiglass chamber for approximately three hours. Seven days following this exposure to $^{14}\text{CO}_2$ a major branch of each plant was harvested and immediately chilled to arrest respiration. An 8-cm diameter orchard auger was used to extract a soil-root core in the vicinity of each plant. This core was separated into two increments, 0-30 cm and 30-60 cm.

Harvested plant samples were separated manually into branches, leaves, flowers, etc. (see Figure 18 in the Results section, Figures 19 and 20 in the Discussion and Tables 1, 2, and 3 in the Discussion for enumeration of plant parts). Roots were passed through a sieve using a water stream to remove adhering soil particles and then floated on water for separation of "living" from "dead" roots. This assessment as to living or dead was based only on color and physical appearance. "Live" roots tend to be white to cream in color and quite elastic as opposed to the brittle and dark-colored "dead" roots. This has been substantiated to a limited degree by observation of autoradiographs of labeled intact roots. Detailed separation of living from dead roots based on microtechniques or autoradiograms is not feasible on the sampling scale required for this study. Following the separation of plant parts to different segments and size classes, the plant samples were dried for 48 hr at 60 C. Plant tissues with moderate to low fiber content were ground in a mortar. A dry in-vial combustion procedure was used as a rapid, convenient method of combustion and allowing accurate determinations of $^{14}\text{CO}_2$ from the plant samples.

2.3.1.6.-6

The in-vial combustion procedure most recently used is a technique similar to one used by Gupta (1966). This procedure involves making a cup container from lens paper soaked in black ink and placing it into a coiled wire holder. The cup container in the wire holder is then placed into an empty scintillation vial. A dried sample is placed into the cup container, the vial is momentarily flushed with a stream of pure oxygen and the vial is immediately capped tightly with a #15 serum stopper cap. The sample in the coiled wire stand is then ignited with a focused light beam from a modified slide projector. The sample ignites and burns to completion in approximately 5 sec. Maximum sample size for this technique is dependent upon caloric content of the material and is usually less than 10 mg dry weight. Larger samples could be combusted in larger containers, but this would decrease the convenience of the in-vial procedure. An 800 C combustion furnace has also been utilized for ignition, but we have found the focused project beam to be more efficient. In all steps, proper shielding and ventilation precautions are taken to provide safety in case of vial breakage or other leakage.

After a 5-min cooling period, 0.5 ml of NCS are injected through the serum stopper cap with a glass syringe (Hamilton Co., Inc., Whittier, California). After an absorption period of 6 hr (sufficient for complete absorption), the serum stopper cap is removed and 10 ml of scintillation grade counting solution are placed in the vial, which is then closed with a cap containing a teflon liner. We have tested several combinations of absorber and scintillation cocktail. Phenethylamine and NCS were used as absorbers in combination with cocktails of either a dioxane or a toluene base. The combination of highest efficiency was found to be NCS and a toluene base scintillation liquid. This combination minimizes problems of chemoluminescence, remains stable for at least several days, and yields consistent counting efficiencies of 70-75%. The samples are counted in a liquid scintillation counter. The counting efficiency for each vial is determined by the channels ratio method and DPM are calculated. The calibration curve is established with a toluene base quenched standard set.

This labeling with radioactive carbon was carried out on all three species (*Artemisia tridentata*, *Eurotia lanata* and *Atriplex confertifolia*) on June 21, September 8 and November 14. Only in June were large segments of the root system extracted from the soil and counted. No root material was counted in September and only the finer roots were counted in the November sample. The same plants will be harvested in 1973 to determine movement of carbon-14 during the past year and to estimate root productivity of the fine roots based on the ratio of C^{14}/C^{12} . The dilution of specific activity of plant carbon during the course of the year in the fine root systems should provide some index of root growth, assuming most of the C^{14} in the initial samples taken from the roots was fixed as cellulose or other compounds that would not translocate out of the root system. Radioactive carbon lost during the course of the year in dead roots or respiration would be included in this productivity estimate. Comparisons will be made in 1973 between this radioactive carbon dilution technique and the regrowth of roots into the root-free soil cores mentioned earlier.

RESULTS

Morphology and phenology of *Artemisia tridentata*.

This species exhibits two distinct types of stem growth: 1. vegetative-perennial and 2. reproductive-annual. There is little dieback of the vegetative branches which are the major means of increasing plant size and productivity. Two types of leaves are formed on vegetative shoots. The primary new leaves which develop along the main stems during the spring are large and typically sharply tri-lobed. As growth continues, numbers of new short lateral branchlets grow from the existing stems and support large quantities of smaller, less distinctly tri-lobed leaves which persist throughout the next winter long after the large initial leaves are shed.

The reproductive shoots are initiated, grow, mature, and bear seed within the span of a single growing season. These shoots then cease functioning and die, although the dead shoots may remain on the plant for some time thereafter. Leaves on the reproductive shoots of this study were often quite different from those on the vegetative shoots, being generally smaller, more sparsely arranged, and oblanceolate to linear in form. The reports of Diettert (1938) and Goodwin (1956) provide a more complete analysis of sagebrush morphology.

At the initiation of this study in early May, the sagebrush appeared to be emerging from winter dormancy-quiescence, as was evidenced by swelling and bursting buds. Within a few weeks the large "spring" leaves had emerged, and by the time of the second test period in early June, the sagebrush was experiencing a time of accentuated stem growth with corresponding increased new leaf emergence and growth. New lateral branchlets supporting smaller leaves were also developing at this time. Maximum longitudinal stem growth rate occurred during approximately the first two weeks of June.

Vegetative stem growth rate began to decline soon after the end of June as reproductive buds and shoots began to grow. The large leaves produced in May and early June had largely abscised by this time. By late July the reproductive shoots had reached maximum size, and were equipped with a full complement of their characteristic leaves, as described above. Flower buds first appeared in late July and reached an advanced state of development by the fourth test period in late August. Also, by this time a number of the oblanceolate leaves on the reproductive shoots had begun to die and abscise. By the time of the final test period in September nearly all the leaves of the reproductive shoots had been shed, the flower buds were fully developed and some were beginning to burst. During the latter stages of reproductive shoot development little or no new vegetative growth was observed.

2.3.1.6.-8

After a procedure of West and Wein (1971), the following numeric phenological code was established for analysis purposes:

- 0 -- Winter dormancy
- 1 -- Post-dormant quiescence
- 2 -- Swelling leaf buds (mid-April to early May)
- 3 -- Emergent large new leaves on vegetative branches (mid-May)
- 4 -- Rapid new vegetative stem and leaf growth;
reproductive shoots initiated (late May to mid-June)
- 5 -- Reduced vegetative growth; reproductive shoot and bud growth;
ephemeral leaves growing on reproductive shoots;
(early July to mid-August) "spring" leaves shed
- 6 -- Reproductive shoots full size; flower buds developing;
little vegetative growth (late August to mid-September)
- 7 -- Flower buds fully developed -- some beginning to burst;
ephemeral leaves on reproductive shoots dying and being shed (late September to
early October)
- 8 -- Flowering (mid-October)
- 9 -- Fruit developing (late October to early November)
- 10 -- Shedding of fruit; predormancy quiescence (mid-November on)

Water potential of *Artemisia tridentata*

Results of the seasonal measurement of plant water potential (Ψ) using the Scholander pressure bomb technique are shown graphically in Figure 1, along with the pattern of precipitation for summer, 1971. Water stress was at a minimum during late May and early June, and began to rise thereafter, reaching a peak in late August. The general trend in Ψ is similar to that noted by Dina (1970) for sagebrush in central Utah and by Love and West (1972), Moore (1971), and Moore and Caldwell (in press) for other desert shrubs in northwestern Utah. A distinct relationship can be observed between plant Ψ and precipitation in which minimum water stress occurred soon after maximum precipitation in early summer and maximum water stress occurred in late summer as a reflection of a long dry period. There did appear to be a one to two week lag between appreciable rainfall and its associated effects on sagebrush Ψ . This relationship was also noticed by Moore (1971) with *Atriplex confertifolia* and *Eurotia lanata*.

Although the general trend in plant Ψ is similar to that described by Dina (1970), the degree of water stress in the present study is much less. For example, the minimum Ψ observed in central Utah was -64 bars in late September, whereas the minimum in this study was only -21 bars in late August. Possible explanations for this difference may lie in the above-average precipitation that occurred over the growing season in 1971, and that our study site was located on a level area at a canyon mouth with a more favorable moisture regime from the standpoint of both surface and subsurface runoff than a canyon side situation such as that studied by Dina. In support of this, pressure bomb data for sagebrush were collected

simultaneously from both the level study site and from nearby upland areas; sagebrush on the upland areas generally exhibited two to three times greater water stress than at the study site.

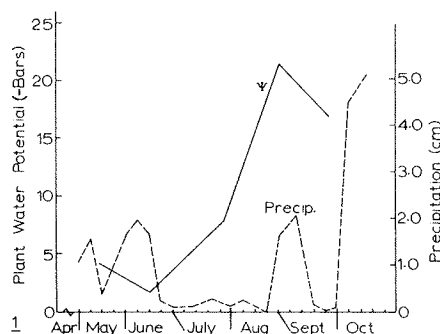


Figure 1. Seasonal pattern of precipitation and *Artemisia tridentata* plant water stress through a growing season at Green Canyon. Water stress values are means of ten to fifteen plants sampled every month.

Gas exchange of *Artemisia tridentata*

Photosynthetic rates at different temperatures and a constant irradiation intensity of $1150 \text{ microeinsteins m}^{-2} \text{ sec}^{-1}$ (400-700 nm) are presented for each phenological stage throughout the summer in Fig. 2. These data were taken on illuminated plants at night. The results dramatically show the variation in rate of net photosynthesis under the same physical condition of irradiation, temperature and windspeed during the course of the growing season. Ambient CO_2 concentrations did not vary appreciably during these experiments and chamber humidity was maintained at ambient levels.

Highest net photosynthetic rates occurred in May and June during periods of maximum vegetative growth (see Fig. 2, phenological stages 3 and 4). These months were also those of the lowest water stress for the plants (Fig. 1). The major drop in photosynthetic rate occurred in July during early reproductive shoot development (phenological stage 5), when the first large increase in plant water stress became apparent. The period of maximum water stress in August, during which flower buds were developing (phenological stage 6), corresponds to the lowest net photosynthesis. In September, early in the period of flowering (phenological stage 7), water stress was somewhat less severe and the rate of net photosynthesis rose slightly. These results suggest that the amount of moisture available to the

plant is a major factor affecting photosynthetic rates throughout the growing season.

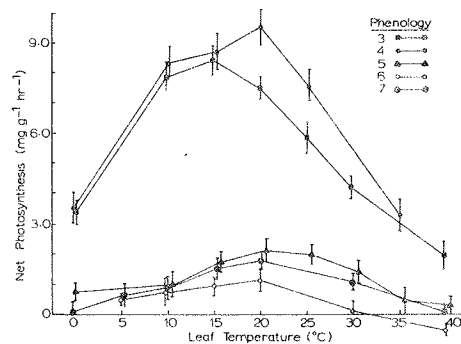


Figure 2. Net photosynthesis of *Artemisia tridentata* at five phenological stages through a growing season under conditions of constant irradiation ($1150 \text{ microeinsteins m}^{-2} \text{ sec}^{-1}$) and varying leaf temperatures. Values are means of measurements of four to six plants, shown with \pm one standard deviation.

There was a gradual shift in the temperature at which peak photosynthesis occurred during each phenological stage from May to September (see Fig. 2). In May the optimal temperature for photosynthesis was 15 C. In June, as higher ambient temperatures occurred, the photosynthetic optimal temperature shifted to 20 C. Although the optimum temperature remained at 20 C for the remainder of the growing season, a decrease in the rate of decline of photosynthesis at temperatures higher than 20 C can be discerned. This trend towards increased relative photosynthetic rates at higher temperatures during each of the summer testing periods may represent an acclimation of photosynthetic rate to the higher general temperatures prevalent, or may simply be a reflection of the greater proportion of new leaves present.

The general seasonal pattern of photosynthetic behavior demonstrated in Fig. 2 is also evident when photosynthetic rates were measured at constant leaf temperature (20 C) and variable irradiation intensities (Fig. 3). Average daily irradiation values for clear days during each test period are also given. The magnitude of net photosynthetic rate with respect to phenological stage followed the same general pattern as in Fig. 2, with the exception of a curious anomaly in July (phenological stage 5). Here, the net photosynthetic rate was close to that of May and June until 9:00 or 10:00 in the morning, where it leveled off. The photosynthetic rate then dropped sharply after 11:00 although irradiation levels were still increasing, and by 13:00 the July rate had fallen into a pattern more closely

akin to that of August and September. Since the July test period was a transition between periods of lower water stress in May and June and higher stress in August and September, this daily pattern is of particular interest. It would appear that in July a transient water stress developed by late morning, inducing stomatal closure thereafter. This reduced stomatal aperture would certainly in part account for the reduction in photosynthetic rate shown in Fig. 3. Consistent with this explanation, stomatal resistances (r_s) calculated from simultaneous transpiration rate measurements were correspondingly lower in the morning and higher in the afternoon, as shown in Fig. 4. These data show the significant effect of water stress in photosynthesis and transpiration via stomatal closure. However, calculated mesophyll resistances, r_m^i , to CO_2 exchange were also found to increase similarly during the afternoon. Therefore, decreased afternoon photosynthesis cannot be solely attributed to stomatal closure.

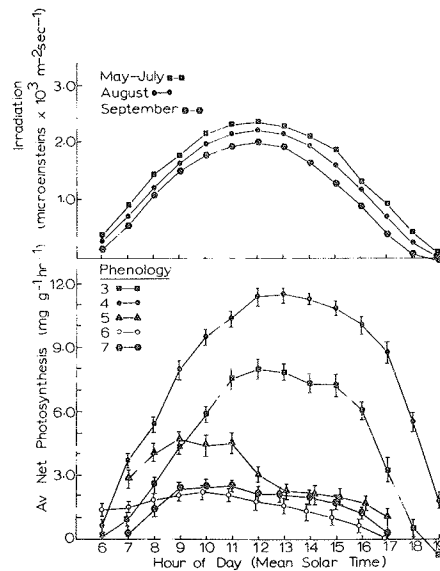


Figure 3. Net photosynthesis of *Artemisia tridentata* at five phenological stages during the course of a growing season under conditions of constant temperature (20 C) and irradiation varying through the course of a day. Gas exchange values are means of measurements of four to six plants, shown \pm one standard deviation, and irradiation values are average for the clear days during which the experiments were run.

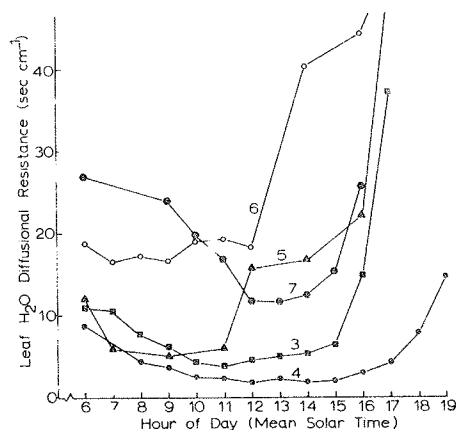


Figure 4. Leaf water vapor diffusional resistance, $r_a + r_s$, of *Artemisia tridentata* at five phenological stages during the course of a growing season under conditions of constant temperature (20 C) and varying irradiation through the course of a day.

Dark respiration as a function of temperature was also measured throughout the growing season (Fig. 5). These data were taken on field plants at night. Respiration increased uniformly with temperature at all stages of phenology and rates of respiration were affected similarly between 0 and 20 C. At temperatures above 20 C during earlier phenological stages (3 and 4), sagebrush exhibited higher respiration rates than it did later in the season (5 through 7). Maximum respiration rates at temperatures above 20 C were attained during the period of lowest water stress in June (phenological stage 4). Changes in plant Ψ may be in part related to these variations in dark respiration, and phenological stage of the plant, e.g., through aging of the leaves, would almost certainly be expected to have an effect on respiration rate as was reported by Hellmuth (1971) for *Rhagodia baccata*.

Seasonal variations in rate of dark respiration were not as pronounced as corresponding variations in rates of net photosynthesis. This was also the case for *Eurotia lanata*, a C_3 halophytic perennial shrub prominent in the Great Basin. However, *Atriplex confertifolia*, a C_4 halophytic shrub, exhibited great seasonal variations in net photosynthesis but little change in dark respiration rates (White, Moore and Caldwell, 1971). These tests of the effects of higher temperatures on dark respiration were only short-term experiments; a subsequent decrease in dark respiration rates may take place after prolonged exposures to high temperatures.

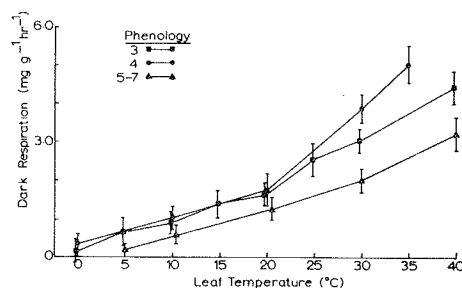


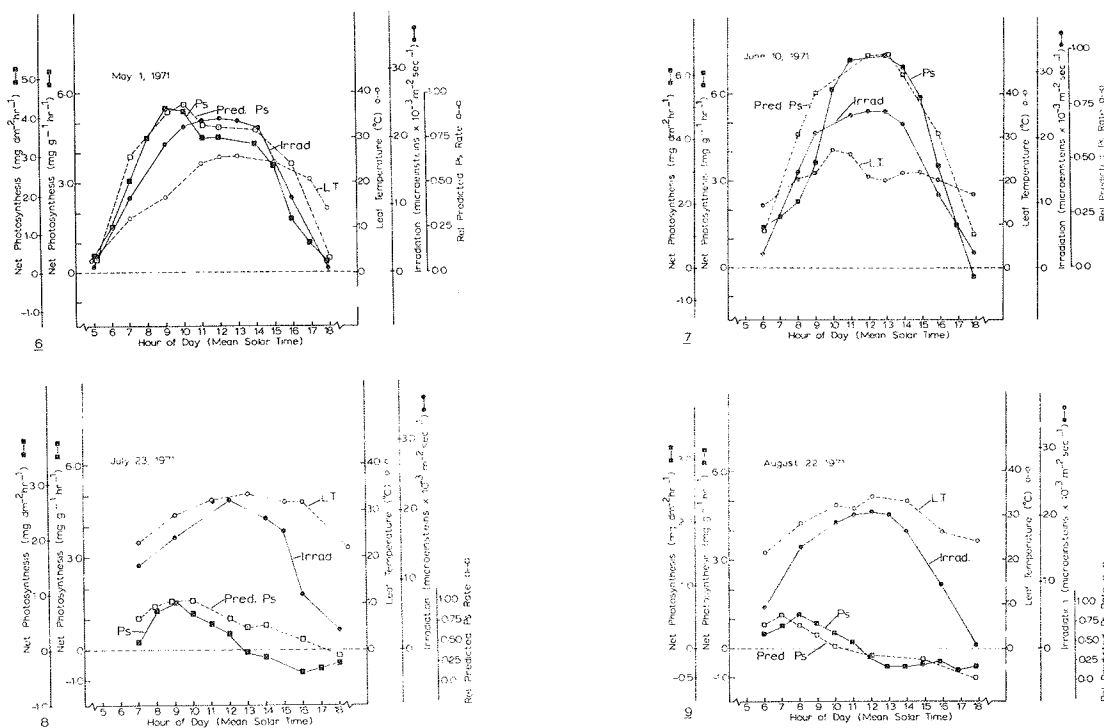
Figure 5. Dark respiration of *Artemisia tridentata* at various phenological stages through the course of a growing season under conditions of varying temperature. Values are means of measurements of four to six plants, shown with \pm one standard deviation.

To determine the actual pattern of sagebrush net photosynthesis through the growing season, measurements of daily variations were made under essentially ambient microclimatic conditions. Results of this type of measurement for four representative plants at progressive phenological stages (3, 4, 5, and 6) are shown in Figures 6-9. Daily variations in net photosynthesis are represented with corresponding variations in irradiation and leaf temperature. Lower absolute rates of net photosynthesis are readily apparent later in the season. Highest net assimilation under natural microclimatic conditions occurred in May and June, during the periods of lowest water stress.

The ambient rates of photosynthesis shown in Figures 6-9 are largely, then, a reflection of four major factors and their interaction: irradiation, leaf temperature, plant water stress, and phenology. In May and June, when plant Ψ did not drop below -7 bars and was presumably not limiting, the course of net photosynthesis and irradiation intensity were parallel as long as leaf temperatures were not excessive. No apparent light saturation of photosynthesis was observed in these data. In July and August, however, the increased water stress and generally excessive leaf temperatures caused the course of net photosynthesis to deviate substantially from that of irradiation after midmorning.

The possibility that endogenous rhythms of photosynthetic activity could be affecting the actual daily course of photosynthesis of sagebrush was not ignored. To test for such a rhythm, an experiment was conducted in May when daily water stress was not limiting in which plants growing *in situ* were exposed to constant microclimatic conditions (i.e. constant

temperature, light intensity, windspeed, etc.) for a period of 72 hr. A constant level of photosynthesis was soon attained and no significant deviation from this level occurred throughout the 72-hr period. As a rhythmic pattern of activity under constant conditions was one of the primary criteria established by Pittendrugh (1954) for true endogenous rhythms, it was thus concluded that sagebrush did not exhibit a marked photosynthetic circadian rhythm. Therefore, determinations of photosynthetic capacity taken at night should be fairly representative of the daytime potential for CO_2 uptake.



Figures 6-9. Net photosynthesis of *Artemisia tridentata* at four times during the course of a growing season under ambient microclimatic conditions through the course of a day. Gas exchange values are for selected individual plants on each date, and concurrent values of leaf temperature, irradiation and relative predicted photosynthesis rate are also given. Figure 6, May 1, 1971; Figure 7, June 10, 1971; Figure 8, July 23, 1971; Figure 9, August 22, 1971.

Gas exchange of *Gutierrezia sarothrae* and *Agropyron spicatum*

Preliminary results for these species are reported here for 1972. Precipitation patterns and the course of plant water potential during the season for *Gutierrezia sarothrae* are indicated in Figure 10. Net photosynthetic response of *Gutierrezia* to varying leaf temperatures at otherwise constant conditions is shown in Figure 11 for various times of the season. These are plotted on a relative basis. The optimal temperature for net photosynthesis was between 15 C and 20 C throughout the season. A single temperature response curve for *Agropyron spicatum* is shown for June, 1972 (see Figure 12). At this time temperature optimum for net photosynthesis was around 25 C. Later in the summer this grass became photosynthetically inactive. Further studies on both of these species will be carried out during 1973. The net photosynthetic response of *Gutierrezia* at three temperatures is shown in Figure 13 for an atmosphere of normal oxygen concentration and an atmosphere of 2% oxygen concentration. The same plant was used in these determinations and all other factors were held constant.

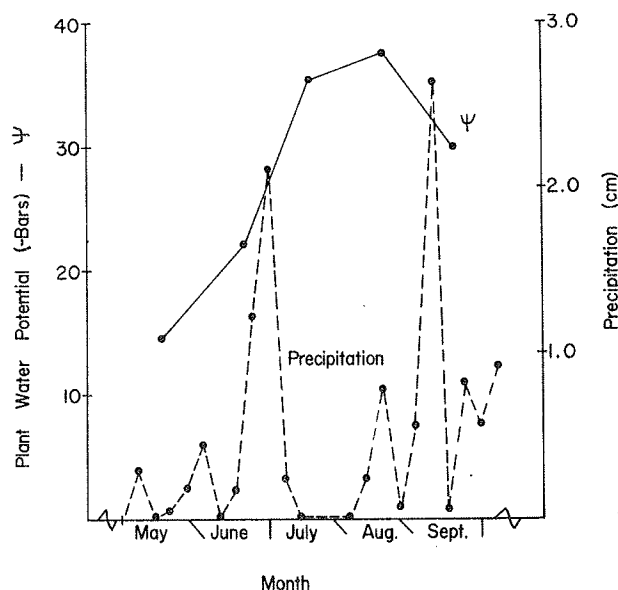


Figure 10. Precipitation and plant water potential of *Gutierrezia sarothrae* as measured by pressure bomb in 1972.

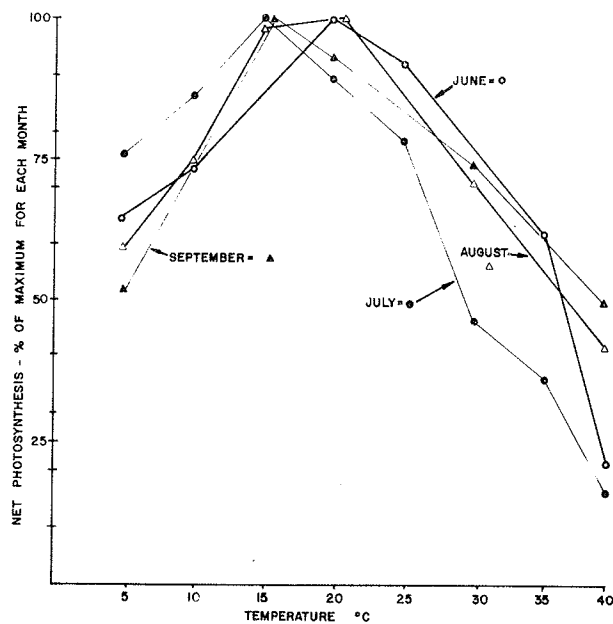


Figure 11. Net photosynthesis of *Gutierrezia sarothrae* as a function of leaf temperature and constant irradiation intensities at different times of the season in 1972.

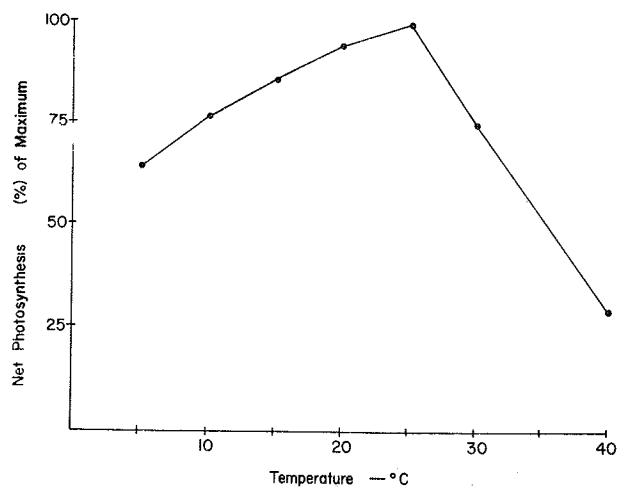


Figure 12. Net photosynthesis of *Agropyron spicatum* as a function of leaf temperature and constant irradiation intensities in June, 1972.

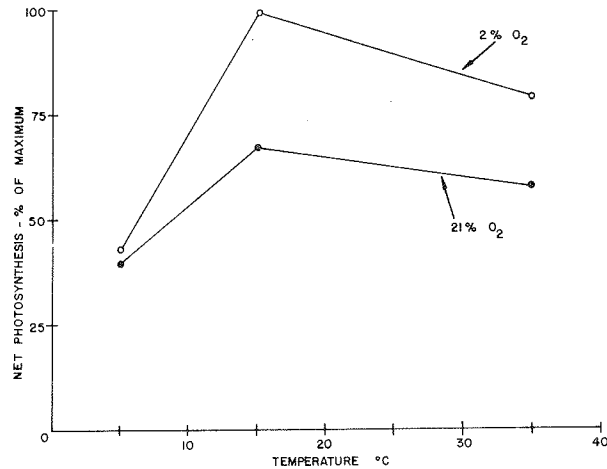


Figure 13. Net photosynthesis of *Cutierrezia sarothrae* as a function of leaf temperature at two levels of oxygen concentration. All other environmental factors were held constant.

Soil Root Observation Chambers

The observation chambers described in the methods section were installed in Curlew Valley in early May, 1972. Two chambers were installed in pure stands of *Atriplex confertifolia*, *Eurotia lanata* and *Artemisia tridentata*. They were installed in such a manner that only 5 to 10 mm of soil was necessary to fill the gap between the outside surface of the plexiglass window and the undisturbed soil-root profile. In the *Atriplex* community, roots were noted on the plexiglass window by June 20. With varying degrees of activity, root growth continued in both of the *Atriplex* observation windows throughout the summer with some perceptible new growth observed in the period between September 22 and October 6 (Figure 14). On July 31 the first roots were recorded on one of the observation panes in the *Artemisia tridentata* stand. No roots were observed during 1972 in the *Eurotia lanata* community. Thermocouple psychrometers for soil water potential measurements and thermocouples for soil temperature determinations were placed immediately adjacent to the observation panes at different depths in the *Atriplex* communities and at a distance of 50 cm from the observation chambers at the same depths. Readings taken on August 11 indicate soil water potentials next to the observation pane to range between -70 at 40 cm

depth to -80 at 25 cm. Soil temperatures were taken between 23 C and 25 C at depths between 25 and 55 cm. Fifty cm away from the observation chambers in the undisturbed community, soil moisture potentials ranged between -60 at 40 cm to -75 at 20 cm. These determinations indicate that the chambers were causing a minimal alteration of soil temperature and water potentials. On August 24 and October 27 soil moisture potentials were not so negative and, if anything, tended to be less negative away from the observation panes. Soil temperatures were somewhat cooler but still above 19 C at all locations.

AI

BOX I - SECTION I - ATR

JUNE 20 ——— AUGUST 11 ———

JUNE 27 - - - - - AUGUST 24 - - - - -

JULY 7 - - - - - SEPT. 8 - - - - -

JULY 18 SEPT. 22 ———

JULY 31 ~~~~~ OCT. 6 - - - - -



Figure 14. Patterns of root growth observed in one chamber during the 1972 season in a pure stand of *Atriplex confertifolia*.

More extensive determinations of soil temperatures and moisture potentials will be carried out in all three communities throughout the season in 1973.

Pattern of root development in *Artemisia tridentata*

Comparative dating of principal elements of the root and shoot system of five *Artemisia tridentata* plants of moderate size and approximately 6 to 7 years of age was carried out in 1972. One representative plant is shown diagrammatically in Figure 15. The principal tap-root element is produced during the first year of growth with no significant elongation beyond that first year. In contrast, the principal branches of the shoot system undergo yearly extension. Branching of lateral roots may occur during any subsequent year of root development. Branch roots were observed in all years of development for each of the plants examined. The proliferation of lateral roots does not form a predictable sequence as occurs in the shoot system. Principal lateral roots of all ages occur at various positions along the main taproot.

The root system of *Artemisia* had many dead roots which only lived one year. On plants six to seven years of age there are many more of these dead one-year roots than on younger plants. These roots which survived only one year appear to have originated during several years in the development of the root system. During some years more of these short-lived roots were produced than during other years. No attempt was made to trace out the proliferation of the fine roots in this particular growth study.

Root growth of *Atriplex* as measured by pulse labeling

The goals of this study were to determine the applicability of the pulse labeling technique to estimates of growth of roots of desert shrubs. Preliminary applications of this technique to corn roots in the laboratory proved successful as described by Wardlaw (1969) for *Lolium*. Since radioactive carbon is permanently incorporated in cellulose of cell walls, among other compounds, the concentration of radioactive carbon will accumulate in that portion of the root where cellulose synthesis took place subsequent to incorporation of $^{14}\text{CO}_2$ in photosynthesis. On an autoradiogram this location of accumulated radioactive carbon would appear as a particularly dark band or region on the root system. The interval between these dark bands would indicate the amount of root growth which had taken place between the pulses of $^{14}\text{CO}_2$ taken up in the plant photosynthesis.

Our attempts to apply this pulse labeling technique to *Atriplex* seedlings in the laboratory were successful if the plants were kept in a vermiculite or sand culture medium and the interval between pulses was only a few days.

In the field, excavation of these shrub root systems has proven to be extremely difficult as far as fine roots are concerned. Curlew Valley silty soils are probably as

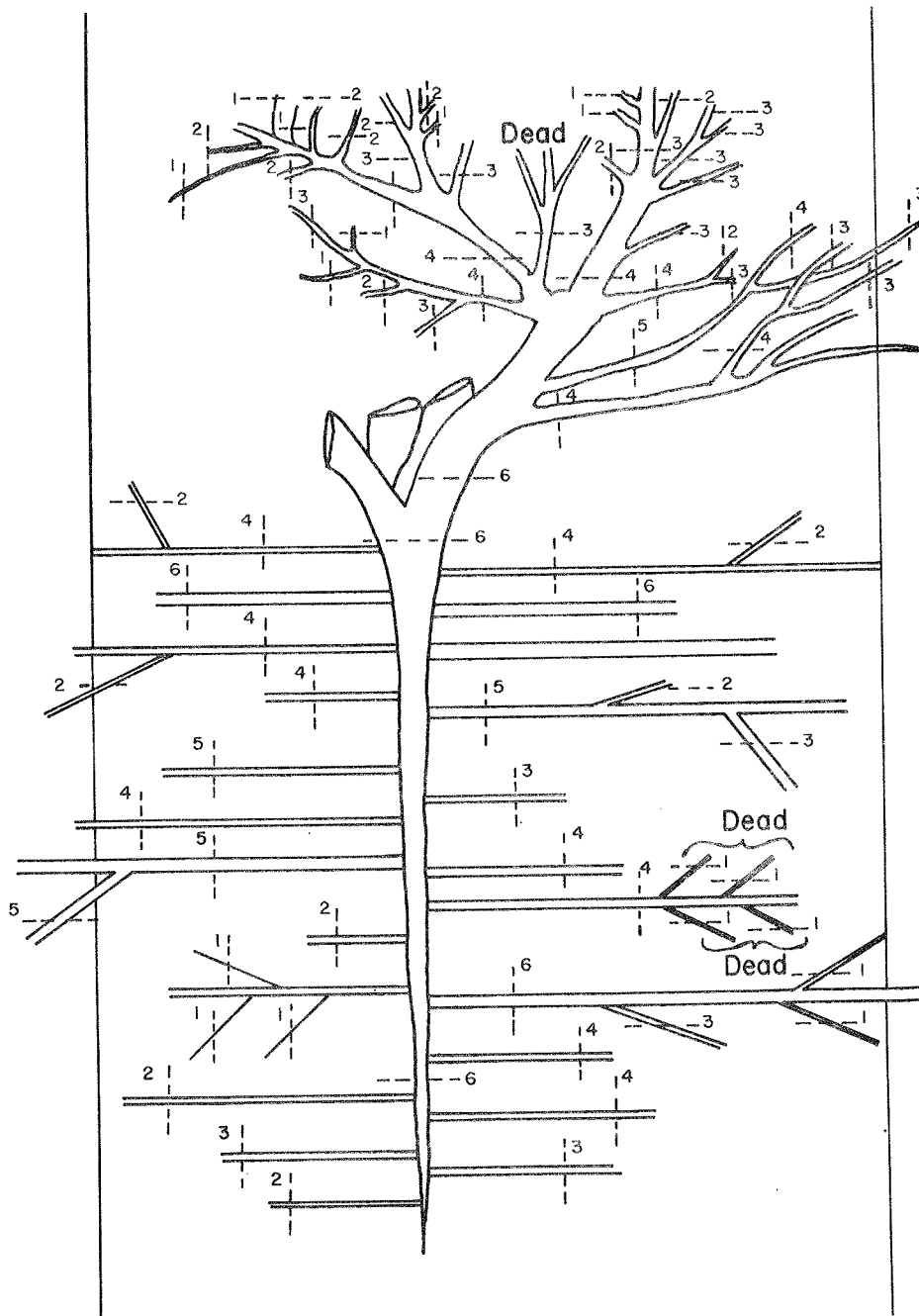


Figure 15. Diagrammatic representation of annual ring counts for the shoot and root system of a 6-year *Artemisia tridentata* plant.

easy as any soils to work with in a field situation. However, there is an immense profusion of fine roots which are difficult to extract from the soil intact even by using the most careful washing techniques. Growth apices are also extremely difficult to locate. In Figures 16, 17 and 18 are photographs of different portions of the root system with a comparable print of the autoradiograms of these roots of a single *Atriplex* plant on which this pulse labeling technique was applied. The plant was labeled with .37 mc of $^{14}\text{CO}_2$ for one hour on October 23, 1970, and again on 22 July, 1971. Roots of the plant were carefully removed from the soil by washing with a jet of water on 8 July, 1972. Almost all roots which were saved were positively traced back to the treated plant. The roots were mounted while still wet on herbarium sheets, covered with plastic film, and dried in a plant press. After drying they were attached permanently with tape to the sheets. Autoradiograms were prepared by exposing x-ray film for 65 days.

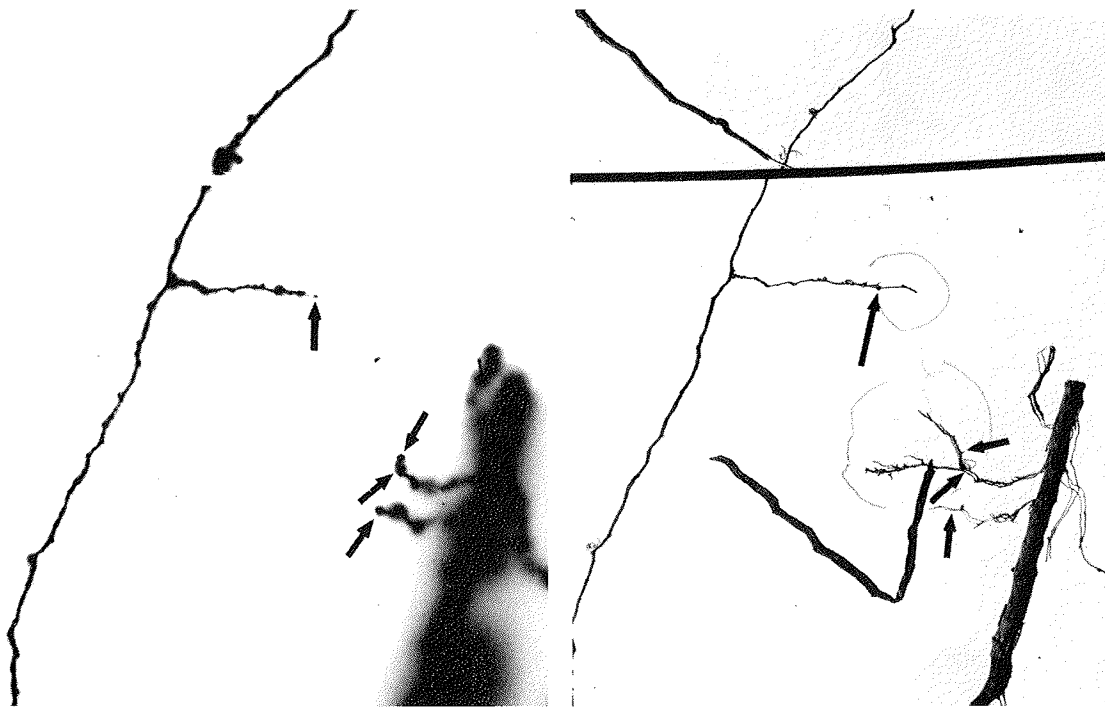


Figure 16. Photograph (left) and autoradiogram (right) of the main root and a long lateral root, each with branch roots, pulse-labeled with ^{14}C -carbon. The arrows point to the terminus of radioactivity on the photograph. Apparently, the portion of the root extending beyond this abrupt termination of radioactivity was dead at the time of labeling.



Figure 17. Photograph (left) and autoradiogram (right) of ^{14}C -carbon pulse-labeled long lateral roots with terminal rootlets. Some of the small terminal rootlets designated by the letter "a" are more heavily labeled than the long lateral root and are thought to have developed shortly after the exposure of the shoot of the plant to $^{14}\text{CO}_2$. Some terminal roots appear only as dots designated by the letter "c" on the autoradiogram.

For convenience these roots are classified into three groups. First are the large main roots, up to 4 mm diameter which branch from the taproot. Second are the many long, thin, lignified lateral roots. These are usually less than 1 mm, often about 0.5 mm in diameter, lignified and perhaps several years old. Such roots may be 50 cm long without appreciable changes in diameter and with only occasional branching. We were not successful in following any of these roots to what might be called actively growing root tips. The third group consists of short lateral roots varying in length from less than 1 mm to several cm long, which are attached to small branch rootlets.

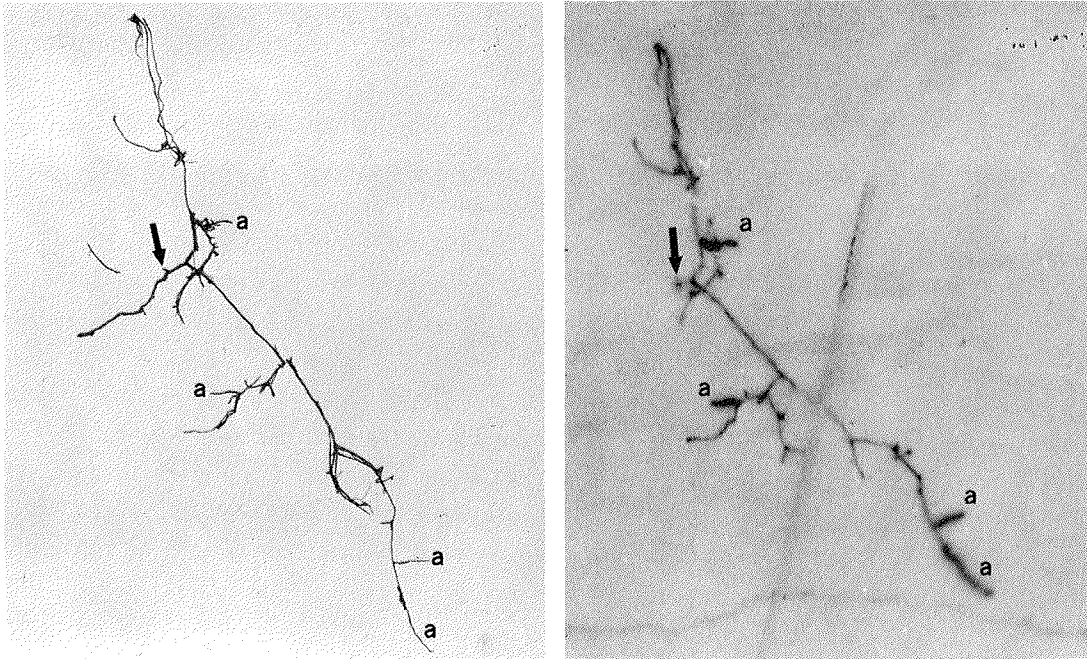


Figure 18. Photograph (left) and autoradiogram (right) of ^{14}C -carbon pulse-labeled terminal root system. The arrow indicates a lateral root which was apparently dead beyond this point at the time of plant exposure to $^{14}\text{CO}_2$. The short terminal rootlets designated by the letter "a" apparently developed concurrently or shortly following the exposure to $^{14}\text{CO}_2$.

The autoradiograms indicated substantial variation in the amount of radioactive carbon accumulated in major roots. Presumably the degree of anatomical linkage with the particular shoot branch being exposed to $^{14}\text{CO}_2$ accounts for at least part of this variability in amount of radioactive carbon in these major roots. The exact location of the labeled carbon within the major root tissue was not studied but it was presumably fairly near the surface because self absorption of the weak beta radiation emitted by C^{14} would not penetrate to the film from internal root tissues. In these long-term studies, most of the labeled carbon was probably in the form of cellulose in secondary xylem and phloem tissue formed soon after photosynthetic uptake of $^{14}\text{CO}_2$. The smaller roots tended to show a fairly uniform accumulation of radioactive carbon throughout. There was no evidence of "banding" or small areas of radioactive carbon accumulation as should be expected with this pulse labeling technique (Wardlaw, 1969). Most likely the label is in secondary growth tissues of these small roots.

The smallest branch rootlets were often very radioactive. These are interpreted as rootlets formed immediately after photosynthetic uptake of $^{14}\text{CO}_2$ by the plant, although they may have been formed at a later time as well. On some of the longer small rootlets there were areas of intense radioactivity. These may have been lateral roots or perhaps even very short lateral rootlets. They may also have been the remaining living stumps of lateral roots which had died. In a few situations on lateral roots, radioactivity was found only on a part of the root, often ending very abruptly or even with an intensified area of radioactivity. These are interpreted as being rootlets which have died in part prior to the date of $^{14}\text{CO}_2$ fixation. The radioactivity actually identified in this case the portion of the root which was still living. The somewhat intensified area of radioactivity found at the termini of the radioactive portion of the root could be due to callus formation or pathogenic activity.

During the excavation it was apparent that roots of all size categories were in various states of decay and some would easily crumble on contact. Healthy roots on the other hand were quite tough and roots in intermediate stages of decay would break down unless they were very carefully handled, and were brown in cross section. These roots were assumed to have died relatively recently.

Root Productivity -- Root Regrowth into Soil Cores

Soil cores removed in 1972 and replaced with root-free soils will be excavated in late summer of 1973. This method of estimating root productivity will then be compared with techniques employing carbon labeling.

Root Productivity and Translocation -- Radioactive Carbon Studies

In Tables 1, 2 and 3 are given radioactivity counts in various plant parts of the three species labeled in 1972. The absolute counts in disintegrations per minute per mg dry weight of tissue are the average of three to six samples in each case. Percentage figures are the percentage of radioactive carbon distributed in each segment of the above-ground portion of the plant relative to the total amount of radioactive carbon in the above-ground portion of the plant. In these preliminary studies it was not possible to do this for the root system since the entire root system was not excavated. Each of the plant part segments are illustrated for the three species in Figures 19, 20, and 21.

Table 1. Distribution of radioactive carbon in *Eurotia lanata* shoot and root structures during 1972

Plant Structure	June		September		November	
	dpm/mg	%	dpm/mg	%	dpm/mg	%
Branches of current year	2228	23%	129	8.2%	4452	6.2%
Fruits and flowers of current year	-----	--	293	1.2%	-----	---
Fully expanded leaves	3738	12.6%	151	1.3%	9410	2.7%
New unexpanded leaves	8452	51.5%	250	86%	15150	86%
New buds	3015	5%	203	2%	9265	5%
1° branches of previous year	340	2.7%	30	0.5%	9	0.0002%
2° branches of previous year	129	1%	62	0.5%	12	0.0004%
Crown	1347	3.3%	---	---	-----	-----
Buds of previous year	1100	0.6%	101	0.2%	156	0.008%
Taproot	1066	--	---	---	-----	-----
1° laterals of taproot (1-2 mm diam)	1061	---	---	---	-----	-----
2° laterals of taproot (0.5-2.0 mm diam)	96	-----	12	-----	46	-----
Small live roots (<0.5 mm diam) at 0-30 cm depth	357	-----	---	---	60	-----
Small live roots (<0.5 mm diam) at 30-60 cm depth	674	-----	---	---	150	-----

Table 2. Distribution of radioactive carbon in *Atriplex confertifolia* shoot and root structures during 1972

Plant Structure	June		September		November	
	dpm/mg	%	dpm/mg	%	dpm/mg	%
Branches of current year	6039	15%	690	10%	2327	19%
Fruits and flowers of current year	-----	-----	2866	7%	-----	-----
Large spring leaves of current year	3051	62%	2497	41%	-----	-----
Rosette leaves	NA		NA		NA	
Small late summer winter leaves	-----	-----	1267	39%	13793	67%
Spines of current year	10629	5%	1877	0.5%	52	1%
1° branches of previous years	4070	8%	532	1%	511	7%
2° branches of previous years	1796	7%	101	1%	1230	5.5%
Crown	1408	3%	---	---	-----	-----
Determinate spines of previous year	159	0.01%	42	0.5%	16	0.5%
Taproot	1105	-----	-----	-----	-----	-----
1° laterals of taproot (1-2 mm diam)	814	-----	-----	-----	-----	-----
2° laterals of taproot (0.5-2.0 mm diam)	139	-----	-----	-----	328	-----
Small live roots (<0.5 mm diam) at 0-30 cm depth	63	-----	-----	-----	185	-----
Small live roots (<0.5 mm diam) at 30-60 cm depth	151	-----	-----	-----	192	-----

Table 3. Distribution of radioactive carbon in *Artemisia tridentata* shoot and root structures during 1972

Plant Structure	June		September		November	
	dpm/mg	%	dpm/mg	%	dpm/mg	%
Branches of current year	18396	19%	2764	13%	1925	14%
Fruit and flowers of current year	-----	---	-----	---	130	0.05%
Fully expanded leaves	26952	57%	4677	77%	482	81%
Reproductive shoot of current year	-----	---	-----	---	41	0.5%
Small leaves formed in current summer	NA		NA		NA	
New buds	-----	---	-----	---	-----	----
Insect galls	-----	---	1077	0.5%	4241	0.05%
1° branches of previous year	8042	9%	501	4.5%	460	2.5%
2° branches of previous year	6021	10%	143	5%	960	2%
Crown	7166	10%	-----	---	-----	----
Buds of previous year	-----	---	-----	---	-----	----
Taproot	4932	---	-----	---	-----	----
1° laterals of taproot (1-2 mm diam)	5051	---	-----	---	-----	----
2° laterals of taproot (0.5-2.0 mm diam)	6281	---	-----	---	22	----
Small live roots (<0.5 mm diam) at 0-30 cm depth	724	---	-----	---	132	----
Small live roots (<0.5 mm diam) at 30-60 cm depth	340	---	-----	---	196	----

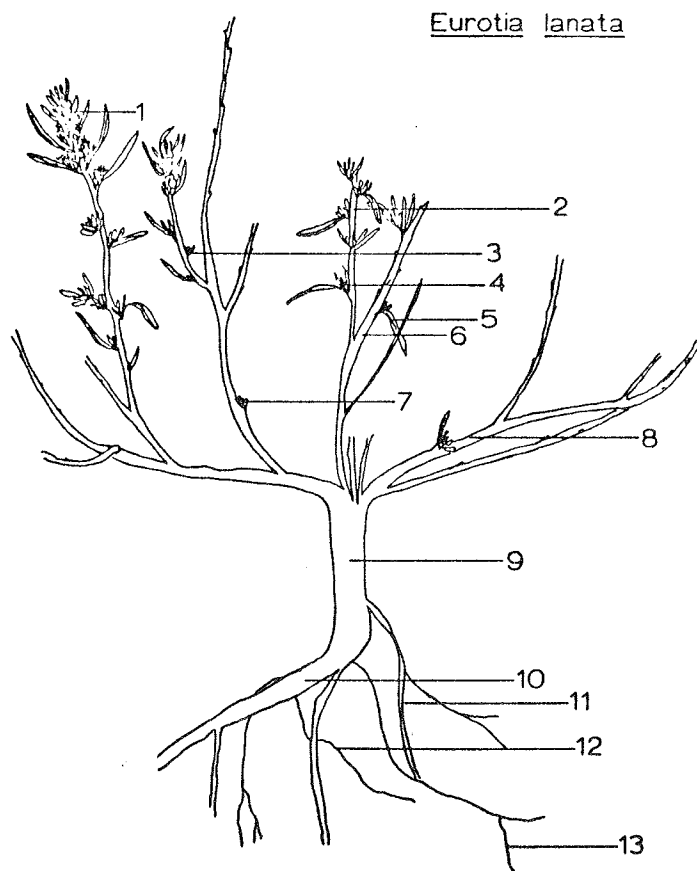


Figure 19. Diagrammatic representation of plant parts sampled for C^{14} for *Eurotia lanata*: 1. Flowers and fruits of current year's growth; 2. Current year's branches; 3. New buds; 4. New unexpanded leaves; 5. Fully expanded leaves; 6. Secondary branches of previous year's growth; 7. Buds on previous year's growth; 8. Primary branches of previous year's growth; 9. Crown; 10. Taproot; 11. Laterals of taproot (1-2 mm diam); 12. Secondary lateral roots from the main taproot (0.5-2.0 mm diam); 13. Small live roots less than 0.5 mm diam.

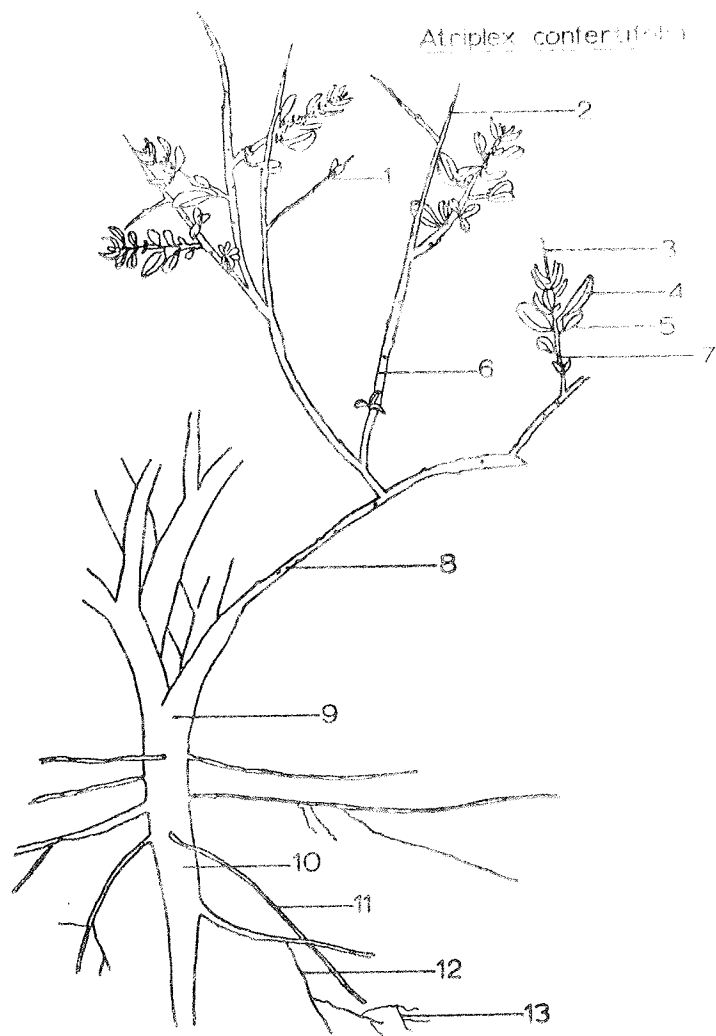


Figure 20. Diagrammatic representation of plant parts harvested for radioactivity determinations in *Atriplex confertifolia*: 1. Fruits and flowers of the current year's growth; 2. Determinate spines of the previous year's growth; 3. Spines of the current year's growth; 4. Large leaves formed in the current year's growth in the spring of the year; 5. Smaller winter leaves formed in the late summer; 6. Secondary branches of previous year's growth; 7. Branches of the current year's growth; 8. Primary branches of previous year's growth; 9. Crown; 10. Taproot; 11. Primary lateral roots of the taproot (1-2 mm diam); 12. Secondary laterals of the taproot (0.5-2.0 mm diam); 13. Fine living roots less than 0.5 mm diam.

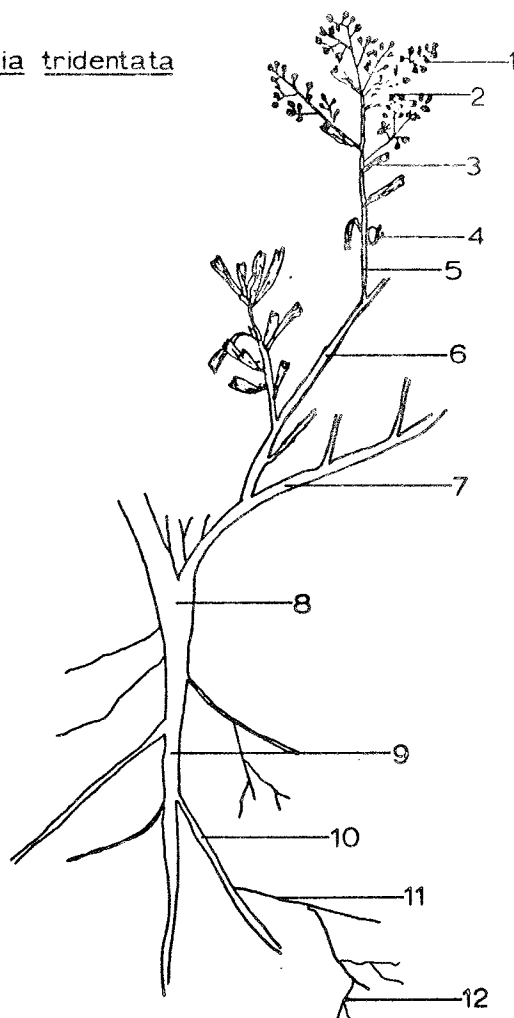
Artemisia tridentata

Figure 21. Diagrammatic representation of plant parts of *Artemisia tridentata* harvested for radioactivity determinations: 1. Fruit and flowers of current year's growth; 2. Reproductive shoot of current year's growth; 3. Fully expanded leaves of current year's growth; 4. Insect galls; 5. Branches of current year's growth; 6. Secondary branches of previous year's growth; 8. Crown; 9. Taproot; 10. Primary lateral roots of the taproot (1-2 mm diam); 11. Secondary laterals of the taproot laterals (0.5-2.0 mm diam); 12. Fine living roots less than 0.5 mm diam.

DISCUSSION

Gas exchange studies

To show the compounding effects of leaf temperature and irradiation on photosynthetic rates of *Artemisia tridentata*, an attempt was made to predict the daily course of relative photosynthesis under ambient conditions with respect to temperature and irradiation. This is not an attempt to predict absolute photosynthetic rates as a function of environmental parameters but merely to predict the pattern of relative photosynthesis based only on temperature and radiation. The predictive equation used was similar to the hyperbolic equation of Brown (1969):

$$RP = \frac{D}{\frac{D}{I} + 1}$$

where: RP = relative photosynthesis

I = irradiation % of maximum for growing season

D = integral exchange coefficient, here defined as a conductance term based on the % of maximum photosynthesis at a given leaf temperature from the data of Figure 2.

This simple equation yielded photosynthetic patterns, plotted on a relative scale in Figures 6-9, which paralleled the measured photosynthesis pattern remarkably well. Except in June, the increased afternoon temperatures, which exceeded temperatures optimal for photosynthesis, appeared to counteract the effect of the concurrent high irradiation levels. Predicted and measured photosynthesis rates then declined. The most plausible mechanism of this high temperature inhibition would appear to be induced stomatal closure, although higher mesophyll resistances may also be involved. In June, the afternoon leaf temperatures did not climb appreciably above the optimum for photosynthesis, and photosynthesis rates, both measured and predicted, roughly paralleled the pattern of irradiation through the course of the day. As June was the month of minimum water stress the degree of stomatal closure in the afternoon, partially a function of leaf temperature, would also be minimal.

We have alluded to the influence of plant Ψ on daily and seasonal net photosynthesis. The principal mechanism by which water stress limits photosynthetic activity of *Artemisia tridentata* appears to be an increased stomatal diffusion resistance, r_s' . Investigations of other species have also shown r_s' to be the major factor limiting photosynthesis under conditions of water stress (Boyer, 1970; Troughton and Slatyer, 1969; Hodges, 1967; El-Sharkaway and Hesketh, 1964; Brix, 1962). However, other more direct effects of water stress on photosynthetic processes should not be ruled out. Increased water stress may indeed induce higher mesophyll resistance values, r_m' . It should be pointed out, however, that some investigations have not found this to be the case (Troughton and Slatyer, 1969). In this discussion we are considering r_m' as the total

resistance, diffusive and metabolic, for the CO_2 pathway from just inside the stomates to carboxylation in the chloroplast.

If water stress is minimal, as it was with sagebrush during May and June of this study, daily variation in the rate of photosynthesis can be largely attributed to two major factors: irradiation and temperature. Helms (1972) found 80-90% of the variation of net photosynthesis in *Pinus ponderosa* could be accounted for by means of irradiation and temperature alone, as long as lack of moisture was eliminated as a complicating factor. Warren Wilson (1967) obtained similar results with respect to both assimilation and growth rate. Photosynthetic patterns for *Artemisia* also can be accounted for largely by temperature and irradiation variations (Figs. 6-9). Moderate temperature variations have been observed with some species to have little direct effect on rate of photosynthesis during periods of low water stress (Warren Wilson, 1966). Response to moderate temperature variations may be very species dependent, since *Artemisia tridentata* was apparently highly responsive to moderate variations of leaf temperature, even during periods of low water stress (Fig. 2). However, the temperature dependence of photosynthetic rate may be complicated by the effects of irradiation. The data of Figure 2 represent night tests during which artificial irradiation ($1150 \text{ microeinsteins m}^{-2} \text{ sec}^{-1}$) was approximately one half of maximum solar intensities. The possibility certainly exists that at higher irradiation intensities the temperature dependence of photosynthesis might be somewhat different.

The limitation of photosynthesis at low water stress by temperature and irradiation may be related to changes in r_m' although Troughton and Slatyer (1969) again found no increase of r_m' with increases of temperature between 22.5 and 38 C. The importance of r_m' in such situations, however, has been demonstrated by Hodges (1967), in which photosynthetic rate decreased in response to increased temperature with no change in stomatal aperture, and by El-Sharkaway and Hesketh (1964) where photosynthesis was curtailed at high temperatures even when the stomates were completely open.

Calculations showed r_m' for sagebrush in this study to change in magnitude at different temperatures and times of the season. This would indicate that variation in r_s' due to water stress cannot be viewed as the sole factor limiting photosynthesis.

The bimodal daily pattern of net photosynthesis observed by Lange et al. (1969) and Hellmuth (1971) in other desert plants was noticeably absent in *Artemisia tridentata*. The major cause of this midday depression cited by Lange et al. was stomatal closure induced by a transient water stress, although other possibilities were not ruled out. With sagebrush during the dry months of July, August and September stomates began to close in the morning and apparently failed to completely reopen the same day, even when leaf temperatures declined again in the late afternoon. Therefore photosynthetic rates once depressed remained low (Figs. 3, 8, 9). Stomatal closure is certainly a major mechanism limiting gas exchange here, since leaf diffusional resistances, $r_a + r_s$, remained high (Fig. 4) throughout the late summer afternoon test periods.

However, increased stomatal resistance cannot be viewed as the sole factor limiting photosynthesis. The negative afternoon net photosynthesis values noted in Figures 8 and 9 confirm this; indeed, increased r_s' values here would tend, if anything, to decrease the CO_2 efflux from the leaves. A possible cause of this negative net photosynthesis is greatly increased rates of dark respiration at the high leaf temperatures prevalent during the late summer afternoons (see Fig. 5 for dark respiration response to high temperature). Such an increase in dark respiration could, if coupled with greatly lowered rates of photosynthesis, account for the negative photosynthesis values of Figures 8 and 9. Although increased photorespiration relative to photosynthesis might partially account for depressed photosynthesis, photorespiration cannot exceed gross photosynthesis causing a negative net photosynthesis. Although agreement on the exact biochemical pathways of photorespiration has not yet been reached, the oxidation of immediate photosynthetic products is certainly involved (Beevers, 1971). Therefore, it would violate stoichiometry if photorespiration exceeded photosynthesis for prolonged periods of time.

The influence of phenology on rate of net photosynthesis through the growing season may well assert itself through effects on r_m' and these effects may be related to the different types of leaves present in differing proportions through the season. The large ephemeral leaves of May and June may indeed have lower r_m' and r_s' values due to such factors as larger intercellular air spaces in the mesophyll, hence lower CO_2 diffusion resistance, and greater light penetration to the chloroplasts allowed by the higher leaf area:dry weight ratios of such leaves. As these leaves are shed, a greater proportion of the foliage is composed of smaller, perennial leaves, perhaps with higher mesophyll and stomatal resistances. Cunningham and Strain (1969) found similar variations in structure and numbers with leaves of *Encelia farinosa* in which photosynthesis was depressed in the perennial, denser, smaller leaves of late summer. The major factor found to be related to these seasonal leaf changes was water availability, and the ability of the plant to produce smaller, denser leaves during dry periods was viewed as a plant adaptation to continued primary production even during periods of high water stress. Such may indeed also be the case with *Artemisia tridentata*, as this study would seem to indicate.

Leaf age may also be a phenological factor contributing to seasonal photosynthetic variations in sagebrush. Aging of both new and older leaves on the plants, or the greater proportion of older leaves on the plants following the loss of the large spring leaves after midsummer, may have been factors inducing lower rates of photosynthesis when coupled with higher temperatures and water stress. For many plant species it has been found that older leaves generally exhibit lower photosynthetic rates in response to high irradiation or temperatures than do more juvenile leaves (Hopkinson, 1966; Singh and Lal, 1935).

Photosynthetic acclimation of leaves had been studied by a number of investigators in recent years. As has been noted, the optimal temperature for sagebrush photosynthesis in early spring (15 C) was lower than the optimal temperature during the remainder of the

season (20 C). Although variations in optimal temperature are not nearly as dramatic as reported for other species (i.e. White, Moore and Caldwell, 1971; Mooney and West, 1964; Strain and Chase, 1966; Adams, 1970), they are still appreciable. These previous studies have shown that plants grown at higher temperatures tend to adapt by exhibiting maximum photosynthetic rates at higher temperatures. As long as water potential is not limiting, leaves acclimated to higher temperatures generally tend to have higher photosynthetic rates than those acclimated to lower temperatures (Mooney and Shropshire, 1967; El-Sharkaway and Hesketh, 1964). This trend appears to be evidenced in the higher rates of photosynthesis in June than in May with sagebrush. The fact that the optimal temperature for photosynthesis did not continue to rise through July and August is perplexing, and may either reflect a limit of acclimative adaptability for this sub-species of sagebrush or compensating factors such as leaf age or changes in leaf structure.

Mooney and West (1964) reported striking differences in the temperature optima for photosynthesis of different ecotypes of sagebrush, e.g. when comparing desert and subalpine populations. However, Mooney et al. (1966) found the optimum temperature for photosynthesis of sagebrush of the subalpine ecotype to shift only slightly through the course of a growing season, as we have reported for the sagebrush ecotype of this study.

Absolute rates of net photosynthesis (see Fig. 2) were quite similar to those reported by Mooney et al. (1966) although temperature optima and acclimation patterns were understandably somewhat different with the subalpine sagebrush, the temperature optimum of which generally ranged between 10 and 15 C.

The results of this study have shown the pattern of net photosynthesis of *Artemisia tridentata* to vary through the course of a growing season, both as a response to changing environmental conditions and as a reflection of phenological changes in the plant itself. The capability of sagebrush to maintain low levels of net photosynthesis during stress periods without becoming fully dormant may be viewed as an adaptation allowing greater overall growth and vigor, and thus a more secure position in the plant community.

Unlike *Artemisia tridentata* and *Atriplex confertifolia* (see 1971 Progress Report) *Gutierrezia sarothrae* did not exhibit a pronounced pattern of temperature acclimation based on optimal temperatures for net photosynthesis. The temperature optimum shifted between 15 and 20 C throughout the season. Whether this shift was significant or not is difficult to say since this is still in need of replication in 1973. The temperature optimum may have been centered around 17 or 18 C throughout the entire season and fluctuations represented in Figure 11 may be statistically insignificant. In any case, there is no drastic shift in photosynthetic performance of *Gutierrezia* as a function of leaf temperature at different times of the year. *Agropyron spicatum* exhibited a temperature optimum for photosynthesis around 25 C (see Figure 12); however, this is only based upon a single determination in June, and will await further replication in 1973.

Inhibition of net photosynthetic rates in plants possessing the normal C_3 photosynthetic pathway is a well-known phenomenon. Whether or not oxygen is simply stimulating photorespiration or actually acts as an agent directly inhibiting carboxydismutase (Osmond and Bjorkman, 1972; Bowes and Berry, 1972), the difference in net photosynthetic rates at normal and 2% oxygen concentrations do provide to some extent an indication of photorespiratory activity. There is an increasing dependency of net photosynthesis on oxygen concentrations with increasing temperature for *Gutierrezia* (Figure 13). Further research in 1973 is planned to evaluate the magnitude of photorespiration for this species under field conditions.

Root growth and translocation

Growth, productivity, and gas exchange of above-ground plant parts is becoming better understood through process studies of the Desert Biome and other research in desert ecosystems. However, even crude assessments of the amount of energy partitioned to underground plant parts per unit of time are conspicuously wanting. Underground plant biomass of pure stands of *Atriplex confertifolia* and *Eurotia lanata* were found to account for 74 to 83% of the total plant biomass in these communities in earlier studies (Bjerregaard, 1971). The turnover rate of this biomass has not yet, however, been assessed.

This year's studies dealing with root growth and translocation have been carried out in the field in Curlew Valley at the sites of previous process study work by Caldwell, West, Goodman, and others. Here, reasonably pure stands of *Atriplex confertifolia*, *Eurotia lanata* and *Artemisia tridentata* can be found. Soils are reasonably uniform, silty in texture and without rocks or heavy clay concentrations. Although in many respects these soils are ideally suited for root growth studies, there is still a great deal of difficulty in extracting the fine profuse network of fine roots which thoroughly permeate these soils. Although living roots of larger size classes are easily distinguished from large dead and decaying roots, fine roots are much more difficult to distinguish as to whether living or dead. Extracting roots from the soil which are intact from the growing apices to the central tap root is extremely difficult. Historically, techniques for studying root biomass and productivity have been very laborious and fraught with difficulties and limitations. We have attempted to apply several techniques to the study of root growth acknowledging that each technique has definite limitations and inherent inaccuracies.

The soil-root observation chambers are providing a technique whereby the timing of root growth activity during the course of the growing season can be observed in the field. Although our preliminary soil moisture potential and temperature measurements indicate no major alterations in these two parameters by the presence of the observation window, more replication is necessary in these measurements. Also, alterations in soil structure and other physical characteristics are unavoidable in the immediate vicinity of the window pane. This technique only provides an observation in two instead of three dimensions, and certainly does not provide quantitative information on root productivity.

Although these observation chambers were only installed this past year some interesting information has already been yielded. Root growth is apparently very sporadic and extends well into the autumn even though shoot growth has terminated much earlier (see Figure 14 and 1972 Progress Report by West). Individual roots apparently have short periods of growth usually spanning only two weeks even though the entire root system is experiencing growth over at least a period of three to four months. Small lateral rootlets may often arise several weeks after the termination of elongation of the main rootlet. Active root growth was also observed when concomitant measurements of soil moisture potential indicated soils to be on the order of -70 to -80 bars water potential. This growth of roots in extremely dry soils may be possible if another portion of the root system, e.g. at greater depths, is in an area of less negative water potential. Cowling (1969) was able to verify root growth of *Atriplex vesicaria* in dry soils for at least 60 days as long as another portion of the root system was held under moist conditions in the laboratory.

Fungal hyphae were observed to be apparently associated with much of the fine root system of *Atriplex confertifolia*. Root cross sections are currently being made to determine the apparent nature of this fungal association. Even though it is possible to accurately observe the timing and nature of root growth of this fine permeating root system, death of these fine roots is difficult to establish through the observation window.

Our studies of the root growth pattern of *Artemisia tridentata* over the course of several years using the annual ring counting technique (Fig. 15) also indicate an irregular pattern of root development. Root branching apparently can occur at many places in the root system during most any year following development of the main taproot. The discovery of a great number of dead roots which were alive for only one year also suggests a great deal of turnover of the finer root systems. Naturally, the annual ring dating technique could not be applied to finer roots that may live less than one year. Observations in the root chambers suggest that most of the small rootlets only grow for a period of one or two weeks although lateral branches may develop several weeks subsequent to the growth of the primary rootlet. Although root death is difficult to observe through this observation window, it might be reasonable to assume that many of these small rootlets have a very limited span of activity and last only a few weeks. If this is the case the turnover time for carbon in the minute root system of these shrubs may be reasonably rapid. If this is the case, a substantial amount of energy would need to be invested in underground plant productivity.

Our attempts at the application of pulse labeling techniques to the study of root growth, while only moderately successful for estimation of root elongation, did indicate the appropriation of radioactive carbon to various portions of the excavated root system. Although some radioactive carbon was concentrated in what would be assumed as actively growing rootlets such as those observed in the observation chambers, a substantial amount

of carbon was also invested in apparently secondary tissue formation in larger roots. Translocation and root growth studies using carbon-14 have also verified this in a more quantitative manner.

Results of the preliminary experimentation using radioactive carbon in these three species indicated substantial differences in allocation of carbon to various plant parts (see Tables 1, 2 and 3). One week following the application of $^{14}\text{CO}_2$ most of the radioactive carbon was still concentrated in the leaves. In *Eurotia lanata* most of the activity was not in the larger leaves but instead in the very small leaves which had not yet expanded. All three species had a moderate amount of activity in branches of the current year's growth. Activity in previous years' growth was usually low, although in June in *Artemisia tridentata* there was approximately 10 percent of the total radioactive carbon in the above-ground portion of the plant concentrated in primary and secondary branches of previous years' growth.

Shoot growth studies of *Eurotia lanata* by West and Fareed correlate reasonably well with Table 1 results.

The relatively high percentage of C^{14} in the current year's branches correlates with the timing of maximum elongation in the current year's lateral shoots examined in the shoot growth study. Also, the reduction in the percentage of C^{14} in the current year's branches in September and November is related to the observed reduction in shoot growth which began in August. In both the fully expanded and unexpanded *Eurotia* leaves, C^{14} activity shows similar patterns to those noted in the shoot growth studies. Activity in the fully expanded leaves tended to decrease between June and November, while the unexpanded leaves showed an increase in activity. The shoot growth studies indicated that the fully expanded leaves, which surround the unexpanded leaves, began dying-back and falling in early May. At about this same time, the unexpanded leaves became more active. Apparently a large percentage of carbon fixed at this time of year is channeled to these new leaves.

Based on *Atriplex confertifolia* shoot growth studies, both regreening of leaves and apical leaf bud swelling was still occurring in *Atriplex* plants in June, but at a somewhat reduced rate than in May. Conceivably, the percentage of C^{14} in these large spring leaves may have been even greater in May than the observed 62% which occurred in June (Table 2). During September, shoot growth studies indicated the occurrence of the first summer dormancy and the shedding of spring leaves in *Atriplex*. This could explain the reduced C^{14} activity in September. The small winter *Atriplex* leaves which began developing in the late summer appeared to become more succulent and darker green in color during the fall. Perhaps this was influenced by the marked increase in precipitation beginning in September. Although there was no noticeable increase in their length, it seems probable that they were active photosynthetically. This might explain the increase in the percentage of C^{14} in these small winter leaves in November.

Table 3 results of *Artemisia tridentata* activity show some interesting correlations with shoot growth observations. During May and June, *Artemisia* shoot elongation was occurring. The relatively higher percentage of C^{14} found in the current year's branches in June is indicative of this period of rapid shoot elongation. Shoot length was maximum during late August and began to decrease thereafter. A similar reduction in the percentage of C^{14} occurred in the current year's branches in September and November. The relatively high percentage of C^{14} in the current year's fully expanded leaves in September and November may have been influenced by the precipitation which occurred following the unusually dry 1972 summer season.

Although taproots and primary laterals of the taproot system were only excavated in June it was apparent that there was much more activity per mg dry weight of tissue in these larger roots than in the small fine root system. This provides some quantitative corroboration with qualitative evidence from the autoradiograms. Surprisingly, radioactivity in what are considered to be living roots of the small fine root system (less than .5 mm diam), was quite low both in June and later in November. Perhaps between these two dates these fine roots would be much more active since root growth activity is known to occur during this part of the year according to the observation chamber studies. Also, many of the extremely fine roots and certainly root hair tissues were usually not recoverable even with most meticulous efforts. It could be that there is still a substantial amount of radioactivity per unit of tissue in these extremely fine elements of the root system. If root turnover of the fine root system, i.e. new growth, death and decay, is extremely rapid as was suggested earlier in this discussion, there may still be a very sizeable increment of carbon invested in these fine roots. In 1973 much more effort will be concentrated on intensive root sampling and further labeling. With acquisition of a carbon train, larger samples can be combusted and thereby reduce the variability in individual samples. Plants labeled in 1972 will be sampled again for various portions of the root and shoot system to determine changes in specific activity, i.e., proportion of carbon-14 to total plant carbon, to estimate root productivity as discussed in the results section. Although there are certainly more implicit assumptions which must be satisfied in this relationship, some estimate of root productivity should be forthcoming. This will provide comparative information for estimates of root growth derived from root regrowth into the soil cores removed the previous year. The conspicuous absence of information on root productivity in all terrestrial ecosystems indicates the drawbacks in all methods attempting to assess root productivity and the meticulous and time-consuming labor involved in such work.

EXPECTATIONS

The pulse labeling technique will be attempted again in 1973 with shorter intervals between the pulse labels. Pulse labeling is designed to identify primary growth and root elongation and is ideally suited for roots without secondary growth. Such secondary diameter growth occurs along almost the entire length of the root and tends to obscure primary pulse labels. Therefore, much shorter intervals between pulses and harvesting the roots within one to two weeks following the second pulse label will be employed in the field. It is anticipated that this technique still may be of some value in confirming root growth observations in the soil-root observation chambers. Also in 1973 the soil cores installed in 1972 will be excavated and root invasion into these cylinders will be determined as an index of root productivity. A major effort will be directed towards further studies of translocation and root growth using the radioactive carbon labeling techniques in the field. Root observation chambers will be monitored at regular intervals from early spring until late fall to further elucidate the nature of timing of root growth activity in these shrubs. Preliminary studies of associated fungal hyphae will be carried out. Soil respiration studies will be initiated in the field in 1973. Finally, in the laboratory a detailed study will be centered on the complete carbon balance of individual desert shrubs bringing into account carbon dioxide exchange of roots and shoots independently and using a concomitant $^{14}\text{C}_2$ labeling to quantitatively assess translocation to various parts of the plant. Much of the 1973 effort is then to be directed to the elucidation of the relationship between plant productivity and gas exchange.

During 1973, further shoot gas exchange studies will be carried out on *Gutierrezia sarothrae* and *Agropyron spicatum* in the field with correlative laboratory studies.

ACKNOWLEDGEMENTS

Although this 1972 study was conducted largely under the financial auspices of the US/IBP Desert Biome, additional financial support by the Utah State University Ecology Center and the Utah Agricultural Experiment Station is gratefully acknowledged.

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1972 PROGRESS REPORT

PHENOLOGY AND FUNCTION OF SONORAN DESERT ANNUALS
IN RELATION TO ENVIRONMENTAL CHANGES

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Research Memorandum, RM 73-14

MAY 1973

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Report Volume 3

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INTRODUCTION

Perennial grasses, shrubs, trees and succulents are usually considered the characteristic plants of the Sonoran Desert; however, the annual herbs may significantly contribute to the desert vegetation cover and biomass during years when there is adequate moisture. The Sonoran Desert has both winter and summer periods of precipitation, each producing a different annual flora. Winter annuals are generally dicotyledons while summer annuals are monocotyledons.

The winter annual vegetation begins to develop shortly after the first winter rains which usually occur in December. If late winter rains do not follow the early rains, the annual herbs may not flower or fully develop. Development of winter annuals during good moisture years may produce more new photosynthetic material than the shrubs. However, as the weather warms, the shrubs far surpass the annuals in total biomass production.

Summer rains occur in late July and August stimulating annual grass production. In lower elevations of the Sonoran Desert, summer rainfall may be irregular and annual plant development may therefore be quite limited. At higher elevations, wet years cause annual grass production to be 80% of the total grass biomass while during dry years annual grass production may be lacking (Martin, 1966).

Germination and development of annuals have been shown to be related to rainfall and temperature (Went, 1949) as well as to the relative position to shrubs (Went, 1942; Müller, 1953). Annual growth also may occur in clumps with high densities in some areas (e.g., 250 plants per dm²) and few plants elsewhere. These irregularities in growth occurrence along with variations in response to environmental stimuli among different annual plant species create an interesting problem for the researcher of desert vegetational development and productivity.

OBJECTIVES

The primary objectives of this study are to relate the growth and development of desert annual plants to environmental parameters in order to determine which factors most influence annual vegetation productivity. Closely correlated with these objectives is the determination of the relationship between the phenological stages of the annuals and the past and present environments of the plants. Productivity of the desert annuals can be measured through field sampling as well as CO₂ exchange analyses. A comparison of these processes shows the relationship between environmental responses of field growth and

A B S T R A C T

Desert annual plants may contribute a high percentage of biomass during "good" years. This study proposes to determine those factors that influence the productivity of desert annuals by 1) monitoring desert microenvironmental conditions in various habitats, 2) periodically measuring biomass accumulation of desert annuals, 3) determining phenological stages of annuals in relation to time and environment and 4) measuring CO_2 exchange functions of annuals in relation to environments.

In 1972, desert annual biomass accumulation did not begin until October, winter rains were lacking and summer rains were apparently insufficient. Biomass accumulation since October has been concentrated under the shrubs, the area of apparent optimum environment. Continual monitoring of annual plant biomass relative to shrub and open habitats is beginning to show the factors necessary for annual plant development in the Sonoran Desert. Growth has been limited to the vegetative stage so flowering, seed set and dispersal, and mortality have not been related to specific environmental variables. This relationship plus CO_2 exchange analyses should help predict productivity rates of desert annuals.

physiological function. All of the measured processes of growth and productivity of the annuals are considered relative to the perennial plants which greatly influence the micro-environments of the desert.

METHODS

A study site near Cave Creek, Arizona, at an elevation of about 2100 feet was selected because it had similar vegetation and rainfall to the Silverbell Validation Site near Tucson, Arizona. Vegetation is typical of the *Larrea-Franseria* desert association with scattered *Cercidium*, *Opuntia* and *Cereus*. This site was mapped and randomly sampled (21 10 x 10 m quadrats) for composition.

Microenvironmental stations were set up in two locations in the study site in order to measure abiotic conditions prior to, during and after annual plant germination, growth, flowering, seed set and dispersal, and mortality. Microenvironmental conditions were measured, starting in April, 1972, in the open and in relation to the canopy of various shrub species, especially *Cercidium microphyllum*, *Larrea divaricata*, and *Franseria deltoidea*. Abiotic parameters measured include: solar radiation by pyrlieliograph (Data Set A3UPB05), precipitation by recording rain gauge (Data Set A3UPB06), air temperatures and calculated vapor pressure deficits at 15 and 120 cm by recording hygrothermographs (Data Set A3UPB07), air temperatures at 1.5 cm by Moeller distance recording thermographs (Data Set A3UPB08), wind velocity at 15 and 120 cm in the open and 15 cm under shrubs by totalizing anemometers (Data Set A3UPB09), soil temperatures at 1.5 and 7.5 cm depths by Moeller thermographs (Data Set A3UPB10), and soil moisture at 0-7.5 cm and 15-22.5 cm depth by gravimetric means (Data Set A3UPB11), and at 1.5, 7.5, 15, and 30 cm by Colman soil moisture blocks (Data Set A3UPB12). Most of the abiotic data have been collected on a weekly basis; however, when periods of rainfall occur and plant growth is stimulated, daily microenvironmental data are recorded.

Annual plants were sampled under shrubs and in the open with 2 x 2 dm quadrats. Under large shrubs sampling was at four aspects (N, S, E, W) from the shrub stem near the stem and under the canopy overhang. Sampling under small shrubs was limited to the north and south sides near the shrub base. Densities of annual plants and total biomass (dry weight) for each sample (2 x 2 dm) were measured under *Cercidium microphyllum*, *Larrea*, *Franseria deltoidea* and in the open (Data Set A3UPB13). Densities and biomass of individual species of annuals, when they could be identified, were measured under *Cercidium*, *Larrea*, *Franseria* and in the open (Data Set A3UPB14). During the sampling, phenological stages of the various species of annuals were also determined.

CO₂ exchange measurements were not made during 1972 because the annual plant vegetation did not develop until near the end of the year, thus the amount of photosynthetic surface was limited.

RESULTS

Vegetation

The relationship between shrubs and the growth and development of annuals is considered important enough that vegetational composition of the study area might be used to ultimately determine productivity of annuals in the area. Table 1 shows that the study area is dominated by *Franseria deltoidea* (I.V. over 100); however, influence of shrub cover probably is more significant when considering annual plant growth. *Cercidium microphyllum* with lower density than *Franseria* practically equals the cover of *Franseria* and thus is probably very important to annual productivity. Many of the perennials produce cover within the canopy of a bigger shrub or tree and thus may not independently influence the annual plant microenvironment.

Abiotic environment

Macroclimate of the study area is represented by temperature data from a standard weather shelter at 120 cm and precipitation data from the open (Fig. 1). The study site is typical of the Sonoran Desert with hot summers and cool winters. 1972 was an unusual year in the study area in that the first half of the year was dry, the normal winter rains never occurring, while the second half of the year was abnormally wet with heavy rains in October. The abnormal rainfall pattern caused a lack of annual plant development in the winter and spring and a lush annual plant development in late fall.

Germination, growth and development of desert annual plants is influenced more by conditions near the ground than at 120 cm; thus microenvironment near the ground, in the open and under shrubs, has been intensively monitored. Proper temperature and moisture conditions initiate annual plant development and maintain growth. Figure 2 shows temperature conditions in the open and under *Cercidium* at 1.5 cm above the ground surface and 1.5 cm in the soil, along with soil moisture conditions in the upper 7.5 cm of soil in the open and under *Cercidium*. In the summer, conditions were extremely hot with subsurface soil temperatures reaching over 50 C. Soil moisture was very low until the July rains, after which soil moisture was not maintained due to evaporation. Not until after the late fall rains did the soil temperature drop in conjunction with a more or less continual maintenance of soil moisture. The influence of the shrubs can be readily seen (Fig. 2). Temperatures near the ground and in the soil subsurface are moderated by the shrub canopy. Soil moisture is also maintained for a longer period under the shrubs.

Growth and development of the annual plants after germination is a function of soil moisture and temperature, but the microenvironment in the area of foliage development must also have some influence. Figure 3 shows the temperature and vapor pressure deficit (VPD) differences at 15 cm above the ground in the open and under the canopy of *Cercidium*. VPD is high during the drought periods and moderate during rainy periods. Only on days of rainfall does VPD drop to zero. From April through December, 1972 temperature and VPD conditions in the open and under the shrubs were not too different except for the slight expected variations due to the influence of shrubs. At times, the VPD under the south-side canopy of *Cercidium* was higher than in the open. This probably was due to the south-side canopy creating a heat pocket.

Table 1. Cover percentages and importance values (IV) of the perennials at the Cave Creek study site

Species	Aerial Cover (%)	I.V.
<i>Fraseria deltoidea</i>	32.3	115.9
<i>Larrea divaricata</i>	23.9	42.6
<i>Cercidium microphyllum</i>	31.3	41.0
<i>Opuntia acanthocarpa</i>	5.3	20.2
<i>Opuntia bigelovii</i>	0.7	15.3
<i>Mammillaria microcarpa</i>	*	10.2
<i>Opuntia leptocaulis</i>	1.9	10.7
<i>Echinocereus engelmannii</i>	*	7.8
<i>Opuntia fulgida</i>	0.6	6.4
<i>Cereus giganteus</i>	*	4.5
<i>Trixis californicus</i>	*	6.0
<i>Opuntia phaeacantha</i>	*	1.6
<i>Prosopis juliflora</i>	1.5	3.4
<i>Fouquieria splendens</i>	0.9	2.3
<i>Krameria grayi</i>	*	1.5
<i>Ferocactus acanthodes</i>	*	4.0
<i>Opuntia arbuscula</i>	*	1.9
<i>Simmondsia chinensis</i>	*	1.4
<i>Acacia greggii</i>	*	0.9
<i>Zizyphus obtusifolia</i>	*	1.0
<i>Calliandra eriophylla</i>	*	0.7
<i>Porophyllum gracilis</i>	*	0.7

*Cover = less than 0.5%.

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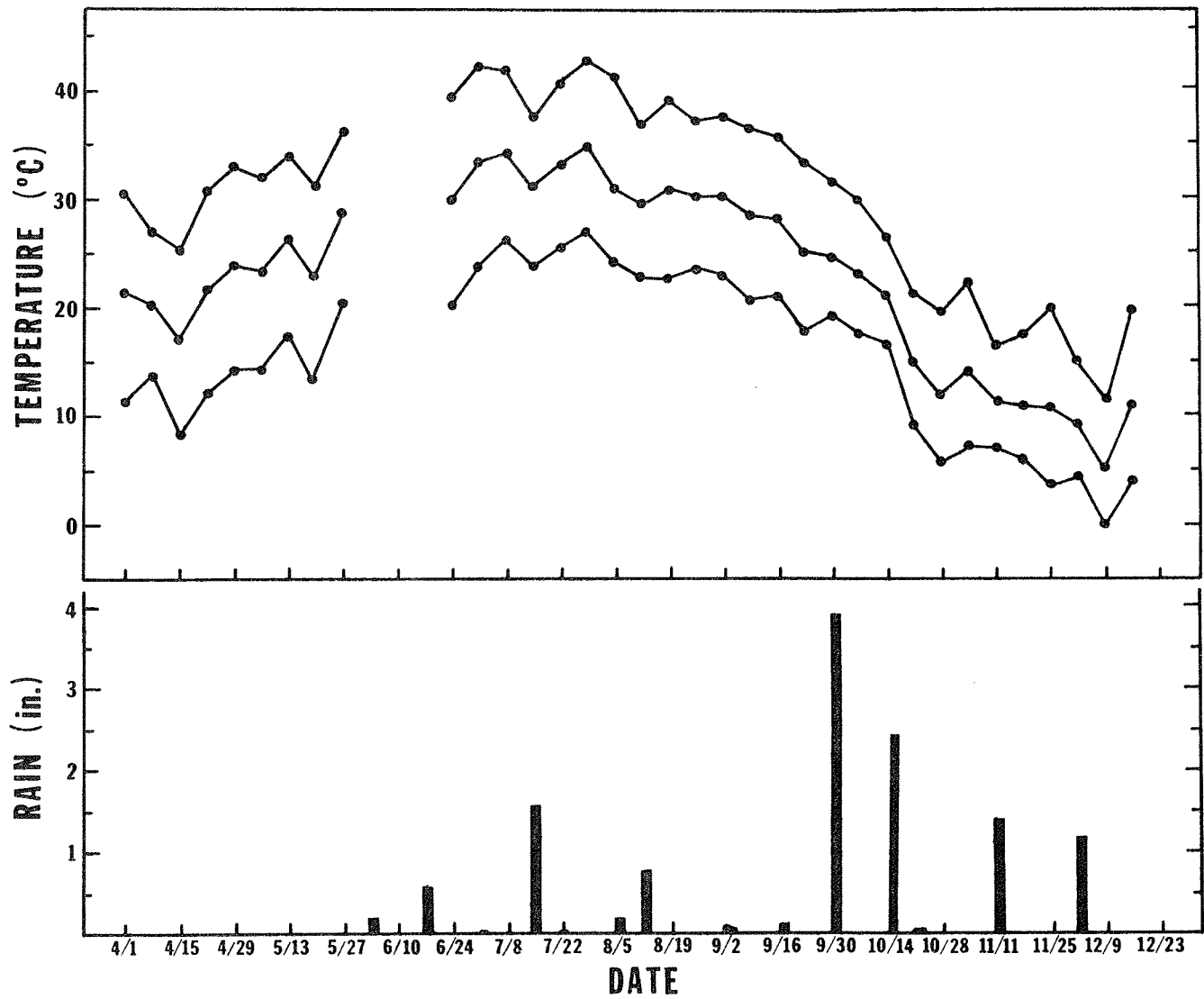


Figure 1. Weekly mean maximum, mean and mean minimum temperatures at 120 cm above the ground, and total weekly precipitation at the Cave Creek study site. Dates indicate the first day of the averaged weekly period. (DSCODES A3UPB06 and A3UPB07)

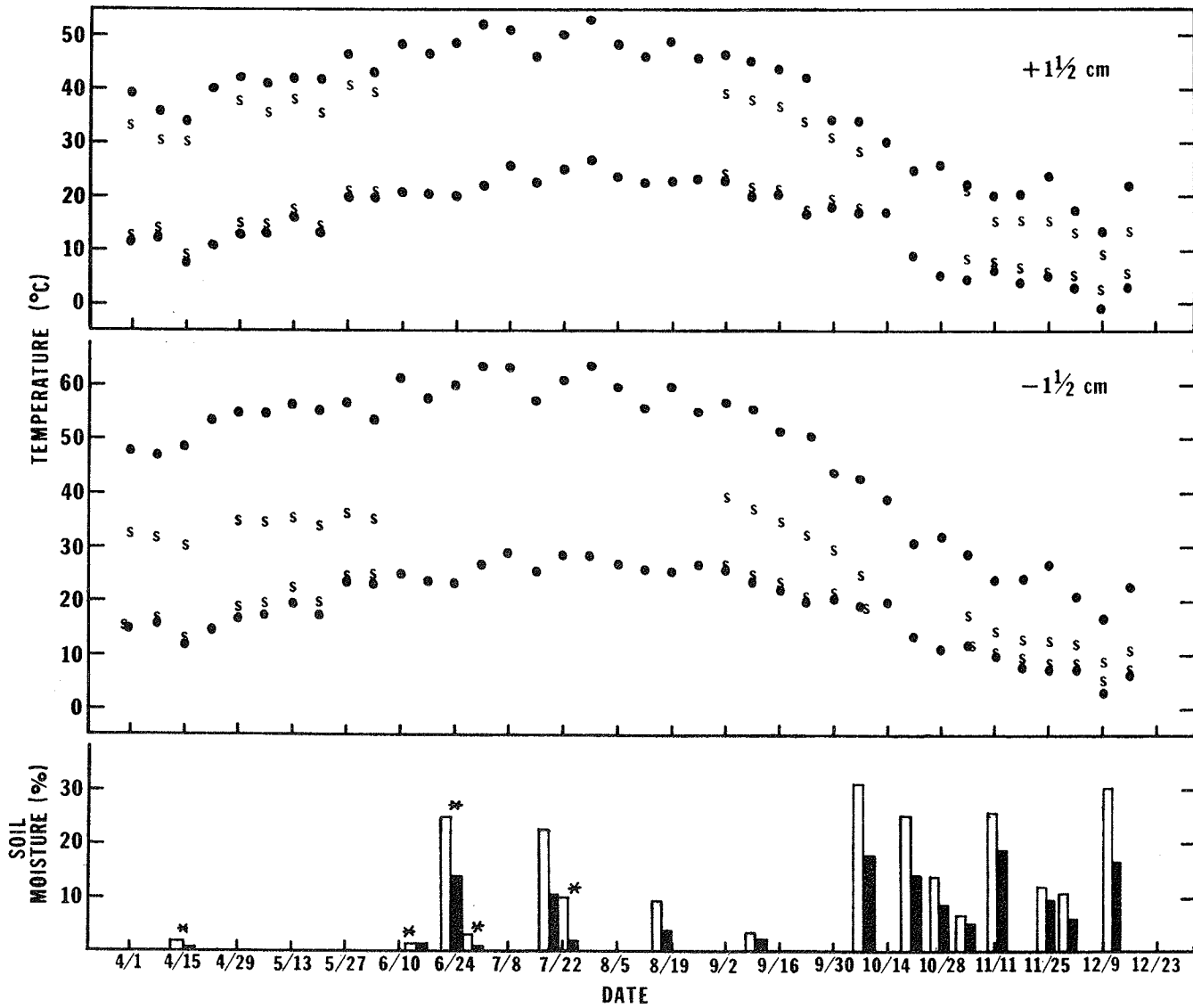


Figure 2. Weekly mean maximum and mean minimum temperatures at 1.5 cm above the ground and 1.5 cm in the soil in the open (solid dots) and under the north side of *Cercidium* (s). Soil moisture (rock corrected) at 0 - 7.5 cm in the open and under *Cercidium* (dark bar) for the date indicated (*not corrected for rocks). (DSCODES A3UPB08, A3UPB10 and A3UPB11)

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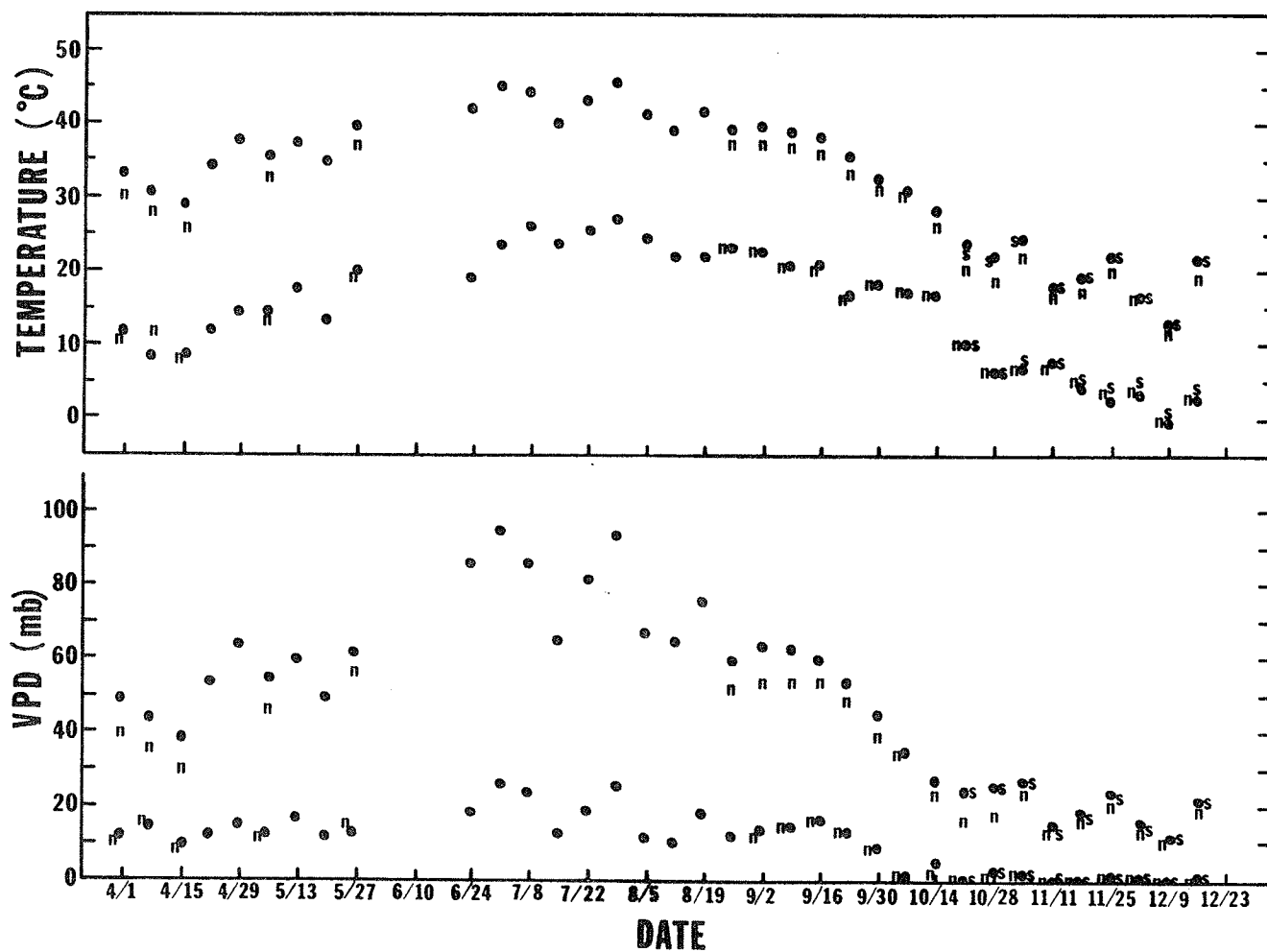


Figure 3. Weekly mean maximum and mean minimum temperatures and mean maximum VPD's at 15 cm in the open (dot), and under the north (n) and south side (s) of canopies of *Cercidium*. (DSCODE A3UPB07)

Biomass

In 1972 there was no annual plant development until following the early October rains. Figure 4 (A) shows biomass accumulation of the annual plants in the open and under the influence of various shrub species. This Figure presents only totals and does not break the totals down into biomass quantities under various aspects of the shrub canopy. Germination and measureable annual plant biomass development occurred first under *Cercidium*, followed by growth under *Larrea*, *Franseria* and out in the open. The second surge in growth was probably due to additional moisture input from later rains followed by clear sunny days. The difference in biomass accumulation between under the shrubs and in the open is great even at an early stage of annual plant development. The amount per unit area is nearly four times greater under *Cercidium* than in the open.

Totaling biomass does not indicate the significance of various aspects under the shrub canopy. Figure 4 (B) shows that the edge of the southside of the canopy of *Cercidium* is very similar to totals in the open shown in Figure 4 (A). On the other hand, biomass accumulation of annuals under the southside of the canopy near the base of the tree is as high as any of the northside canopy figures (Fig. 4 (B)). Position under the shrub thus appears to be important for maximum annual plant growth and development.

Phenological stages of the characteristic annual species are being followed but in most cases germination and vegetative growth is all that has been recorded. A few individuals of a few species show signs of beginning to flower.

The following is a list of the identified annual plant species at the Cave Creek study site following the fall, 1972, rains:

<i>Bowlesia incana</i>	<i>Calandrinia ciliata</i>
<i>Parietaria floridana</i>	<i>Tillaea erecta</i>
<i>Draba cuneifolia</i>	<i>Erodium texanum</i>
<i>Eucrypta chrysanthemifolia</i>	<i>Schismus barbatus</i>
<i>Lotus salsuginosus</i>	<i>Sonchus</i> sp.
<i>Lotus tomentellus</i>	<i>Thelypodium</i> sp.
<i>Astragalus nuttallianus</i>	<i>Plantago</i> spp.
<i>Poa bigelovii</i>	<i>Amsinckia</i> spp.
<i>Pectis papposa</i>	<i>Spermolepis echinata</i>
<i>Pectis prostrata</i>	<i>Plagiobothrys</i> spp.
<i>Erodium cicutarium</i>	<i>Filago</i> sp.
<i>Sisymbrium irio</i>	<i>Lepidium</i> sp.
<i>Pterostegia drymarioides</i>	<i>Descurainia</i> sp.
<i>Lotus humistratus</i>	

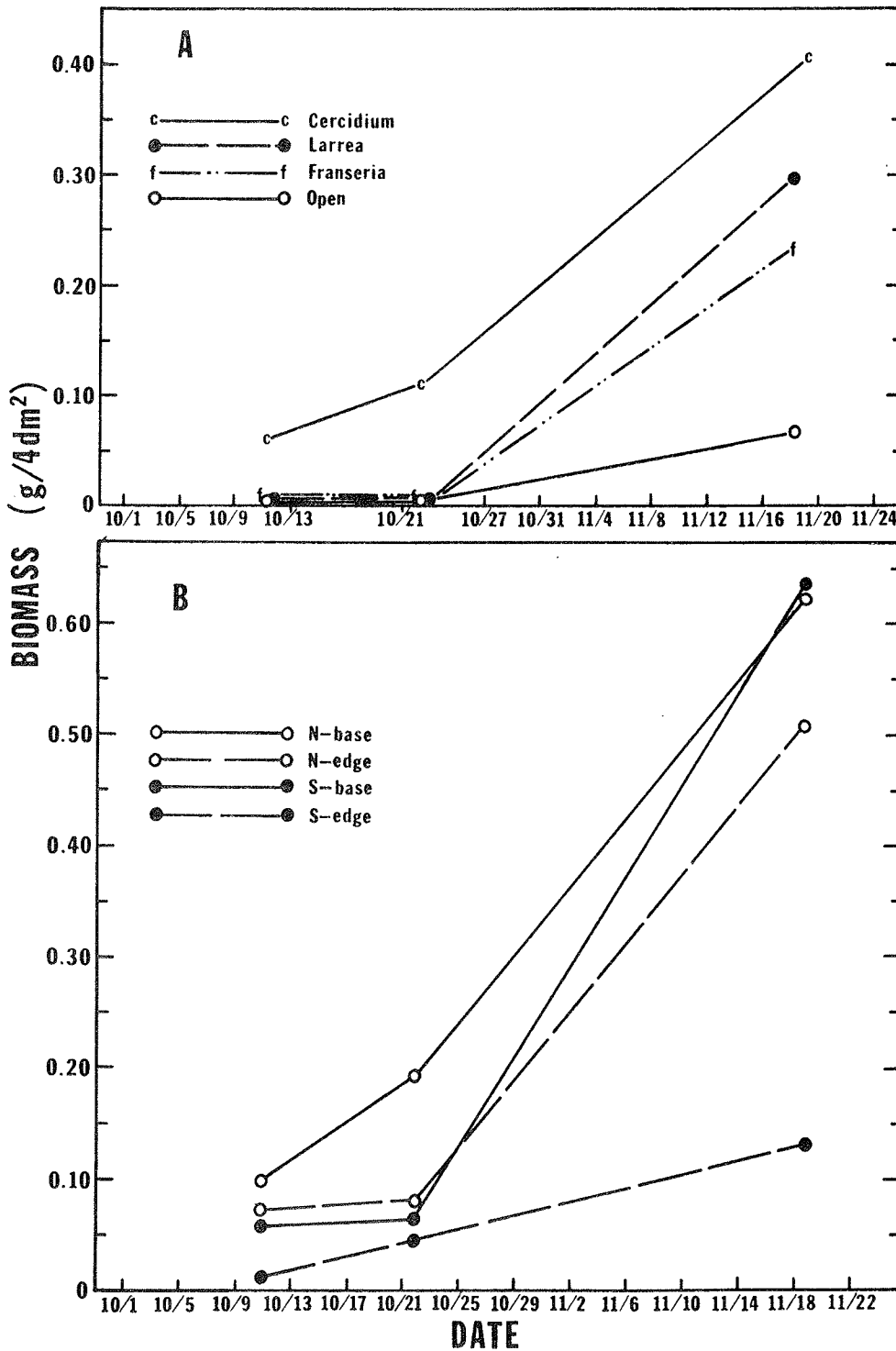


Figure 4. A. Total annual plant biomass (dry weight) in the open and under *Cercidium*, *Franseria* and *Larrea* in relation to time. (DSCODE A3UPB13)

B. Total annual plant biomass under the north and south canopies of *Cercidium* near the canopy edge and near the base of the tree, in relation to time. (DSCODE A3IIPR13)

DISCUSSION

Many factors influence the germination and growth of desert annual plants. Probably the most important are moisture and temperature or the combination of these two. No annuals developed in the study site in July when the moisture was non-limiting. Extremely high ground temperatures or the lack of seeds from heat-requiring species probably accounted for this. However, the rains that occurred in October brought on the development of many annual plants; some are considered to be summer annuals. October soil temperatures were not as high as July but they were hot. Soil moisture was maintained longer in October and high soil temperatures did not last as long. These could be factors permitting annual plant seed germination and growth.

Once conditions were generally right for development of annuals in all areas, they were optimum in certain areas under the shrubs. That these areas under the shrubs produced more annual plants and biomass than in the open is probably due to microenvironment but it may also be due to a greater seed reserve under the shrubs; a product of greater annual plant survival in these areas.

EXPECTATIONS

The production of biomass of desert annuals in late 1972 is only the beginning of the potential biomass accumulation that should occur into 1973. Continuation of monitoring of the macro- and microenvironment will indicate what factors most influence the biomass accumulation and developmental stages of the annuals. Factors which will be looked at more closely will be VPD and low temperatures (frost damage).

In late 1972, the annual species were beginning to be identifiable. When certain identification is possible, biomass accumulation will be separated as to species and totaled. In the winter and spring of 1973 as annual plants flower and begin to die, micro-environment will be followed very closely to determine the conditions influencing each stage of each species.

With the development of enough plant volume to permit measureable gas exchange, CO₂ exchange analyses will be made on clumps of annuals in the field in different locations (shrubs, open, etc.). The measurements will be compared with the actual biomass accumulation data to enable estimates of productivity rates.

Phenological studies of annuals will be continued in 1973 until all the plants have set seed and died.

Laboratory analyses of germination requirements of annuals will be made after an adequate seed reserve is collected. Germination tests will also be made using the desert soil after the annuals at the study site have completed seed development and dispersal.

A comparison of the various microenvironmental regimes where annuals germinate, grow and flower with the relative biomass accumulation rates of the species and CO_2 exchange rates, should give a composite picture of the environmental spectra in which productivity is possible for each annual plant species and the annual plants as a whole.

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1972 PROGRESS REPORT

A MODEL OF NET CO₂ EXCHANGE RATE FOR C-4 GRASSES

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Research Memorandum, RM 73-15

MAY 1973

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A B S T R A C T

A mathematical model for the prediction of net CO₂ exchange rates of C-4 grasses was developed. The independent variables in the model are irradiance, soil water potential, air temperature, and ambient CO₂ concentrations. Infrared gas analysis was employed to measure net CO₂ exchange rates for use in developing the model. A multiple non-linear regression technique was used to obtain least squares estimates of coefficients in the model. The model provides reasonably accurate estimates of net CO₂ exchange rates for *Hilaria mutica* and *Panicum obtusum*.

INTRODUCTION

In any model of a desert ecosystem one of the most important submodels will be for the prediction of net primary production. This submodel will have to be sensitive to changes in the environmental parameters which most closely determine rates of net primary production. It should also allow for integration of rates of production over any desired time interval to give updated standing crop values.

The net primary production of a plant can be determined over any desired time interval by:

$$P = C_{ip} - (C_{op} + C_{on}) \quad (1)$$

where:

- P = net primary production for the desired time interval,
- C_{ip} = net carbon uptake by photosynthetic organs during the light period of the desired time interval for updating standing crop,
- C_{op} = net carbon loss by photosynthetic organs during the dark period of the desired time interval for updating standing crop,
- C_{on} = net carbon loss by nonphotosynthetic organs during the desired time interval for updating standing crop.

Clearly an important subroutine of the net primary production submodel will be a calculation of net CO_2 exchange of the photosynthetic organs in the light. This subroutine should calculate expected rates of net CO_2 exchange as a function of the environmental variables which control the process.

On the Jornada Validation Site the playa community is dominated by two grass species, *Hilaria mutica* and *Panicum obtusum*. The modelling of this will therefore require an accurate estimation of net CO_2 exchange rates of these grasses as a function of environmental variables being measured on the site. A general mathematical model of CO_2 exchange in C-4 grasses was developed. Coefficients for the model were then determined using CO_2 exchange data and an intrinsically non-linear regression algorithm.

OBJECTIVES

The objective of the research was to develop a mathematical expression which can be used to calculate expected rates of net CO_2 exchange for *Hilaria mutica* and *Panicum obtusum* from environmental measurements being made on the Jornada playa site.

THE GENERAL MODEL

The process of photosynthetic CO_2 exchange can be viewed as a temperature-dependent enzyme-catalyzed reaction. The maximum rate of this reaction will be dependent on the maximum level of CO_2 in the plant's environment. The rate can be reduced from this maximum value by lowering the CO_2 concentration in the environment or imposing resistances to CO_2 flux in the pathway from ambient air to the chloroplast. A general equation expressing these ideas is:

$$\phi = R \cdot S \quad (2)$$

where:

ϕ = rate of net CO_2 exchange in $\text{mg CO}_2 \cdot \text{dm}^{-2} \cdot \text{hr}^{-1}$.

R = temperature-controlled rate of net CO_2 exchange at normal ambient CO_2 concentration with no resistances to CO_2 flux to the chloroplasts in $\text{mg CO}_2 \cdot \text{dm}^{-2} \cdot \text{hr}^{-1}$.

S = rate of CO_2 supply to the chloroplasts relative to the maximum rate at normal ambient CO_2 concentrations and no resistances to CO_2 flux to the chloroplasts. This is a dimensionless coefficient.

R is the product of the non-enzyme limited rate and a scaling coefficient which corrects for enzyme denaturization at increased temperature:

$$R = Q \cdot E \quad (3)$$

where:

Q = non-enzyme limited temperature-controlled rate of net CO_2 exchange in $\text{mg CO}_2 \cdot \text{dm}^{-2} \cdot \text{hr}^{-1}$

E = dimensionless coefficient that varies from 1 at optimum enzyme concentration to 0 at zero enzyme concentration.

Q is an exponential function of leaf temperature:

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$$Q = e^{k_1 T} \quad (4)$$

where:

e = base of natural logarithm.

k_1 = coefficient in $\text{mg CO}_2 \cdot \text{dm}^{-2} \cdot \text{hr}^{-1} \cdot ^\circ\text{C}^{-1}$

T = leaf temperature in $^\circ\text{C}$.

For the present study the assumption has been made that leaf temperature is equal to air temperature. This was necessary because no information is yet available on leaf temperatures of the plants on the validation site.

E is also an exponential function of leaf temperature:

$$E = k_2 - e^{k_3 T} \quad (5)$$

where:

k_2 = dimensionless coefficient related to maximum enzyme activity.

k_3 = coefficient in $^\circ\text{C}^{-1}$.

Substituting equations (3) and (4) into equation (2) gives:

$$R = e^{k_1 T} (k_2 - e^{k_3 T}) \quad (6)$$

S is a function of the CO_2 concentration gradient from the ambient air to the chloroplast and of the resistances to CO_2 flux from the ambient air to the chloroplasts. Since the grasses involved in this study have a C-4 carbon fixation pathway they exhibit no photorespiration and the CO_2 concentration at the chloroplast can be assumed to be zero.

$$S = \frac{[\text{CO}_2]_a - [\text{CO}_2]_c}{K r_t} = \frac{[\text{CO}_2]_a}{K r_t} \quad (7)$$

where:

$[\text{CO}_2]_a$ = CO_2 concentration of the ambient air in $\text{mg} \cdot \text{dm}^{-3}$.

$[\text{CO}_2]_c$ = CO_2 concentration at the chloroplast in $\text{mg} \cdot \text{dm}^{-3} = 0$.

K = scaling coefficient to make S a relative number from 1 to 0 in $\text{mg CO}_2 \cdot \text{dm}^{-2} \cdot \text{hr}^{-1}$.

r_t = total resistance to CO_2 flux from the ambient air to the chloroplast in $\text{hr} \cdot \text{dm}^{-1}$.

The total resistance to CO_2 flux from the ambient air to the chloroplast is assumed to have two components in series. One of these is assumed to be dependent upon the

irradiance at the leaf surface. The other is assumed to be a function of the leaf water potential. Since data are not available on the variation in leaf water potential it is assumed to be generally equivalent to the soil water potential.

Therefore:

$$r_t = r_I + r_\psi \quad (8)$$

where:

r_I = irradiance-dependent resistance to CO_2 flux in $\text{hr} \cdot \text{dm}^{-1}$.

r_ψ = soil water potential-dependent resistance to CO_2 flux in $\text{hr} \cdot \text{dm}^{-1}$.

Substituting equation (8) in equation (7) gives:

$$S = \frac{[\text{CO}_2]_a}{K(r_I + r_\psi)} \quad (9)$$

Data in the literature indicate that r_I should be a hyperbolic function of the irradiance (see, for example, Turner and Begg, 1972).

Thus:

$$r_I = k_4 \frac{1}{I} \quad (10)$$

where:

k_4 = coefficient in $\text{watts} \cdot \text{m}^{-2} \cdot \text{hr} \cdot \text{dm}^{-1}$.

I = irradiance in $\text{watts} \cdot \text{m}^{-2}$ in the wavelengths between 400 and 700 nm.

Although not much data appear in the literature it seems reasonable to assume that r_ψ is an exponential function of soil water potential. This function should be minimal at zero soil water potential and reach some maximum value at some lower soil water potential. This relationship can be described by:

$$r_\psi = k_5 - e^{k_6(k_7 + \psi)} \cdot 1 \text{ dm} \cdot \text{hr}^{-1} \quad (11)$$

where:

k_5 = dimensionless coefficient

k_6 = coefficient in bar^{-1}

k_7 = coefficient in bars

ψ = soil water potential in bars

Substituting equations (10) and (11) into equation (9) gives:

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$$S = \frac{[CO_2]_a}{K \left[k_4 \frac{1}{1} + [k_5 - e^{k_6(k_7 + \psi)}] \right]} \quad (12)$$

Table 1. Values of model coefficients estimated by the non-linear regression analysis

	<i>Panicum obtusum</i>	<i>Hilaria mutica</i>
K	13.9732	23.3083
k ₁	0.115361	0.136288
k ₂	1.89578	1.88255
k ₃	0.0143206	0.0149059
k ₄	45.8484	34.4111
k ₅	15.0759	15.0599
k ₆	0.0541470	0.0542243
k ₇	50.00	50.00

Further substituting equations (6) and (12) into equation (2) gives:

$$\phi = \frac{[CO_2]_a}{K \left[k_4 \frac{1}{1} + [k_5 - e^{k_6(k_7 - \psi)}] \right]} R \cdot e^{k_1 T} (k_2 - e^{k_3 T}) \quad (13)$$

METHODS

Rates of net CO₂ exchange were measured as previously described (Cunningham and Balding, 1972). Rates were measured on both *Hilaria mutica* and *Panicum obtusum* under various combinations of levels of the three environmental variables in the model. The values of the coefficients in equation (13) were found by using the equation as a multiple non-linear regression model and determining the values for the coefficients which give the best fit to the measured CO₂ exchange rate data. This was done using an algorithm proposed by Marquardt (1970). Special thanks are due to Dr. N. Scott Urquhardt, Department of Experimental Statistics, New Mexico State University, for making an APL program for the non-linear regression available to us.

RESULTS AND DISCUSSION

The model accounted for 83% of the variability in the *P. obtusum* CO₂ exchange data and 89% of the variability in the *H. mutica* data. The predicted values for the coefficients are given in Table 1. The F values indicate the equation and predicted values of the coefficients provide a significant fit to the data at the 0.001 level of probability. T statistics indicate slopes given by all coefficients are very significantly different from zero.

The model not only allows prediction of rates of net CO₂ exchange as a function of the environmental variables, but also allows comparisons of effects of each variable. Figure 1 shows the response of net CO₂ exchange rate to temperature assuming an ambient CO₂ concentration of 315 ppm and no resistances to CO₂ flux to the chloroplasts. The temperature responses of the two species are generally the same. *Hilaria* has a higher non-CO₂-limited rate of net CO₂ exchange. The optimum temperatures are about the same for both species and relatively high as expected in C-4 species.

The effect of irradiance on resistance to CO₂ flux can be seen in Figure 2. The shapes of the curves are generally the same for both species. *Panicum obtusum*, however, has a higher light-dependent resistance.

The soil water potential-dependent resistance of *Panicum obtusum* varies from 0 to 1 hr · dm⁻¹ (Fig. 3). Although the curves for both species have the same shape the soil water potential-dependent resistance of *Hilaria mutica* varies only from 0.6 to 0.643 hr · dm⁻¹. This clearly indicates that changes in soil water potential will have much less of an effect on the net CO₂ exchange rate of *Hilaria mutica*. In this regard it is interesting to note that *Hilaria mutica* occupies the more xeric sites on the playa.

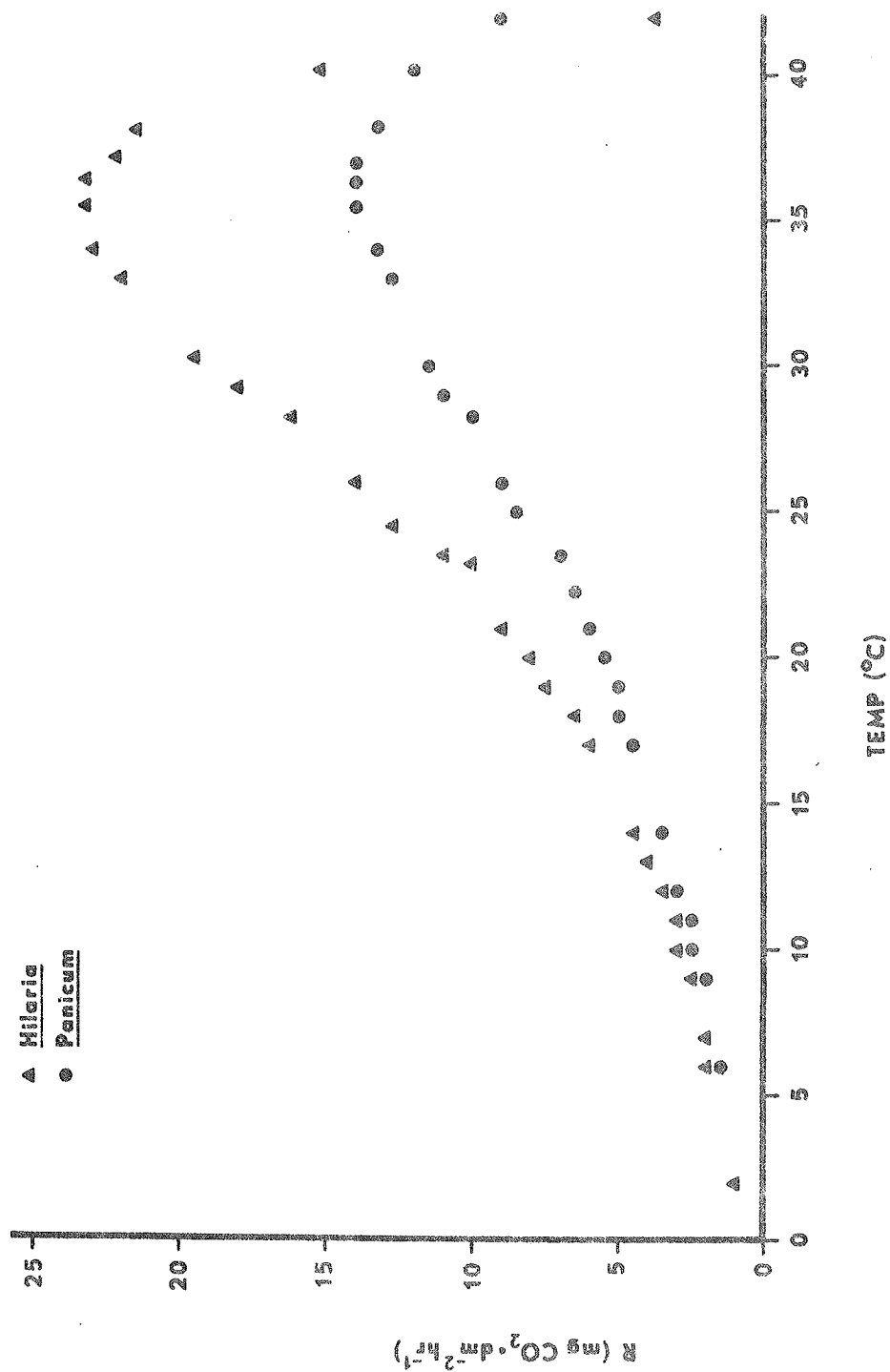


Figure 1. Response of net CO₂ exchange rate (R) to temperature assuming an ambient CO₂ concentration of 315 ppm and no resistances to CO₂ flux to the chloroplast for *Panicum obtusum* and *Hilaria mutica*.

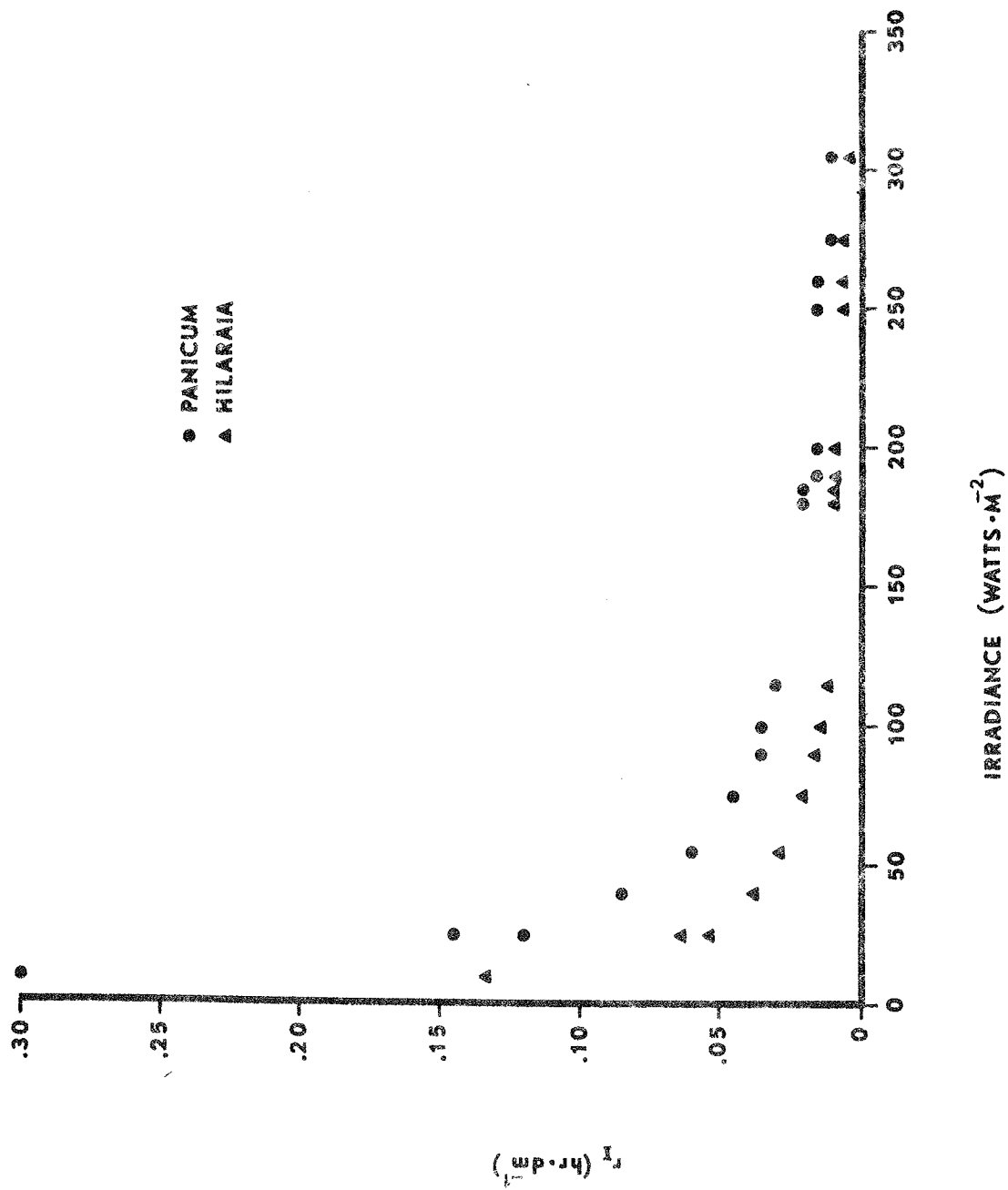


Figure 2. The effect of irradiance (PAR) on resistance to CO₂ flux in *Panicum Obtusum* and *Hilaria mutica*.

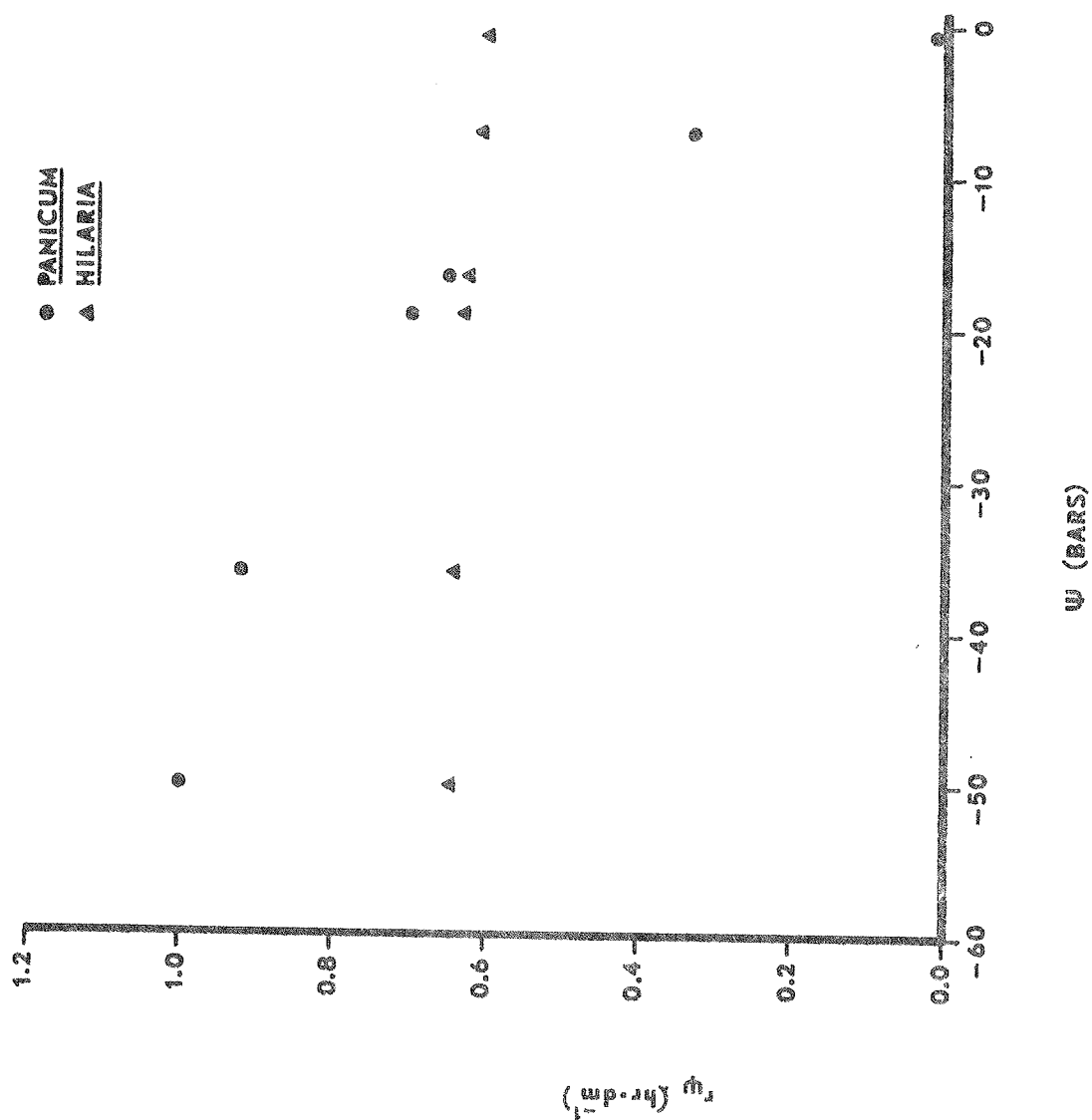


Figure 3. The effect of soil water potential (ψ soil) on resistance to CO₂ flux in *Panicum obtusum* and *Hilaria mutica*.

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1972 PROGRESS REPORT

GROWTH AND DEVELOPMENT OF *Sitanion hystrix* AND *Poa sandbergii*

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Research Memorandum, RM 73-16

MAY 1973

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A B S T R A C T

Poa sandbergii seedlings produced more root biomass when grown in soil maintained at 15 C, but produced less shoot biomass. Poorest root development and lowest root:shoot ratios were obtained by seedlings grown in 32 C soil.

CO₂ compensation point of *Poa sandbergii* in relation to plant water stress was about -25 bars. The compensation point for *Sitanion hystrix* was near -35 bars. *Poa* development was found to be controlled by photoperiod. Long daylength (18 hours) induced dormancy and short daylength (12 hours) promoted growth. The critical daylength period was not determined.

Growth and development rates of *Poa sandbergii* from communities supporting *Sitanion hystrix* var. *hystrix* and var. *californicum* indicate that the later-developing "ecotype" is related to the distribution of var. *hystrix*.

INTRODUCTION

Poa sandbergii and *Sitanion hystrix* are perennial grasses that occur in varying amounts in most sagebrush-grass and other cold-desert plant communities. *Poa* is primarily a constituent of climax sagebrush communities but persists in deteriorated communities that have been highly disturbed. Recently-abandoned cultivated lands are exceptions, however.

Sitanion hystrix is a seral species and is one of the first perennial grasses to re-establish by seed as secondary succession progresses. In sagebrush vegetation *Sitanion*, being a short-lived perennial, is gradually replaced by long-lived climax grasses, such as *Agropyron spicatum*, *Stipa thurberiana* and *Festuca idahoensis*. *Sitanion*'s status in shade-scale vegetation is unclear, but it is suspected that it may be climax and co-dominant with *Oryzopsis hymenoides*.

Both *Poa sandbergii* and *Sitanion hystrix* have broad ecological amplitudes. Only recently has *Sitanion hystrix* been recognized as being composed of at least two varieties, var. *hystrix* and var. *californicum* (Wilson, 1963). The general distribution of the two varieties differs. Var. *californicum* occurs in mesic sagebrush communities, whereas var. *hystrix* occurs in the shade-scale and xeric portion of the sagebrush zone.

Poa sandbergii has not been taxonomically divided although its distribution is as extensive as *Sitanion hystrix*. Because it was suggested that the *Poa sandbergii* which occurs in the same communities as *Sitanion hystrix* var. *hystrix* was different from the *Poa* in communities supporting var. *californicum*, two sources of *Poa sandbergii* were included in the study. The Crane Creek source represents *Poa sandbergii* from a mesic habitat and grows in the same communities as *Sitanion hystrix* var. *californicum*. *Poa sandbergii* from Saylor Creek represents the xeric form and grows in the same communities as var. *hystrix*.

This year's report emphasizes the research findings on *Poa sandbergii*, whereas last year's research concentrated on *Sitanion hystrix*.

OBJECTIVES

Objectives of study were basically the same for the two species. In most cases, results for *Sitanion hystrix* were reported previously (Hironaka and Tisdale, 1972). Additional information on *Sitanion* is included in this report.

The objectives were to study:

1. Growth and development of seedlings as affected by soil temperature.
2. Growth and development of vegetative growth as a function of soil moisture, plant water stress and photosynthesis.
3. Growth and development of the root system as a function of soil moisture.
4. Transpiration rate in relation to plant growth and moisture stress.
5. Carbohydrate root reserve in relation to plant growth.

Soil moisture determinations were not made in 1972.

METHODS

Seedling development in relation to soil temperature (DSCODE A3UHH03) was determined by growing seedlings in 200 cc containers placed in constant temperature baths maintained at 5, 15, 20, and 32 C. Seedlings were grown for 2 weeks in the greenhouse before being moved to water baths. Light source was provided by gro-lux fluorescent lights with an intensity of 1000 ft. candles. Daylength was 12 hours. At weekly intervals six seedlings from each treatment were monitored for CO₂ exchange rates in a closed system for 30 minutes. Leaf area determination was made with a photocell planimeter. Plant material was oven-dried at 70 C.

Field studies were conducted at the Saylor Creek Experimental Range (U.S. Forest Service) in southwest Idaho. The annual precipitation averages about 20 cm in the experimental area. Plants were grown in 10 x 600 cm tubes planted "flush" with the soil surface. Plant material was obtained from naturally occurring summer dormant *Poa* that were brought to the greenhouse in late September and divided into 2.0 - 2.5 cm squares and planted in small containers. These plants were permitted to "green up" and a month later they were transplanted to the field. *Poa* materials were from Saylor Creek (20 cm precipitation area) and Crane Creek (40 cm precipitation area). The first observation was made on March 28 and subsequently at periodic intervals throughout the growing season. Water in addition to which the area received naturally as rainfall was added periodically. At each sampling period 1/3 of the plants received no additional water; 1/3 received 1.0 cm and the remaining 1/3 of the plants received 2.0 cm of water at each of six visits. This amounted to 0 additional water, 4 cm of added water and 8 cm of added water for the season.

Carbon dioxide exchange rates (DSCODE A3UHH04) were monitored with a Beckman infra-red gas analyzer connected in a closed system. The entire tube with plant was extracted from the field and placed in a close-fitting, metal cylinder. A water-cooled plexiglass chamber was attached to the top of the metal cylinder and sealed. Transpiration measurements were made in an open system with a dewpoint hygrometer.

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Later in the season, plant water stress determinations were made with a sample chamber psychrometer. After gas exchange and transpiration measurements were obtained, a green leaf blade was cut into short segments and placed in the sample chamber. An equilibrium period of 15 minutes before measurement was observed.

Carbohydrate root reserve determinations were made from root and crown material of plants from which gas exchange measurements were made. Total nonstructural carbohydrate (TNC) was determined by the procedure outlined by Smith (1969).

RESULTS

Poa sandbergii

The growth of *Poa* seedlings in relation to soil temperature (DSCODE A3UHH03) demonstrated that higher root:shoot ratios were obtained when seedlings were grown in soil with temperatures maintained below 32 C (Table 1). *Poa* produced the most shoot biomass when grown in soil maintained at 20 C whereas root biomass tended to be greater for plants grown in 15 C soil. Higher root:shoot ratios were obtained at 15 C soil temperature than other temperatures tested. Plants grown in 32 C soil produced more top growth than those grown at lower temperatures but produced the least amount of root material. The cooler soil temperatures favored root development over shoot development.

Net photosynthesis rates as determined by measurement of CO₂ exchange were erratic and difficult to interpret (Table 1). In general, plants grown in soil of 32 C consistently showed negative net photosynthesis. This may be partially due to high water stress. Plants were watered whenever they appeared to be under stress. They were not watered prior to sampling, however. Plants in the 32 C bath required watering nearly daily because of high evaporation and transpiration. Unfortunately, plant water stress measurements were not obtained to test the hypothesis of the effect of plant water stress on seedlings in relation to photosynthesis. The relatively low net CO₂ exchange during photosynthesis may be partially attributed to the low light intensity of 1000 ft. candles.

Dark respiration CO₂ exchange measurements (Table 1) showed a decline in CO₂ release per unit leaf area as the seedling developed. Plants grown in 32 C soil showed the highest dark respiration rates, whereas the other plants showed no marked trend in response in relation to seedling age.

In the field, differences in growth and development characteristics of *Poa sandbergii* from two distinct habitats and grown in the same environment were obscured by the great variation of individual plants in this experiment (DSCODE A3UHH04). The effects of additional water on *Poa* from the two sources were masked and no detectible trend was noted (Fig. 1 and Fig. 2).

Table 1. Averages of leaf area, shoot weight, root weight, root:shoot ratios, CO₂ exchange rate measurements and tiller numbers of *Poa sandbergii* seedlings grown under conditions of constant soil temperature for 39 days DSCODE—A3UHH03

Soil Temperature C°	Days of Growth					
	0 Day	11 Days	17 Days	24 Days	31 Days	39 Days
Leaf Area (cm ²)						
5°	1.7	2.6	2.9	3.9	4.3	4.3
15°	1.7	3.6	4.0	5.7	6.2	6.0
20°	1.7	3.0	6.2	5.0	7.8	8.1
32°	1.7	2.5	4.0	5.5	6.3	8.5
Shoot Weight (mg)						
5°	4	9	9	15	17	25
15°	4	11	13	23	26	29
20°	4	10	24	22	35	43
32°	4	8	13	21	26	40
Root Weight (mg)						
5°	3	17	20	37	52	79
15°	3	26	30	53	73	90
20°	3	14	41	43	70	57
32°	3	9	17	26	41	45
Root:Shoot Ratios						
5°	.65	1.92	2.56	2.43	3.14	3.31
15°	.65	2.55	2.41	2.42	3.14	3.31
20°	.65	1.45	1.64	2.05	2.09	2.17
32°	.65	1.02	1.40	1.20	1.63	1.18
Tiller Numbers						
5°	1.3	3.0	2.3	3.3	3.7	4.5
15°	1.3	3.0	3.2	4.7	5.7	5.8
20°	1.3	3.0	4.7	4.5	7.0	7.8
32°	1.3	2.8	3.8	4.8	8.0	7.3
Net Photosynthesis (mg CO ₂ /dcm ² /hr)						
5°	---	---	.29	.68	.17	.13
15°	---	---	-.32	.43	.02	-.17
20°	---	---	-.01	.42	.37	.86
32°	---	---	-.98	-.15	-.25	-.33
Dark Respiration (mg CO ₂ /dcm ² /hr)						
5°	---	---	15.15	7.17	9.16	8.19
15°	---	---	12.03	6.93	7.91	6.89
20°	---	---	8.00	9.61	6.37	8.02
32°	---	---	16.04	11.07	12.37	9.33

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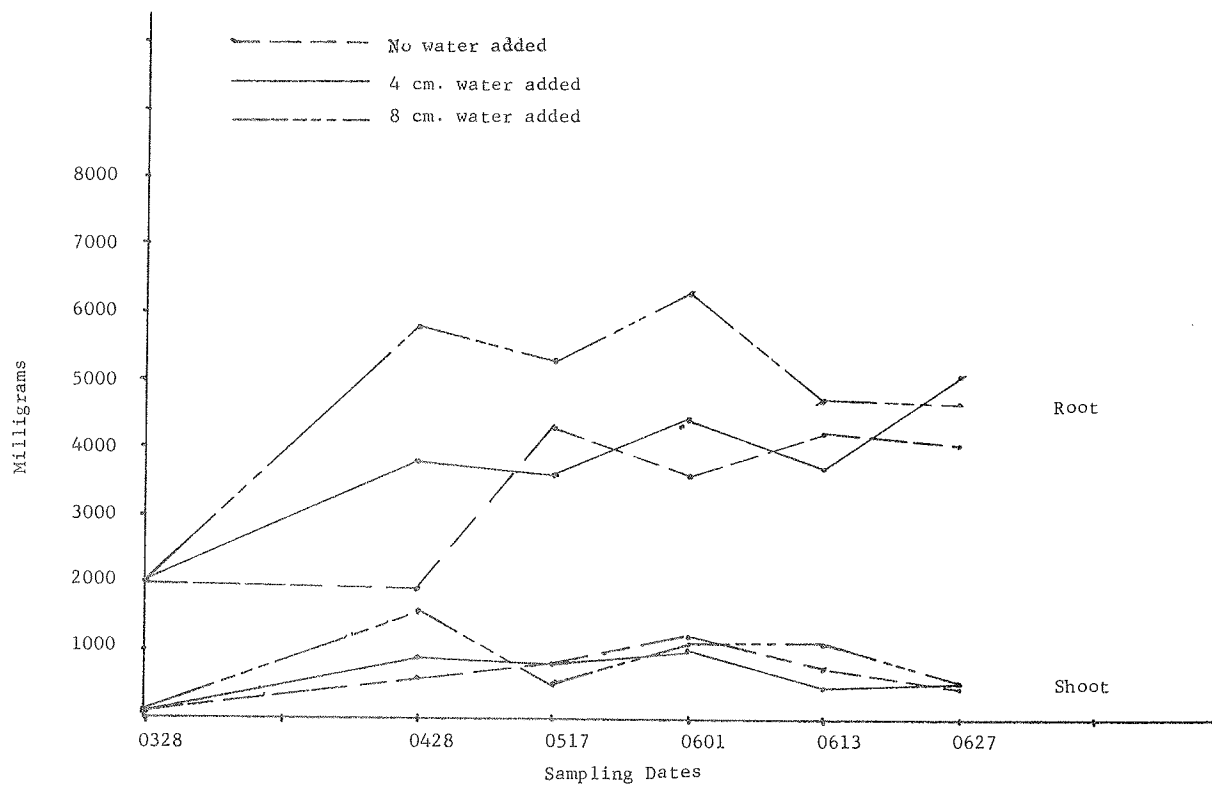


Figure 1. Averages of shoot and root biomass of Saylor Creek *Poa sandbergii* during the 1972 growing season (DSCODE A3UHH04).

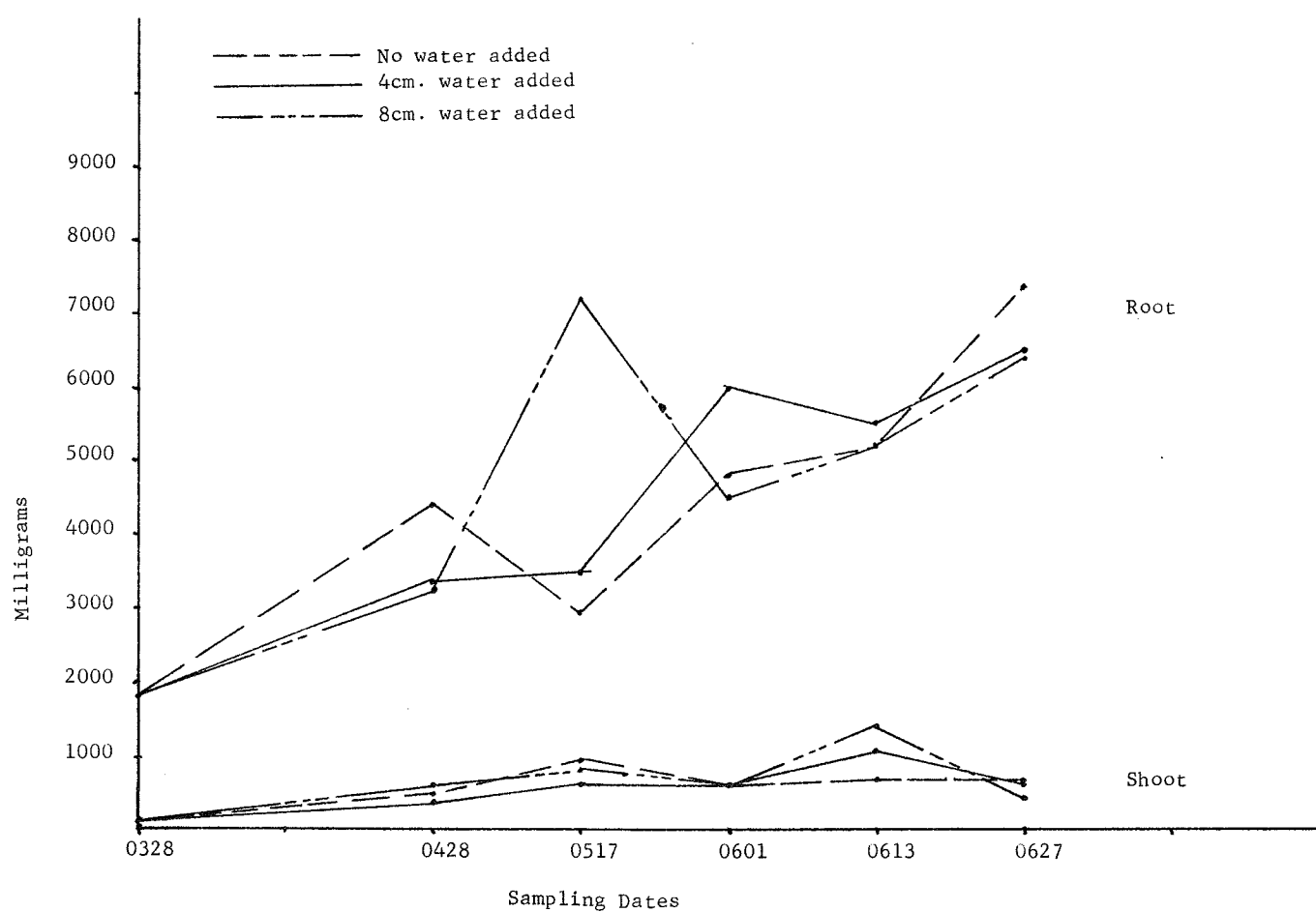


Figure 2. Averages of shoot and root biomass of Crane Creek *Poa sandbergii* during the 1972 growing season (DSCODE A3UHH04).

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Comparison of *Poa* between the two sources showed that the Crane Creek plants produced greater root biomass than plants from Saylor Creek (Fig. 3). Root:shoot ratios of the Crane Creek plants tended to be higher, also (Fig. 4). The Crane Creek *Poa* was slower to develop and attained the seedhead stage 1-2 weeks later than the Saylor Creek plants. The Saylor Creek *Poa* had reached the seedhead stage during the subsequent 2 weeks. By June 27, the Saylor Creek plants had cured and were summer dormant while the *Poa* from Crane Creek had cast its seeds but still retained some green leaves and culms.

The monitoring of CO_2 exchange rates yielded data that were difficult to interpret. *Poa* from both sources responded similarly when positive net photosynthesis was indicated, i.e. the rates were low (Tables 2 and 3). An average of nearly $4 \text{ mg CO}_2/\text{dcm}^2/\text{hr}$ was the highest rate attained (from 9 individuals) for any single day. The response was erratic; some indicated positive net photosynthesis while others indicated negative rates.

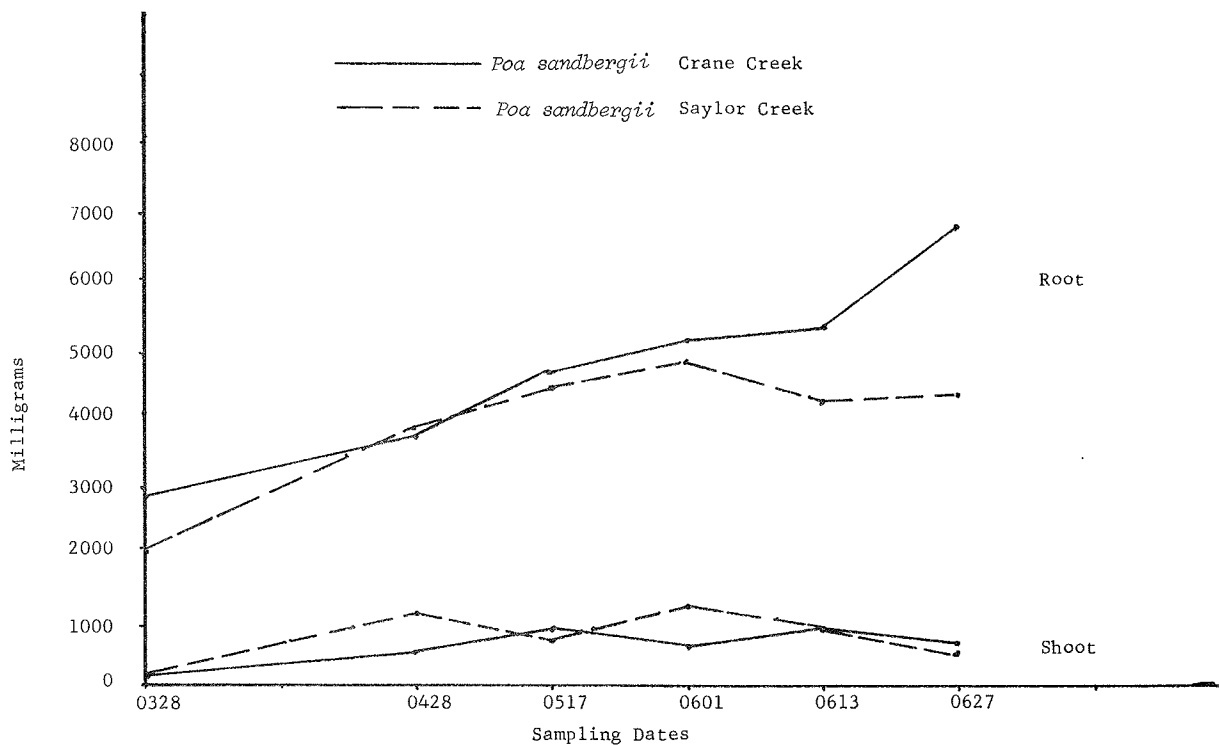


Figure 3. Averages of shoot and root weights of *Poa sandbergii* from Crane Creek and Saylor Creek sources during the 1972 growing season (DSCODE A3UHH04).

Table 2. Average CO₂ exchange and transpiration rates of Saylor Creek *Poa sandbergii* in 1972 DSCODE—A3UHH04

Date	Photo. mg CO ₂ /dcm ² /hr	Resp. mg CO ₂ /dcm ² /hr	Transp.* mg H ₂ O/dcm ² /hr	Transp.** mg H ₂ O/g/hr
3/28	3.68	33.80	3837	4546
4/28	-5.06	26.18	1715	979
5/17	2.91	20.45	1147	1196
6/01	-1.12	12.55	----	----
6/13	-24.62	26.07	1525	267
6/27	----	----	----	----

*Based on green leaf area

**Based on total shoot weight

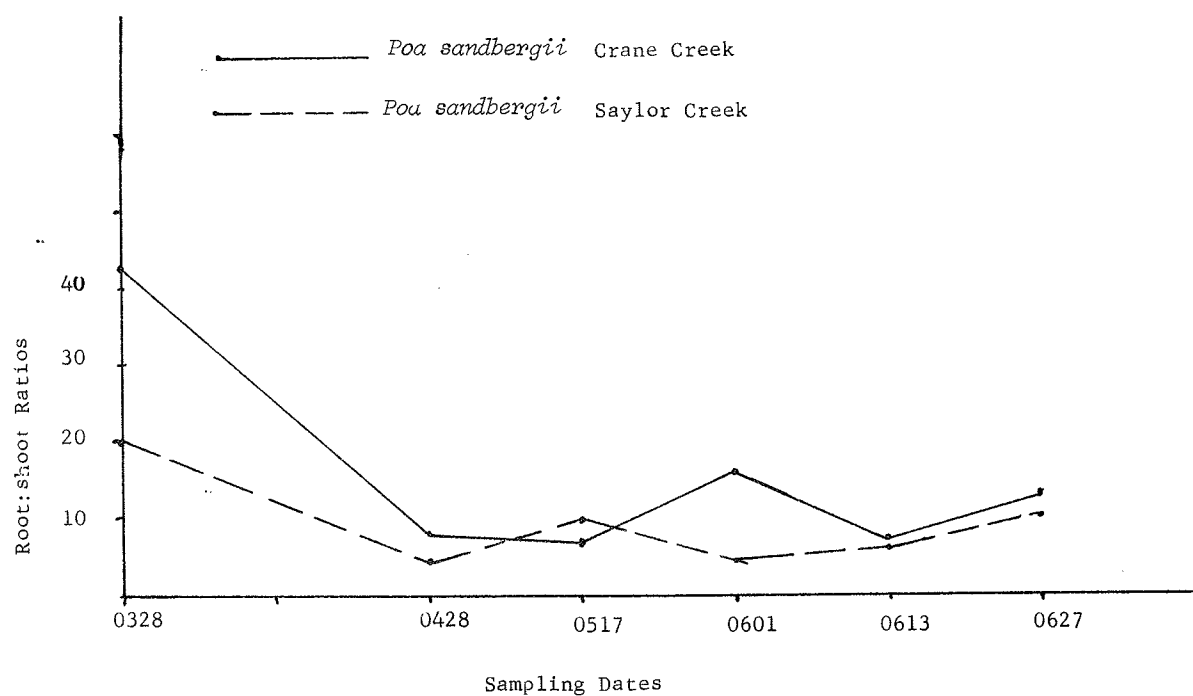


Figure 4. Averages of root:shoot ratios of *Poa sandbergii* from Crane Creek and Saylor Creek sources during the 1972 growing season (DSCODE A3UHH04).

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Table 3. Average CO₂ exchange and transpiration rates of Crane Creek *Poa sandbergii* in 1972 DSCODE—A3UHH04

Date	Photo. mg CO ₂ /dcm ² /hr	Resp. mg CO ₂ /dcm ² /hr	Transp.* mg H ₂ O/dcm ² /hr	Transp.** mg H ₂ O/g/hr
3/28	-0.42	25.54	2731	6620
4/28	2.60	24.07	1415	1126
5/17	0.81	16.39	794	446
6/01	-0.98	14.29	----	----
6/13	-4.21	11.56	949	427
6/27	-13.37	16.97	1788	360

*Based on green leaf area

**Based on total shoot weight

In late March and April, occurrence of morning frost was common and affected the plants. Plants that showed visible effects of frost from the previous night often indicated reduced or negative net photosynthesis. The duration of the effects of frost damage on net photosynthesis was not determined.

The relation between plant water stress and net photosynthesis rate of *Poa* indicated that the CO₂ compensation level was near -25 bars, at least for plants in the late development stages (Fig. 5). It was observed that reduced or negative photosynthetic rate could be reversed by increasing the CO₂ concentration level, however. The effects of plant water stress in the range of 0 to -20 bars stress were not monitored so the maximum net photosynthetic rate in relation to plant water stress was not ascertained for *Poa sandbergii* under field conditions.

Transpiration rates based on green leaf area (Tables 3 and 4) showed a bimodal response. During early spring rates were high and as development and growth progressed transpiration sharply declined. A second high was recorded as plants approached dormancy and green leaf area was greatly reduced. A similar response was observed for *Sitanion hystrix* the previous year. On the basis of total shoot biomass, transpiration rates decreased as the season progressed and very low rates were recorded as plants became dormant.

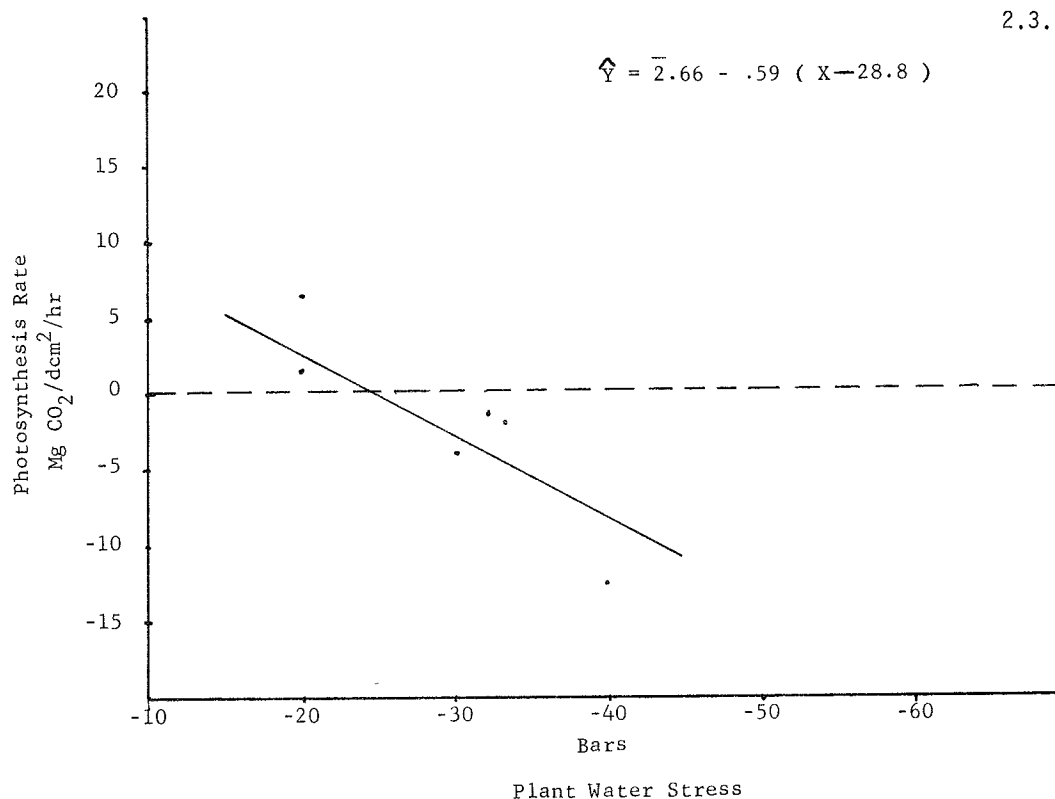


Figure 5. Relationship between net photosynthetic rates and plant water stress of *Poa sandbergii* during the 1972 growing season (DSCODE A3UHH04).

Table 4. Average CO₂ exchange and transpiration rates of 2nd season *Sitanion hystrix* var. *hystrix* DSCODE—A3UHH04

Date	Photo. mg CO ₂ /dcm ² /hr	Resp. mg CO ₂ /dcm ² /hr	Transp.* mg H ₂ O/dcm ² /hr	Transp.** mg H ₂ O/g/hr
4/28	2.07	8.0	----	----
5/17	9.36	9.0	----	----
6/01	-1.52	23.0	567	217
6/13	4.82	----	----	----
6/27	-19.67	30.0	----	453
7/11			CURED	

*Based on green leaf area

**Based on total shoot weight

2.3.1.9.-12

Sitanion hystrix

Measurements were made on second season *Sitanion* plants. Due to limited number, it was not possible to stratify for uniformity and much variability was encountered. In general, var. *californicum* produced larger plants than var. *hystrix* (Fig. 6). This was observed with the first season plants also. The root:shoot ratios for var. *hystrix* were higher than for var. *californicum* (Fig. 7) but were not greatly different from those during the first season (Hironaka and Tisdale, 1972).

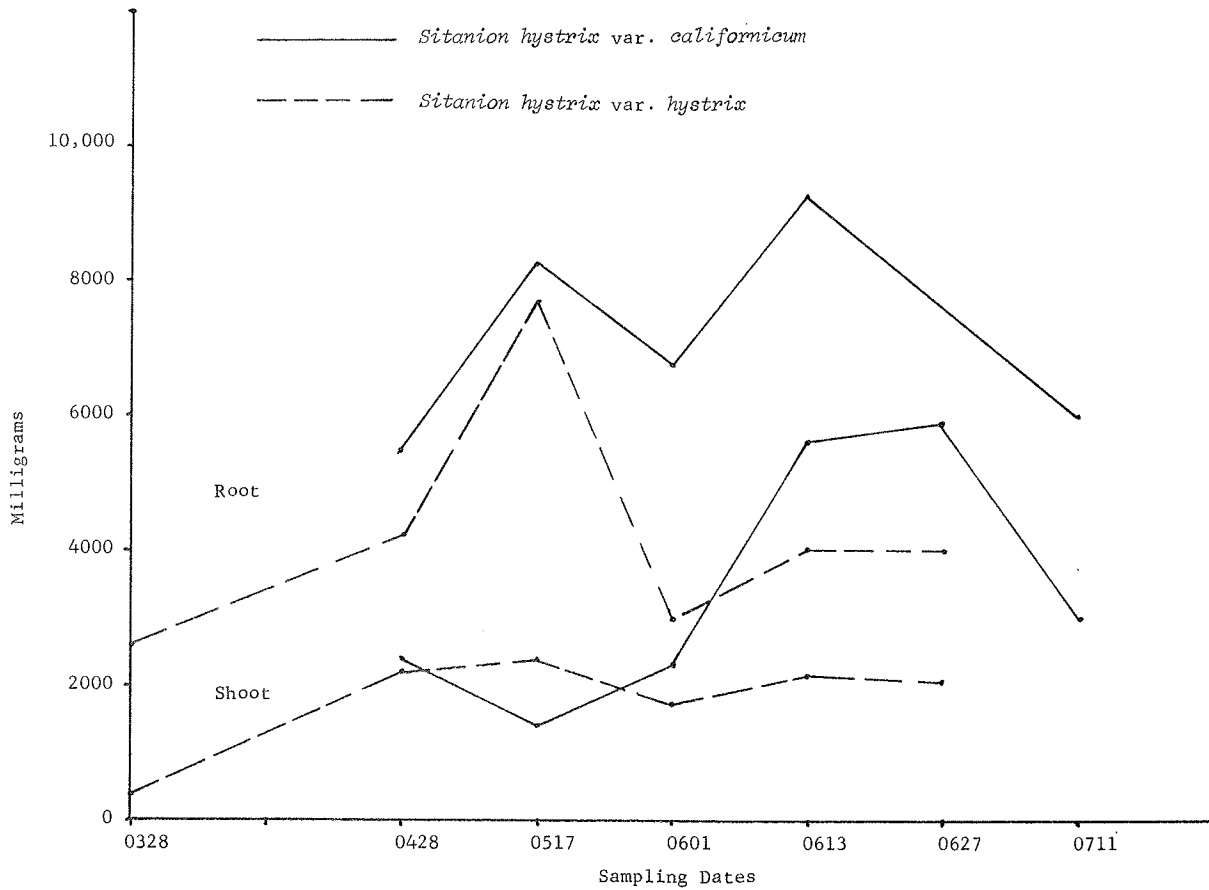


Figure 6. Averages of shoot and root weights of *Sitanion hystrix* var. *hystrix* and var. *californicum* during the second growing season (1972) (DSCODE A3UHH04).

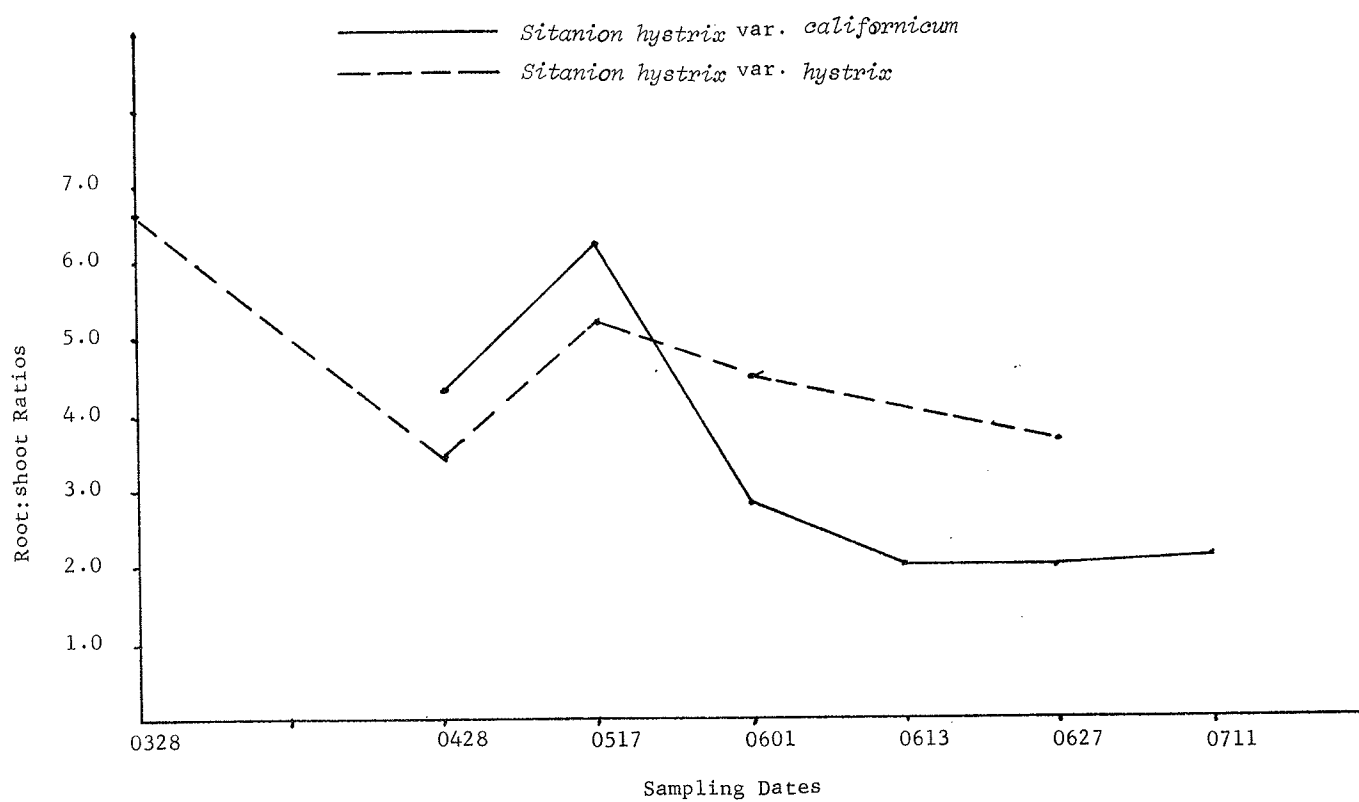


Figure 7. Averages of root:shoot ratios of *Sitanion hystrix* var. *hystrix* and var. *californicum* during the second growing season (1972) (DSCODE A3UHH04).

2.3.1.9.-14

The net photosynthetic rates in 1972 did not attain the high rates obtained in 1971 when the plants were in their first season. In 1971, the maximum average measured was about 14 mg CO₂ fixed per dcm² per hour while in 1972 the maximum reading was less than 10 mg CO₂ (Tables 4 and 5).

Table 5. Average CO₂ exchange and transpiration rates of 2nd year *Sitanion hystrix* var. *californicum* in 1972 DSCODE—A3UHH04

Date	Photo. mg CO ₂ /dcm ² /hr	Resp. mg CO ₂ /dcm ² /hr	Transp.* mg H ₂ O/dcm ² /hr	Transp.** mg H ₂ O/g/hr
4/28	1.64	21.88	----	----
5/17	7.69	11.40	589	304
6/01	8.19	12.18	----	----
6/13	-2.41	8.50	1223	94
6/27	-10.25	15.92	924	84
7/11	-4.35	11.06	1294	121

*Based on green leaf area

**Based on total shoot weight

Var. *hystrix* showed its characteristic early development by as much as 2 weeks. Maximum photosynthetic activity occurred during the latter part of April for var. *hystrix*, whereas for var. *californicum* high activity was recorded two weeks later.

It appeared that the effect of plant water stress on photosynthesis rate was conditioned by the stage of development. Temporary high water stress did not appear to affect photosynthesis rate to the same degree in the early stages as compared to late developmental stages. The CO₂ compensation level in relation to plant water stress was near -35 bars (Fig. 8), which indicated that *Sitanion* can function under considerable plant water stress. When compared to the lower CO₂ compensation point of *Poa sandbergii* (about -25 bars), *Poa* must make its growth early in the spring when moisture is ample, whereas *Sitanion* is able to grow later in the season. This differential growth response is not entirely a function of plant water stress of *Poa sandbergii*. Another controlling factor was disclosed in a growth chamber experiment.

Poa sandbergii from Crane Creek was grown under two daylight periods, 12 and 18 hours. Plants under the short daylength treatment continued to produce vegetative shoots while plants under the 18-hour day went into dormancy. When the treatment was reversed, dormant plants resumed growth under the 12-hour day condition and the green plants went into dormancy within a period of 3 weeks.

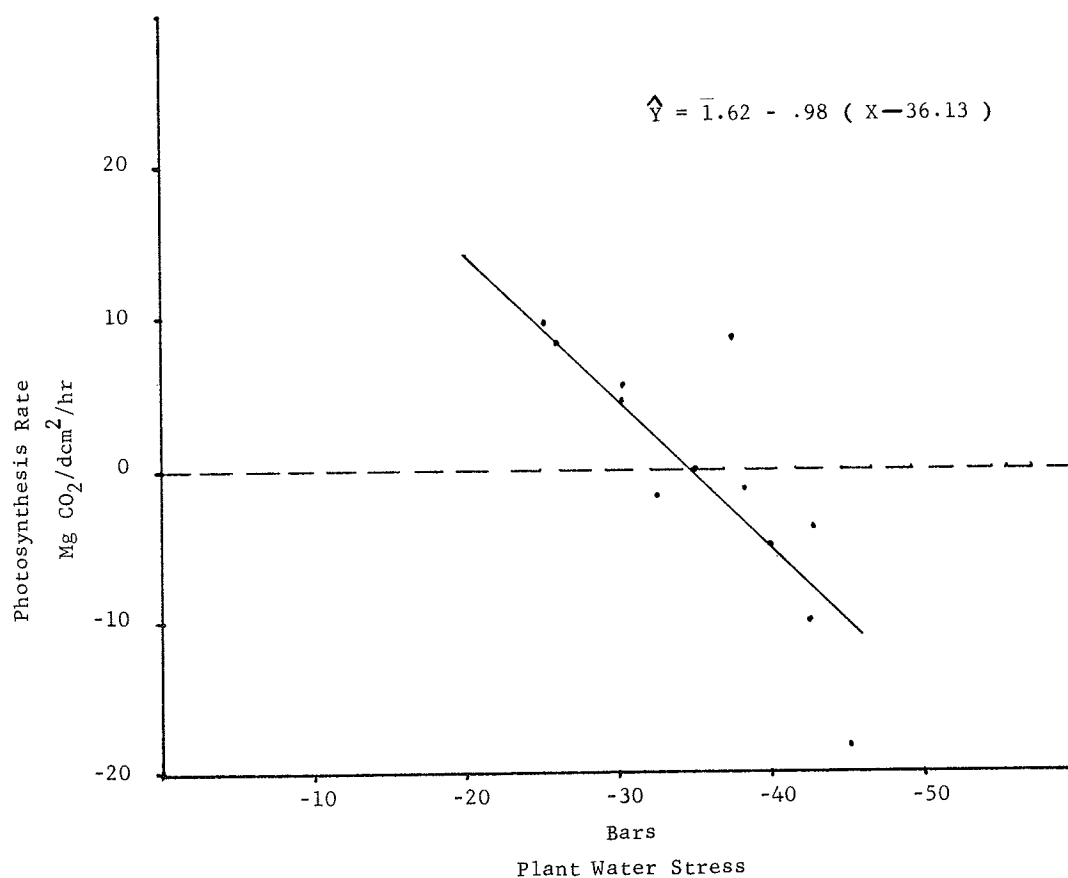


Figure 8. Relationship between net photosynthetic rates and plant water stress of *Sitanion hystrix* during the second season of growth (1972) (DSCODE A3UHH04).

Root carbohydrate reserve status (Table 6) as expressed by total non-carbohydrate (TNC) showed that *Sitanion* tended to accumulate less reserves than reported by Coyne and Cook (1970). *Poa* also indicated a relatively low root reserve accumulation. The TNC data may reflect the results of not stopping enzyme activity immediately after root recovery, however.

Table 6. Average total non-structural carbohydrate percentages (TNC%) of root crown of *Poa sandbergii* and *Sitanion hystrix* in 1972 DSCODE—A3UHH04

Date	<i>Poa sandbergii</i>		<i>Sitanion hystrix</i>	
	Saylor Creek	Crane Creek	v. <i>hystrix</i>	v. <i>californicum</i>
	TNC%			
3/28	----	3.8	----	----
4/28	5.9	7.6	7.5	4.8
5/17	10.9	7.8	11.2	5.2
6/01	6.9	8.0	5.1	6.4
6/13	8.1	6.0	10.3	9.0
6/27	8.5	7.7	8.3	8.7
7/11	----	----	----	9.4

DISCUSSION

Although plant growth and development of individuals of the two sources of *Poa sandbergii* included in this study were highly variable, the Crane Creek plants tended to produce more biomass but were slower in development than those from Saylor Creek. This supports the hypothesis that the slower-developing race of *Poa sandbergii* from Crane Creek tended to occur in similar habitats as *Sitanion hystrix* var. *californicum*. Whereas, the distribution of the early-developing race of *Poa sandbergii*, as represented by plants from Saylor Creek, tends to co-habit with *Sitanion hystrix* var. *hystrix*.

The reasons for the relatively low rates of net photosynthesis obtained for *Poa sandbergii* can only be speculated because of inadequate frequency of sampling during the rapid growth period. This period occurred while moisture was ample and temperatures were cool to moderate. It appeared that plant water stress affects rate of CO₂ exchange to a greater degree than most other species of the cold desert. The level of plant water stress at which depression in net photosynthetic rate was induced was not determined but the CO₂ compensation point occurred at a lower stress level for *Poa sandbergii* than for *Sitanion hystrix*. Furthermore, it was found that daylength governed plant development in *Poa sandbergii*. Long daylength induced dormancy, whereas short daylength promoted growth. The factors of light intensity and quality were not investigated.

Further research is recommended to ascertain the interactions of plant water stress, CO₂ exchange rates, plant development and daylength on the growth and development of *Poa sandbergii*.

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1972 PROGRESS REPORT

ROLE OF ANNUAL GRASSES AND SHRUBS IN NUTRIENT CYCLING
OF GREAT BASIN PLANT COMMUNITIES

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Research Memorandum, RM 73-17

MAY 1973

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Report Volume 3

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A B S T R A C T

High seasonal precipitation is the triggering mechanism for explosive population increases by winter annuals in semi-arid plant communities. It has been suggested that such increases in biomass tie up a considerable portion of the community nutrient capital and may limit growth of associated perennials and subsequent annual growth potential.

Investigation centered on the nutrient cycling patterns within an annual grass-sagebrush (*Bromus tectorum* -- *Artemisia tridentata*) plant community of the Great Basin in northern Utah. The effect of added precipitation during the spring growth period on *B. tectorum* productivity was studied in relation to shrub canopy cover, soil nitrogen and water content, shrub productivity and competition from other associated annual grasses (mainly *B. japonicus*). Six 10 x 10 m study plots were established on a homogeneous sagebrush-annual grass plant community situated 33 kilometers west of Logan, Utah, on the benchlands of the Wasatch Front. Three plots were irrigated during April and May. Bromegrass and soil samples were collected throughout the spring and summer from both shrub understory and interspace habitats. Shrub stem samples were collected during the study period to assess biomass and nutrient changes in perennial cycles.

After treatment, irrigated plots had significantly greater bromegrass biomass in both habitats than did control plots (300 vs 215 g/m² in the understory and 90 vs 50 g/m² in the interspace). Regardless of treatment, *B. tectorum* productivity was significantly greater than that of *B. japonicus* in the understory but not in the interspace (175 vs 135 g/m² in irrigated understory and 135 vs 80 g/m² in control understory). The *B. tectorum* competitive advantage is attributed to rapid nitrogen uptake and subsequent root growth which permits more efficient utilization of available soil moisture. In all cases bromegrass productivity was greater in the understory than in the interspace. This phenomenon is attributed to the germination "safe site" concept.

A supplementary report will discuss the results of the analysis of shrub stem biomass and nitrogen content, bromegrass nitrogen content, and soil water and nitrogen content data.

INTRODUCTION

Emphasis in the first year of study (1971) was to develop methods of procedure which would provide the needed data sets for an understanding of the nutrient cycling patterns of the cheatgrass-sagebrush (*Bromus tectorum* L. -- *Artemisia tridentata* Nutt.) community in northern Utah. Sampling methods for biomass and nitrogen content analysis of ecosystem components were refined, while initial data provided information on the variability of parameters and the degree of future sampling intensity required. This year (1972) a detailed study of the nitrogen relationships between cheatgrass (BROTEC) and big sagebrush (ARTTRI) was conducted. At this time it is appropriate to review the literature concerning the impact of BROTEC on desert ecosystems so as to gain a broad perspective in assessing the study undertaken in this research effort.

BROTEC was introduced to the North American continent from Europe in the middle of the nineteenth century. It made its first appearance in the western states at the turn of the century and has rapidly spread throughout the Great Basin and Columbia River Basin regions of the West (Klemmedson and Smith, 1964).

The most probable causes of this invasion were the practices of the early settlers. Overgrazing and indiscriminate burning led to the retrogression of the Palouse grassland climax and the resultant dominance of ARTTRI and BROTEC (Stoddart, 1941). Hull and Pechanec (1947) reported that the invasion of BROTEC was so complete in southern Idaho that it is now considered an important forage plant in that area. Similar findings have been reported for Utah (Pickford, 1932), Nevada (Fleming et al., 1942) and Oregon (Platt and Jackman, 1946), with the greatest problem area being Idaho (Stewart and Hull, 1949; Tisdale et al., 1969).

The semi-arid climate of the Great Basin greatly affects the annual productivity of BROTEC due to the extreme variation in annual rainfall. The variable forage production associated with fluctuations in rainfall distribution in the critical fall and spring growth periods of this grass has necessitated a reduction of the stocking rate on these deteriorated lands (Stewart and Young, 1939; Hull, 1949).

The nutritive value of BROTEC compares favorably with that of many desirable grass species (Bovey et al., 1961) but the short growing season and fluctuating productivity combine to reduce the forage value of invaded ranges. Thus, lands dominated by BROTEC serve as marginal spring-fall ranges, with fall range use requiring water and protein supplements. This situation has prompted the seeding of BROTEC ranges to exotic species of wheatgrasses -- primarily crested wheatgrass, *Agropyron spicatum* (Cook and Harris, 1952). Attempts at seeding have had mixed results, usually at the expense of the more desirable species (Rummel, 1946; Hull and Stewart, 1948; Evans, 1961; Hull, 1963, 1964; Kay and Evans, 1965; Evans et al., 1970).

Young et al. (1969) studied the population dynamics of BROTEC in an effort to clarify the failures of revegetation attempts. They concluded that variations in seed production and the phenomenon of continuous seed germination were primary factors in the competitive advantage enjoyed by BROTEC.

Other studies dealing with the competitive advantage of BROTEC indicate that complete utilization of available soil moisture is the primary reason for its success (Hulbert, 1955; Harris, 1967). Its fibrous root system and late fall or early spring growth initiation provide a considerable competitive advantage over slower growing perennial species (Hull, 1963). These factors were especially important in seasons of below-average precipitation (Evans et al., 1970).

Studies by Hironaka (1961) disclosed that BROTEC root growth precedes that of medusahead (*Taeniatherum caput-medusa* Nev.) by one phenologic stage and that BROTEC roots penetrate to a greater depth. BROTEC apparently enjoys a competitive advantage for available soil moisture even against this other weedy grass species.

The matter of interspecific competition seems quite clear but that of intraspecific competition is more involved. Harris (1967) observed that both sparse and dense stands of BROTEC underwent the same degree of soil moisture depletion. These observations suggest that factors other than soil moisture limit BROTEC productivity.

Kay and Evans (1965) reported increases in BROTEC productivity due to the addition of nitrogen fertilizer. Fertilization also increased competition for soil moisture between BROTEC and intermediate wheatgrass. They concluded that nitrogen stimulated root growth and therefore the depletion of soil moisture. Similar studies by Smika et al. (1961) and D'Aoust and Taylor (1968) support this hypothesis.

Early studies by Muller (1953) revealed that two desert shrub species were capable of producing toxins which killed other plant seedlings in laboratory cultures. However, the effect of these toxins in natural systems was overcome by the ability of the longer lived shrub crowns to intercept and collect airborne soil and other debris which provide suitable environments for herbaceous plant germination and growth. Robertson (1947) noted much the same phenomena with sagebrush. The shrub crown reduced wind movement and evaporation of soil moisture. Crown dominance over BROTEC was positively correlated with crown area and extended to a distance of one meter from the crown center. No causative agent for this dominance was suggested.

Garcia-Moya and McKell (1970) studied the relation of shrubs to the nitrogen economy of a desert wash ecosystem. They found that in such arid regions the shrubs and their immediate environs acted as reservoirs of the community's nitrogen supply. Bjerregaard (1971) reported that while the soil was the greatest reservoir of nitrogen in salt desert shrub communities, the nitrogen existed in forms which were "microbial in origin and thus

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a very stable terminal residue of decomposition not subject to further transformation of any consequence by microorganisms". He concluded that the small quantities of nitrogen present in litter and its partly decomposed residue served as the most available sources of nitrogen for the plant community.

OBJECTIVES

This project was initially undertaken to:

1. Clarify the function of the annual *Bromus tectorum* (BROTEC) in the utilization of added seasonal precipitation in *Artemisia tridentata* (ARTTRI) rangelands.
2. Assess the magnitude of nutrient tie-up in short-duration cycles and the time required for the release of nutrients through mineralization.
3. Correlate the short-term or opportunistic productivity represented by the increase of annual plant biomass with the longer-term cycling patterns represented by the perennial shrubs.

The effect of shrub crown dominance on BROTEC productivity necessitated the inclusion of the following objectives to better assess the nitrogen economy of the study site:

1. To compare ARTTRI understory and interspace habitats with respect to BROTEC productivity and nitrogen content of plant tissue and litter.
2. To compare ARTTRI understory and interspace habitats with respect to soil moisture and nitrogen content.

The discovery that two additional species of annual brome-grasses, *B. japonicus* (BROJAP) and *B. brizaeformis* (BROBRI) were associated with BROTEC in the study site gave rise to the third additional objective of comparing species productivity differences in both shrub habitats. BROBRI variability on the site was so great that it was disregarded in biomass and nitrogen analysis procedures.

The low annual brome-grass biomass evidenced in the shrub interspace habitat was partly compensated for by the vigorous growth of the annual weed *Ranunculus testiculatus* (RANTES). A side study was conducted to estimate the contribution of this species to the nutrient status of the community.

METHODS

Study site

A relatively homogeneous sagebrush-brome-grass plant community served as the study site. It was located 33 km west of Logan, Utah, on the benchlands of the Wasatch Front.

The soil is gravelly loam of the Sterling Series. It is a member of the loamy-skeletal, mixed, mesic family of Typic Calciustolls (Davis-Weber Soil Survey, 1968; Box Elder-East Soil Survey, No date). Sterling soils are formed on mixed lake sediments predominantly from limestone and quartzite. The upper 36 cm is gravelly loam with a bulk density of 1.25 and is underlain by highly calcareous gravel beds. The slope is 10 to 20 percent. Mean annual precipitation is 510 mm at this particular site (USGS, No date) and the frost-free period is 120 to 150 days. Elevation is 1400 m above sea level

Six study plots were established within a 75 X 35 m cattle-proof fenced area located one-half mile southeast of the highway intersection in Deweyville, Utah. Each plot measured 10 X 10 meters and was at least 5 meters distance from all other plots. Line intercept measurements of each plot showed that the mean shrub canopy cover was 43%.

No grazing was observed on this site during the two-year study period. The landowner had grazed his livestock on better forage grasses at high elevations for several years prior to this study.

Experimental design

Annual plant growth was assessed in relation to nitrogen cycles within this shrub-annual grass plant community. To determine productivity a means of quantifying the biomass of each system component was developed. The biological system was divided into four components: 1) annual grasses; 2) shrubs; 3) annual weeds; and 4) soil. Each component was further subdivided into ecologically significant parts as described in the following sections.

The basic sampling unit for each of the system components was an individual ARTTRI shrub. Each shrub from which samples were to be collected was randomly selected from a plot according to a grid system. The closest living shrub to each grid point was used as the sampling unit.

In each of the 10 X 10 meter study plots the shrub community was stratified into shrub understory and interspace habitats to reduce the variability in assessing bromegrass productivity, soil nitrogen and water content due to competitive effects of the shrub canopy. The understory was considered to be that area immediately under the shrub canopy as well as the area extending 20 cm out from the shrub canopy perimeter. The 20 cm distance was used to reduce the edge effect of the shrub canopy. Shrub interspace habitat was that area of the community not falling within the shrub understory (Figure 1).

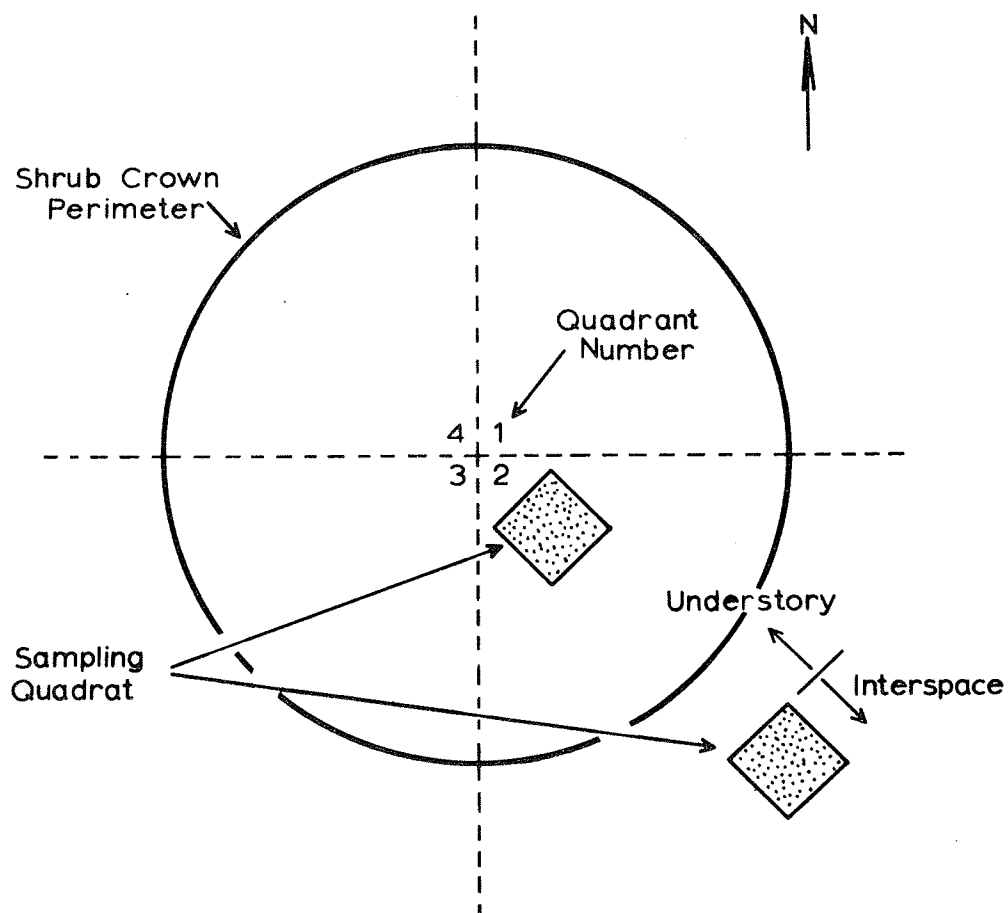


Figure 1. Bromegrass biomass sampling scheme.

Experimental methods

An irrigation treatment was applied to three of the study plots. This treatment simulated conditions of above-normal rainfall during the spring growth period from April to June.

Irrigation water was added at a calculated average rate of 12-15 mm per week during the spring. This amounted to 1925 l of water per week per 10 X 10 m plot. The irrigation treatment was applied for eight weeks.

Water status: Natural precipitation was measured using two standard 8-inch diameter rain gauges. Precipitation measurements were taken twice a month during the spring and monthly at all other times (A3UMD10).

Soil moisture content (A3UMD08) was measured gravimetrically. Soil samples were collected at 1 cm and 15 cm depths in both understory and interspace habitats every two weeks during the spring and monthly thereafter.

Annual grass biomass: Bromegrass biomass samples (A3UMD01) were obtained from 10 randomly selected shrubs within each study plot. A 20 X 20 cm quadrat was used to obtain samples from each shrub habitat. In the shrub understory the quadrat was butted against the shrub's main stem. In the interspace the quadrat was placed at a distance of 20 cm from the shrub crown perimeter. The quadrats were placed in randomly selected quadrants about the shrubs (Figure 1). Placement of the quadrat was not recorded with respect to aspect about the shrub.

Bromegrass biomass samples were collected in April (beginning of treatment), June (maturity) and September (decomposition loss). Only in June did sampling provide an estimate of productivity by species.

Additional bromegrass samples were also collected at frequent intervals between biomass sampling dates. These samples were used for nitrogen content analysis (A3UMD02) and no biomass estimates were made.

Shrub biomass index: ARTTRI stems were subdivided into new and old growth portions. New growth consisted of the current year's production of stem and leaf tissues as well as the carryover of leaves from the previous year. Inclusion of carryover tissue was necessary due to difficulty in distinguishing old from new leaves, especially at later sampling periods. Old growth consisted of stem tissue produced in the previous two years.

At each monthly sampling period five ARTTRI shrubs were randomly selected in each plot using the grid system. Two stem samples were clipped from each shrub and returned to the laboratory for separation into new and old growth stem fractions based on branching patterns, bark coloration and texture, and bud scale position. Stem fraction weights were used to compute a new stem/old stem biomass ratio (A3UMD03) for use in statistical analysis.

Shrub stem growth rate: To further determine the effect of irrigation treatment on shrub growth an investigation into the rate of stem growth was conducted. Stem length measurements were taken monthly and recorded as length increases since the previous measurement (A3UMD09).

Weed biomass: An estimate of the biomass (A3UMD06) of the annual weed *Ranunculus testiculatus* (RANTES) was made. Samples were collected from both interspace and under-

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story habitats in the early spring before maturity. These samples were also analyzed for total nitrogen content (A3UMD07).

Nitrogen analysis: All vegetative material and soil samples (see below) were analyzed for total nitrogen content. The Semimicro-Kjeldahl method described by Bremner (1965) and modified by Bjerregaard (1971), to account for the low nitrogen levels in the desert soils, was used to analyze the 1500 samples collected during the project.

Shrub biomass samples were composited by growth type, plot and date. Bromegrass biomass samples were composited by species, growth type, habitat, plot, and date. Duplicate samples of shrub (A3UMD04) and grass (A3UMD02) material were then analyzed for total nitrogen content.

Soil samples (A3UMD05) were obtained from the shrub understory and interspace habitat at depths of 1 cm and 15 cm and analyzed for total nitrogen content. These depths were selected on the basis of being areas of major change within the rooting zone of the annual grasses. The cobbly nature of the soil profile also limited the depth to which samples could easily be obtained.

RESULTS

The results presented below are those available through the month of September. The remainder of the data and analysis will be presented in a supplementary research memorandum early in 1973. Contents of the supplement are outlined in the Expectations section of this report.

Precipitation data (A3UMD10) are presented in Figure 2. The 20-year (1951-1970) monthly average data are adjusted values computed from records at the Garland, Utah, weather station (8 km NW of study site) where the annual precipitation is 380 mm compared to the 510 mm average for the study site (U.S. Geological Survey, No date). Irrigation treatment is incorporated in the graph as the calculated amount (12-15 mm/week) added per month.

Statistical analyses for bromegrass biomass data (A3UMD01) collected in April and June is presented in Tables 1 and 2. Mean values for each treatment, habitat, date, and species are presented in Tables 3, 4, 5, and 6. A graphic display of these means is given in Figures 3 and 4.

Results of the statistical analysis of the bromegrass biomass data show significant interactions between 1) date and habitat biomass values, and 2) date and treatment biomass values (Table 1). Further analysis of the data using the *a posteriori* LSR (Least Significant Range) test to evaluate the differences between these interacting means resulted

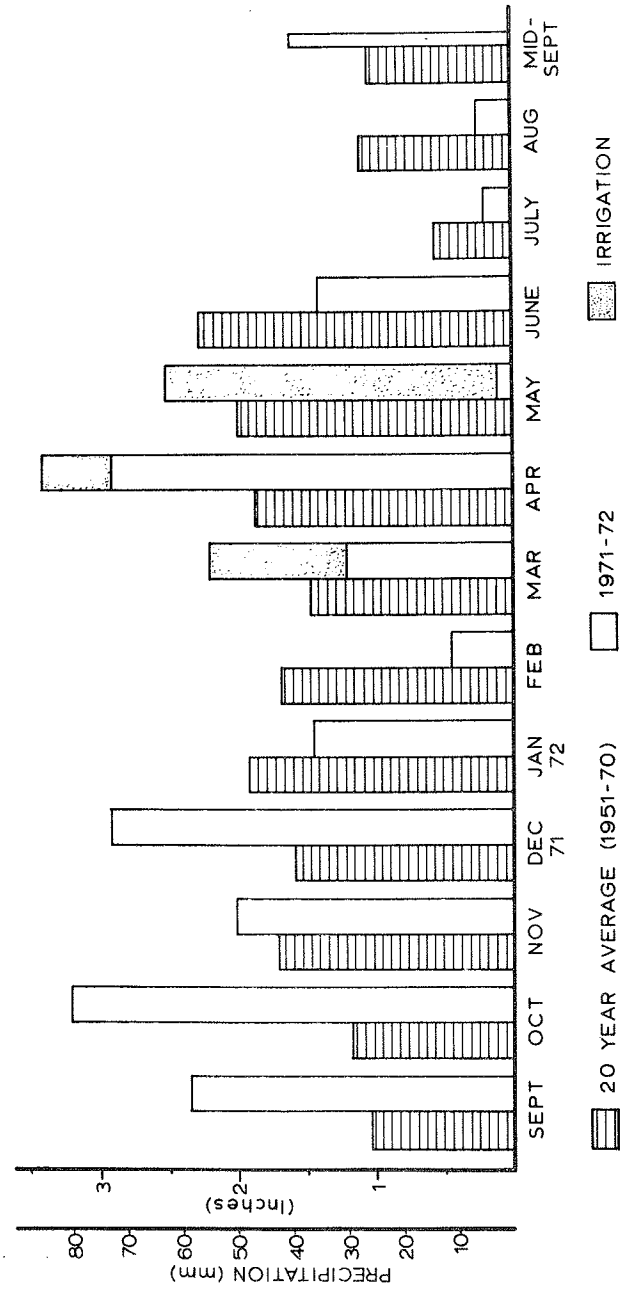


Figure 2. Precipitation record (A3UMD10) for Deweyville Experimental Site, Deweyville, Utah.

Table 1. Factorial analysis of variance for April and June 1972 brome grass biomass at Deweyville Experimental Site, Deweyville, Utah (DSCODE—A3UMD01)

Source	df	MS
Date	1	906.56 ^{xx}
Treatment	1	89.36 ^{xx}
Habitat	1	1956.53 ^{xx}
Date X Treatment	1	126.94 ^{xx}
Date X Habitat	1	216.50 ^{xx}
Treatment X Habitat	1	9.74
Date X Treatment X Habitat	1	12.17
Error	232	4.59

^{xx} = Significant at .01 level.

Table 2. Factorial analysis of variance for June 1972 brome grass productivity at Deweyville Experimental Site, Deweyville, Utah (DSCODE—A3UMD01)

Source	df	MS
Species	2	456.46 ^{xx}
Habitat	1	579.12 ^{xx}
Treatment	1	71.55 ^{xx}
Species X Habitat	2	177.99 ^{xx}
Species X Treatment	2	19.26 ^{xx}
Habitat X Treatment	1	7.28
Species X Habitat X Treatment	2	2.33
Error	348	4.09

^{xx} = Significant at .01 level.

Table 3. April 1972 treatment means (g/20 x 20 cm quadrat) and standard deviations (in parentheses) for brome grass biomass estimates at Deweyville Experimental Site, Deweyville, Utah (DSCODE—A3UMD01)

Habitat	Treatment	
	Irrigation	Control
Understory	4.59 (2.27)	4.87 (1.96)
Interspace	0.83 (0.61)	1.01 (0.75)
	n = 30	

Table 4. June 1972 treatment means (g/20 x 20 cm quadrat) and standard deviations (in parentheses) for brome grass productivity estimates at Deweyville, Utah (DSCODE—A3UMD01)

Habitat	Treatment	
	Irrigation	Control
Understory	12.28 (3.88)	8.75 (2.16)
Interspace	3.82 (2.30)	2.00 (1.28)
	n = 30	

Table 5. June 1972 BROTEC treatment means (g/20 x 20 cm quadrat) and standard deviations (in parentheses) for productivity estimates at Deweyville, Utah (DSCODE—A3UMD01)

Habitat	Treatment	
	Irrigation	Control
Understory	6.92 (5.24)	5.36 (1.82)
Interspace	1.61 (1.21)	1.02 (1.06)
	n = 30	

Table 6. June 1972 BROJAP treatment means (g/20 x 20 cm quadrat) and standard deviations (in parentheses) for productivity estimates at Deweyville, Utah (DSCODE—A3UMD01)

Habitat	Treatment	
	Irrigation	Control
Understory	5.34 (3.01)	3.35 (1.61)
Interspace	2.14 (1.91)	0.95 (0.56)
	n = 30	

1. In april there was no significant (.05) difference in biomass in either habitat due to treatment (which was initiated only the week before); in June irrigated plots had significantly (.01) greater biomass than control plots in both habitats.
2. In irrigated plots June biomass in both habitats was significantly (.01) greater than that in April; in control plots only the understory habitat biomass was greater (.01) in June than April.
3. Regardless of treatment and date, biomass was significantly (.01) greater in the understory habitat than in the interspace.

Statistical analysis of the June brome grass biomass data show significant interactions between species and habitat, and species and treatment (Table 2). Due to the extreme variability in BROBRI biomass values only BROTEC and BROJAP species were analysed further. Means comparisons using the LSR test gave the following results:

1. Regardless of treatment BROTEC productivity was significantly (.01) greater than that of BROJAP in the understory habitat but not the interspace.
2. Understory habitat productivity of both species was significantly (.01) greater in irrigated plots than in control plots; in the interspace habitat BROJAP had a significantly (.05) greater productivity in irrigated plots than in control plots compared to BROTEC.
3. Regardless of treatment and species, productivity was significantly (.01) greater in the understory habitat than in the interspace.

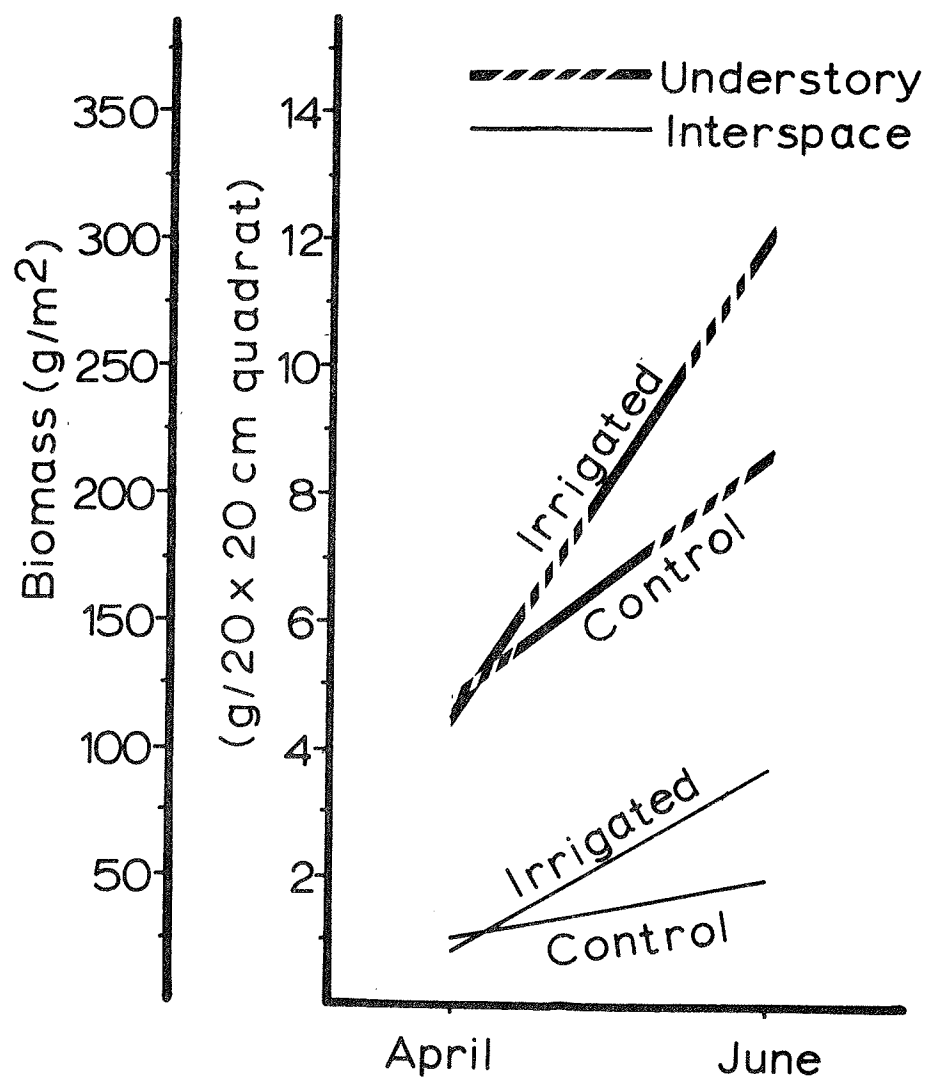


Figure 3. April and June 1972 bromegrass biomass estimates from Deweyville Experimental Site, Deweyville, Utah. (A3UMD01).

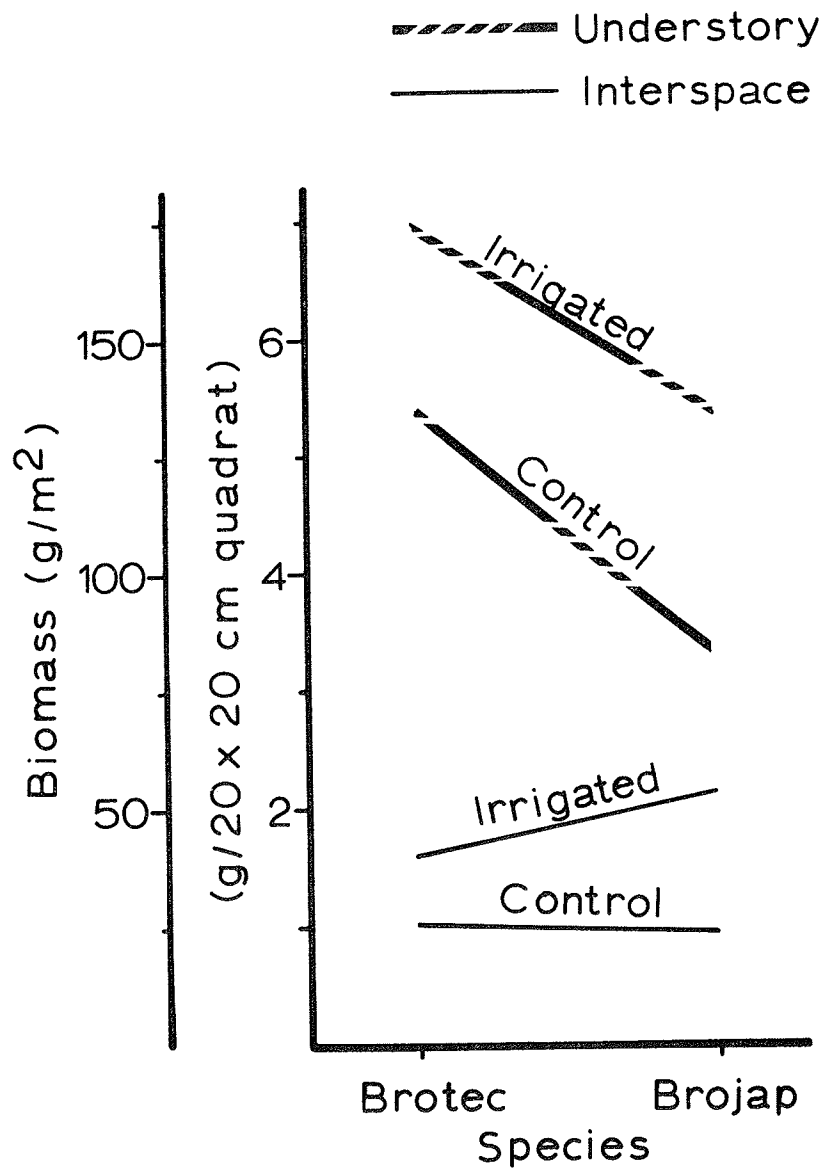


Figure 4. June 1972 bromegrass productivity comparisons between species from Deweyville Experimental Site, Deweyville, Utah. (A3UMD01).

DISCUSSION

Precipitation measurements (Figure 2) were obtained during one complete BROTEC life cycle. Germination occurred in September, 1971, with the breaking of the summer drought by heavy fall rains. Precipitation that month was twice the 20-year average. Hull and Pechanec (1947) noted that 50 mm of concentrated rainfall is needed for good fall growth of BROTEC. Precipitation throughout the fall and winter was above average except for January and February, and thus insured good seedling establishment. Snow-melt began in early March due to an abnormal two-week warm spell. Irrigation treatment began in late March and continued through the end of May. During this period each irrigated study plot received more precipitation than the 20-year average. Irrigation was especially valuable in May when only 6 mm of natural precipitation were recorded. Irrigation in this dry period permitted the treatment effect to become clearly established from both a productivity and a nitrogen content standpoint. Summer month precipitation was below the 20-year average but the drought was ended in mid-September. Seedling germination occurred in September and final biomass and soil samples were then collected.

April brome grass biomass samples compared favorably with observations made in the 1971 study. Treatment differences were not significant but understory biomass was at least four times greater than interspace. This difference is attributed to the phenomenon of shrub crown dominance noted by Robertson (1947). Evans and Young (1970) found that BROTEC failed to germinate in sites with a small litter component. This finding was consistent with the "safe site" germination concept. The relatively large but light-weight caryopses of BROTEC require a rough microrelief to bury themselves and germinate. The presence of abundant litter in the understory acts as an insulating layer which moderates temperature and moisture fluctuations and thus provides favorable microsites ("safe sites") for seed germination.

June brome grass biomass was greater than April's in all plots and habitats except the interspace of control plots. In a study of the perennial *Bromus inermis*, Power (1971) suggests that the Percentage Stress (reduction in growth rates) of nitrogen deficiency was greatest where available nitrogen was lowest; this stress also increased with maturity. Percentage stress for water deficiency was greatest where nitrogen availability was lowest. Preliminary examination of this year's soil nitrogen and water content indicate that both factors are lowest in the interspace of control plots. Our 1971 study also found the lowest soil nitrogen levels in interspace habitats. Evans (1960) somewhat contradicts the above conclusions. His study of competition between the two annual grasses *Bromus mollis* and *Festuca megalura* and the annual forb *Erodium botrys* leads to the conclusion that shading and differential ability for nitrogen uptake were primary factors in annual grass-forb interactions. This was notably so at

high nitrogen levels. The shading provided by increased growth of the forb at moderate nitrogen levels also increased grass productivity. At high nitrogen levels (455 kg/hectare) neither grass species exhibited increased response to nitrogen when grown with the forb. In this case the forb was the sole beneficiary of the increased nitrogen. When grown bi-specifically at the high nitrogen level the grasses exhibited an increased response with no competitive effect on one another. The presence of high soil nitrogen levels in the forb understory would argue for increased productivity as is the case in the ARTTRI community study. Perhaps ARTTRI does not take advantage of the increased nitrogen availability as does the fertilized forb. If the analysis of shrub productivity shows no irrigation treatment difference then this may be the explanation for the different response obtained by Evans at high nitrogen levels. It may be that the difference in forb and shrub response to nitrogen is a function of the amount of nitrogen applied, or available, as the case may be. That is, the two experiments may differ by several orders of magnitude with respect to nitrogen availability.

The species' mean comparisons for June brome grass biomass indicate that BROJAP exhibited a greater response than BROTEC only in the irrigated interspace habitat. Again one must remember that environmental stress is greatest in the interspace habitat. Hulbert (1955) reported that BROTEC had given way to BROJAP in Kansas for several years and attributed this phenomenon to the change of the annual precipitation distribution maximum from spring to early summer. This shift would favor BROJAP due to its later maturity date (2-3 weeks later on the study site in Utah and also on Hulbert's Lewiston, Idaho, site) and more extensive root system. Hulbert further suggests that BROTEC is able to successfully compete against BROJAP in the more severe control interspace due to its earlier maturity date.

The carryover of viable caryopses by BROTEC accounts for the continuous germination potential exhibited by this species (Young et al., 1969). The continuous germination phenomenon is consistent with the "safe site" concept, especially when temperature and water are limiting. That is to say, the simultaneous germination characteristics of fresh caryopses can be environmentally conditioned to continuous germination. With "safe sites" being more frequent in the understory habitat it is conceivable that continuous germination should account for the advantage BROTEC maintains in this particular habitat. This in no way overcomes the possibility that BROJAP might also be capable of continuous germination. Newman (1961) noted that for winter annuals in Great Britain the later the germination date the smaller the plant and the lower the seed productivity. In fact, Hulbert (1955) notes that BROTEC must be subjected to cold temperatures for normal flowering to occur; if not, then spring germination usually results in vegetative plants only. In the event that continuous germination is a characteristic of both species it may be that the new BROTEC seedlings are able to

outcompete BROJAP in the same manner as they do medusahead (Hironaka, 1961) or intermediate wheatgrass (Kay and Evans, 1965). Thus the new BROTEC seedlings, while of small stature, may be of sufficient density, due to "safe site" frequency, that BROTEC productivity remains greater than BROJAP in the understory habitat regardless of treatment.

At this time it is impossible to comment further on the results of this study. With the completion of the data analysis (as noted in the following section) it should be possible to integrate the biomass and nitrogen level results into a comprehensive final report.

EXPECTATIONS

A supplementary report containing the final results of this project will be published in early 1973. Data for these expectations are presently in the Desert Biome Data Bank. The following material will be included in that report:

1. September 1972 brome grass biomass (A3UMD01) values and analysis for differences due to treatment and habitat compared to similar values in June.
2. ARTTRI biomass index (A3UMD03) values and analysis for growth rate differences due to treatment and date.
3. ARTTRI stem growth length (A3UMD09) values and analysis for period of maximum growth rate.
4. RANTES biomass (A3UMD06) values and analysis for differences due to treatment and habitat.
5. Soil nitrogen (A3UMD05) and soil moisture (A3UMD08) content values and analysis for differences due to treatment, habitat, depth, and date.
6. Brome grass nitrogen content (A3UMD02) values and analysis for differences due to treatment, habitat, date, and species.
7. ARTTRI nitrogen content (A3UMD04) values and analysis for differences due to treatment and date.
8. RANTES nitrogen content (A3UMD07) values and analysis for differences due to treatment, habitat, and date.

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1972 PROGRESS REPORT

EFFECT OF DENSITY ON THE POPULATION DYNAMICS OF *Perognathus*
formosus AND ITS RELATIONSHIPS WITHIN A DESERT ECOSYSTEM

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Research Memorandum, RM 73-18

MAY 1973

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Report Volume 3

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A B S T R A C T

The population dynamics of *P. formosus* were observed in 3 enclosures, which initially had densities of this pocket mouse in a ratio of 10:4:1. The high density was obtained by adding mice, the medium density by reducing natural number by half. The low density occurred naturally and was near the extinction level; reproduction in this population began late, but then continued longer. Density dependent effects were observed. The relative amount of sexual activity (incidence X duration) was inversely related to density. The number of young weaned per successful pregnancy was highly correlated with density ($r = -0.999$). At the low density all pregnancies were successful and all young were weaned. Survival of resident mice (RS) was high and unaffected by density. Survival of introduced mice (INT) was lower and inversely related to density. The first mice born survived as well as RS, but survival of later cohorts was less and was inversely related to density. The integration of these effects was that the artificial increase was not maintained and the reduced population quickly recovered. After the late start the low density population increased continuously, but it never reached carrying capacity.

A growth curve is given for mice 20-140 days old in the field. Males grew more rapidly than females; in some comparisons growth rate was inversely related to density. Survival is affected by experience with an area, sudden introduction into a foreign area, density, and age. The observed density effects may result from interactions of mice in overlapping home ranges. Home range was negatively correlated with density. We hypothesize that if sensory perception of the mice can be reduced, and interaction thus be reduced, carrying capacity will be increased. This will be tested in 1973.

In February 1972 seed density was an average of 832 seeds/m² of habitat, or about 4.16 kg/ha. Seed density was significantly higher under shrubs and was directly related to canopy size; in the open areas, seed density was inversely related to distance from shrubs.

I N T R O D U C T I O N

The purpose of the study in 1972 was to observe the responses of a relatively well-known desert ecosystem to an artificial increase and decrease in the density of its most abundant mammal, *Perognathus formosus*, the Long-tailed Pocket Mouse. A good way to learn about an ecosystem is to observe the consequences of upsetting it. These observations can then be the basis for experimentation with the system, which can lead to answers about its functioning more quickly than if one "waits upon Nature's experiments".

Three kinds of forces impinge upon a population: the physical environment, other species, and itself. It is important to know the relative importance of each of these forces in the regulation of a population. The study sites have been studied by French et al. (1973) from 1964 to 1968. The influence of the physical environment is suggested by their observations that the numbers of *P. formosus* varied erratically from year to year and the changes were generally synchronous in different sites within the same valley. The effect of the biota upon itself is suggested by the fact that the densities of the different sites did not always change proportionately. The density-ranking of the sites changed several times in 4 years. The abiotic environment probably affects an herbivore population by the influence of the weather on plant production. A population affects itself by competition for space and food and by effects on its food supply.

A *P. formosus* population can show the influence of biotic and abiotic interactions in several ways: in reproduction, survival, body weight, growth of young, and home range. Since mice of different sexes and sources (resident, introduced, young of year) can respond differently, the heterogeneity in composition of the population increases its usefulness as an indicator. There are obvious expectations as to how a population will respond to density, but only in a few cases have these expectations been put to a test in desert ecosystems. The interaction of *P. formosus* with its food resources is being tested by measurements of seed reserves in the upper 2 cm of soil in February, June and October.

We hope to see how closely the responses of the experimental populations follow the opportunities of the environment and what limits numbers of mice. If a low population density can be artificially raised, say by 100%, this suggests there was a considerable lag in the ability of the population to increase to carrying capacity. If an artificial increase cannot be sustained, this suggests that population size closely follows changes in carrying capacity. In any case we hope to discern what is the limiting factor.

The results of the 1972 work suggest that behavioral interaction is the limiting factor on *P. formosus* density, and this will be experimentally tested in 1973.

OBJECTIVES

The specific objectives in 1972 were:

1. To manipulate the densities of *P. formosus* by removing half the residents present in one 4.4 ha enclosure in March and to increase the number to 250% in another 4.4 ha. A third enclosure was left without modification.
2. To observe the consequences of the manipulation and other events by periodic live trapping of all rodents and measurement of intensity and duration of reproduction, body weight and growth rates, survival and home range.
3. To observe the distribution and quantities of seeds in the upper 2 cm of soil by sampling at three times of the year, and possibly relate seed numbers to pocket mouse density.
4. To look for interspecific relationships of rodents in the enclosures.

METHODS

Study site

The study was conducted in two enclosures, each about 8.8 ha in size, in Rock Valley, Nye County, Nevada, which were established in 1964 (French, 1964). These are circular enclosures, Plot A and Plot C in the original terminology of the area, and Area 1 and Area 3, respectively, in the description of the Rock Valley Validation Site (Turner, 1972). Plot C was divided in half by a fence, and *P. formosus* density in the southern half was reduced by 50% in March 1972 and density in the northern half was increased. Since the naturally occurring density in Plot A happened to be lower than either part of Plot C, these three areas form a sequence of treatments: high density of *P. formosus* (C, north), medium density (C, south) and low density (A). High, medium and low density are categories of "treatment", and not necessarily the actual ranking of densities in these areas at all times.

The soil, weather and vegetation of Rock Valley have been described by French et al. (1973) and Turner (1972, 1973).

Characteristics of *Perognathus formosus*

P. formosus is a medium-sized pocket mouse, with an adult size of 18 to 22 g. Pocket mice are usually described as seed feeders, but the data of French et al. (1973) on stomach contents of *P. formosus* show that seeds ordinarily compose less than half of the diet, and as little as 20% in winter. *P. hispidus* caches seeds in nature (Blair, 1937) and presumably other pocket mice do also. *P. formosus* caches seeds in captivity.

P. formosus, like other species of pocket mice, have lower metabolic rates than non-desert-inhabiting mice (Chew, Lindberg and Hayden, 1965a). In the laboratory

2.3.2.1.-4

P. formosus become hypothermic when denied food or kept at low temperatures. Some individuals kept at 10 C showed a consistent circadian rhythm of deep torpor and arousal (Chew, Lindberg and Hayden, 1965b). This may be their metabolic behavior in winter, when from about November to February they are rarely active above ground (Mullen, 1971; French et al., 1973). Measurements of metabolic rates in free-living animals suggest winter torpor (Mullen, 1971). Survival is usually quite high during winter, probably a benefit of the winter inactivity, and decreases as soon as the mice appear above ground again (French et al., 1973). High winter survival is one reason for the exceptional life span of *P. formosus*, 11.4-14.4 months average life expectancy at age of 1 month (French et al., 1973).

Various authors have recognized that *P. formosus* occur on coarser, gravely and rocky soils. The soils of the northern portion of the validation site are generally fine and sandy, and *P. longimembris* is the most abundant rodent there. However, on the southern or upslope part of the site and beyond, where Plots A and C are located, the soil is coarser and *P. formosus* predominates (Turner, 1972).

Eisenberg (1963) gave an extensive account of the behavior of pocket mice in the laboratory. Much of behavior is oriented to isolation of adults. The male-female response varies with the estrous cycle. Visual, auditory and olfactory interactions occur. The evidence is that pocket mice are almost always solitary in nature.

Other species

Eight other rodents are present in the Plot C with *P. formosus*. These are Heteromyidae: *P. longimembris*, *Dipodomys merriami* and *D. microps*; Cricetidae: *Neotoma lepida*, *Peromyscus crinitus* and *Onychomys torridus*; Sciuridae: *Ammospermophilus leucurus*; and Geomyidae: *Thomomys bottae*. All but the last two species are routinely taken by live trapping in the study plots. On March 8, 1972, *P. formosus* constituted 73.8% of the numbers and 68.1% of the biomass of captured rodents in Plot C.

Probably only the heteromyids are significant competitors with *P. formosus* for seeds, and there is probably some differentiation of seed sizes used by the four species. *D. microps* may feed primarily on leaves (Kenagy, 1972). *O. torridus* is potentially a predator of pocket mice.

Live trapping

Live trapping was carried out on the 15-m grid in the plots, one trap per grid point, using the procedures long established for the site (French, 1964). Generally, traps were set for three consecutive nights, every other week (dates in Table 1) from March 6 through August 15, with an additional 2-day trapping on October 13-14. This spans almost the

entire period of time when *P. formosus* are consistently active above ground. The frequency of trapping was reduced in May in order to minimize trauma to pregnant and lactating females, which could have affected mortality of unborn and weaned young.

Table 1. Numbers of *P. formosus* in different categories at different sampling times in the three treatment areas DSCODE—A3UCC01

Category	Approximate Sampling Time											
	Mar 13	Mar 27	Apr 11	Apr 24	May 19	Jun 13	Jun 27	Jul 11	Jul 24	Aug 2	Aug 14	Oct 13
High Density Treatment												
RS♂	6	6	5	5	5	4	4	3	3	3	3	2
RS♀	13	12	9	8	8	7	7	7	6	6	6	3
INT♂	2	11	6	3	21	14	14	12	10	9	7	4
INT♀	15	21	14	12	31	27	23	22	20	20	18	15
B♂					11	36	31	31	25	22	21	14
B♀					10	39	32	28	20	19	16	8
Total	36	50	34	28	86	127	111	103	84	79	71	46
Medium Density Treatment												
RS♂	4	3	3	3	3	3	3	3	3	3	3	3
RS♀	6	5	4	4	4	4	4	3	2	2	2	1
INT♂				2	5	7	2	3	3	2	1	1
INT♀	3	4	6	6	12	12	11	11	10	10	10	7
B♂			1	4	16	36	38	37	35	34	30	19
B♀				3	14	37	44	42	35	34	30	18
Total	13	12	14	22	54	99	102	99	88	85	76	49
Low Density Treatment ^a												
	Mar 6	Mar 20	Apr 3	Apr 17	May 16	Jun 20	Jul 18	Aug 7	Oct 13			
RS♂	5	5	4.5	4	3.5	3.5	3	3	3			
B♂					1	3	5	6.5	7.5			
B♀					4.5	5.5	9.5	12	11.5			
Total	5	5	4.5	4	9	12	17.5	21.5	22			

a/ values are 1/2 of number for Plot A (8.8 ha) in order to put them on a comparable basis with other plots (4.4 ha)

RS = resident, INT = introduced, B = born

2.3.2.1.-6

The following items were recorded for each capture: species, identification number, sex, reproductive condition, pelage, body weight, capture location. The first time an animal was captured in any trapping period, it was taken to a field laboratory in the trap, weighed to 0.1 g, and then released at its point of capture. Information was copied from field data sheets to IBM cards, which were then run through a verification program that checks for consistency of the new data with previous information. The verified cards constitute data set A3UCC01.

Traps were set beginning at about 1500 hr. Each trap was baited with 2 g of crushed oats from a calibrated spoon. Oats were recovered from traps and from the animals' cheek pouches during weighing, so we know how much food was artificially added to the study plots. Traps were checked starting at 2100 hr on nights when air temperature was expected to go below 5 C, at 2230 hr when the expected minimum 5-15, and 0530 hr on warmer nights. The adequacy of the sampling procedure is shown by the fact that an average of 97.7% of the mice known to be in the area was actually captured each time.

P. formosus were trapped near Mercury, Nevada, and released into the high density area at six different times from February 4 to May 12. Animals were held in the laboratory for 4 to 247 hr before release; they were released in the field at times ranging from 0900 to 1630 hr.

Most of the methods of analysis are simple and will be obvious in the presentation of results. Other methods are as follows.

Growth rate

Growth rates were calculated from the detailed information on the consecutive weights of recaptured mice that were born in the three areas. Rates were calculated for 1-gram weight classes, with animals categorized as to sex and area. A tabulation was made of the mice that were in each weight class at a particular sampling time. Percentage growth rate (K) was calculated from the weight (m_1) at this time of capture (t_1) and the weight at the next sampling time (m_2 , t_2), according to Brody (1945:508):

$$K = \frac{\ln m_2 - \ln m_1}{t_2 - t_1} .$$

The difference, $t_2 - t_1$, was expressed in days and m in grams. Animals that were repeatedly captured entered into several calculations, for different weight classes.

Comparison of survivorship curves

Survivorship curves have irregular shapes (Figures 1-3), which we have not tried to define mathematically. In order to compare the survival of different categories of animals

we calculated a simple index of the area under the curve and applied a Chi-square test. The index was calculated as the sum of the percentage surviving at consecutive 15 or 20-day intervals, with the % values being read from the graph.

Home range

Home range was calculated in terms of the sigma of the normal distribution function, as described by Calhoun and Casby (1958):

$$s = \left[\frac{\sum_{j=1}^K \{(X_j - \bar{x})^2 + (Y_j - \bar{y})^2\}}{2(K - 1)} \right]^{1/2}$$

Here, \bar{x} , \bar{y} is the computed center of activity; X_j , Y_j is the point of the j'th capture; and K is the number of captures for each animal. Sigma (s) is the value of a radius within which the probability of the animal being present is 39.4%, if the animal's movements can be described by a bivariate normal density function. A 2-sigma radius encloses 86% of an animal's activity; we used this to represent home range of *P. formosus*. Maza, French and Aschwanden (1973) used this method in their analysis of 7 years of information on *P. formosus* in Rock Valley. They applied the tests given by Calhoun and Casby (1958) and demonstrated that the distribution of captures of *P. formosus* is sufficiently circular in pattern for the sigma home range to be an appropriate measure.

Sigma was calculated only for those mice captured at least 10 times at 4 or more locations. If any point had a radius greater than 5 sigma, it was excluded and a new center and sigma were calculated.

Correlations of variables with density

For prediction one needs an empirical relationship of the dependent variable with density. But, in this study the actual density in any plot was always changing. In order to make comparisons reference densities were chosen at logical points in the continuum, as follows:

1. For relating success of reproduction to density, the density of the population at the median time in the frequency distribution of its births was used (from Figure 4).
2. For relating home range to density, the density at the midpoint in the trapping of the particular category of animals concerned was used. For example, resident pocket mice were captured in 11 sampling periods; their home ranges were based on all captures. The density at the time of the 5th sampling, halfway through the sequence of captures, was used as the reference density. Other categories, such as young of the year, had fewer sampling periods and a different reference density.

2.3.2.1.-8

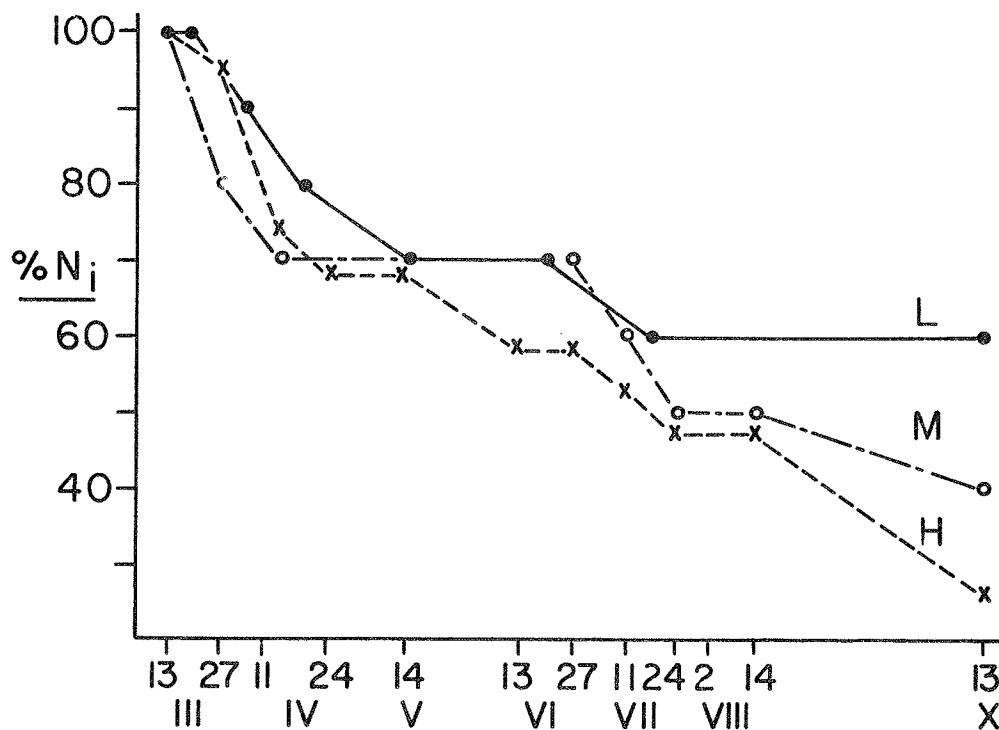


Figure 1. Survival of resident *P. formosus* in the three treatment areas, high (H), medium (M) and low (L) density. Percent N_i is percentage of initial number.

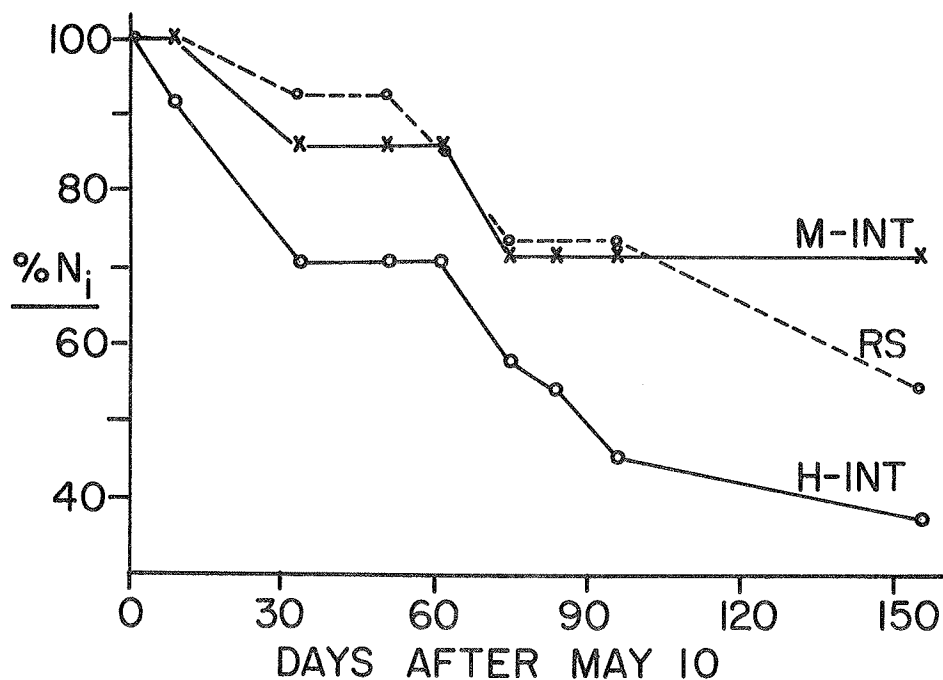


Figure 2. Survival of *P. formosus* introduced into high (H-INT) and medium (M-INT) density plots, compared to residents of all areas (RS). Comparison of three groups is for the same calendar period, the 155 days after May 10, 1972. Percent N_i is percentage of initial number.

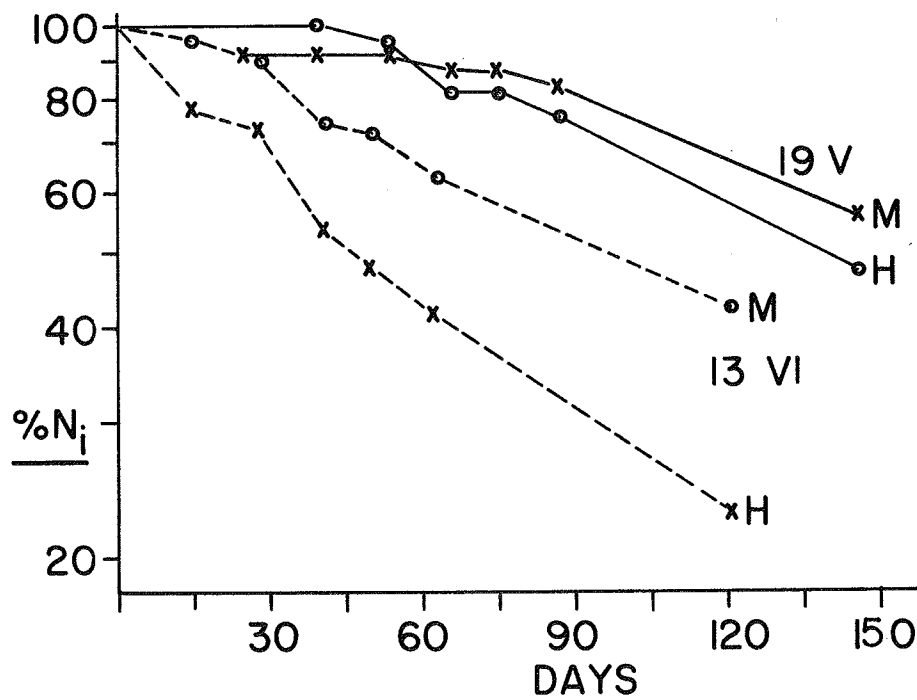


Figure 6. Semilogarithmic plot of the survival of two cohorts of *P. formosus* young of the year, those first captured on May 19 and June 13, in the high (H) and medium (M) density areas. Percent N_i is percentage of initial number.

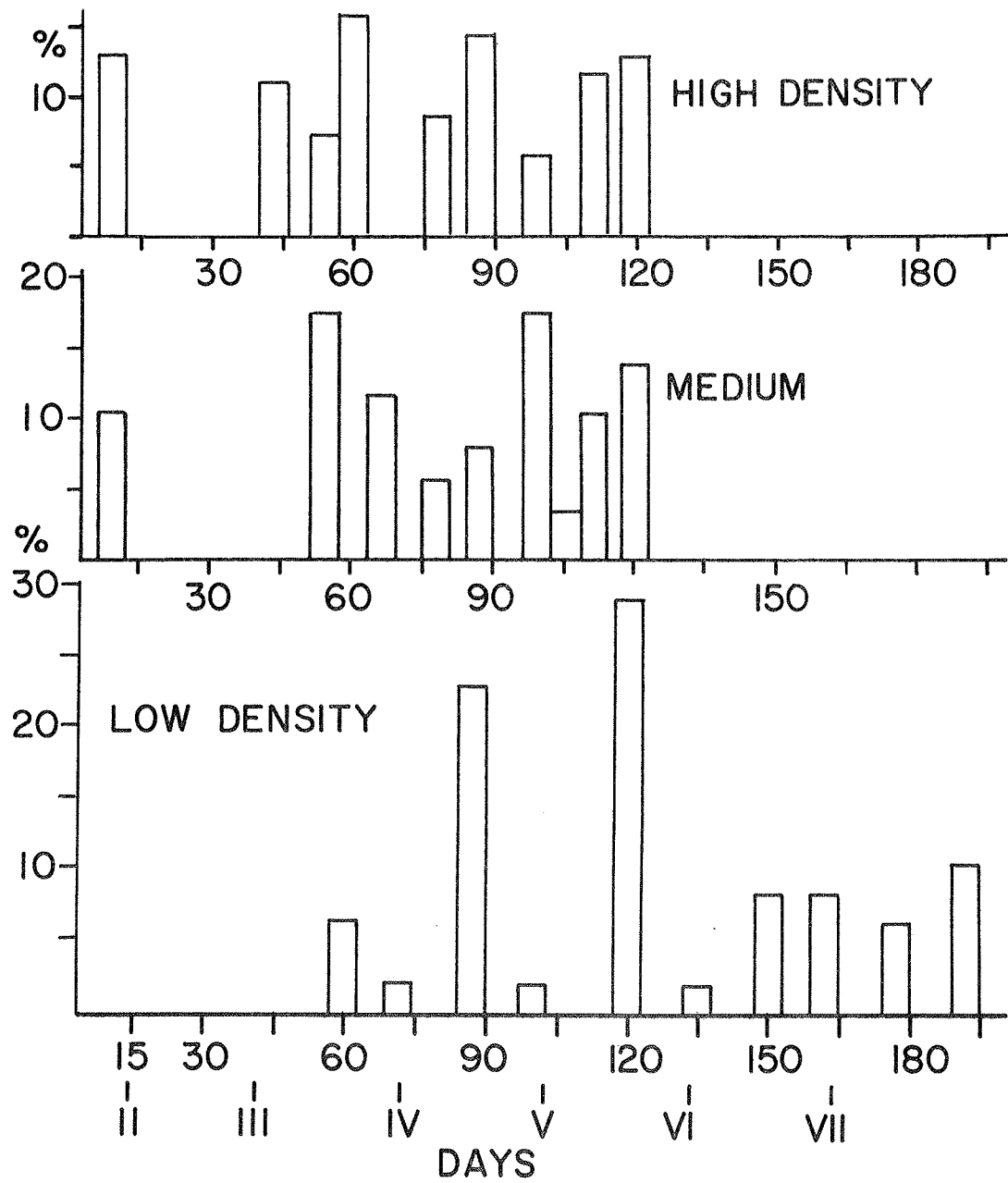


Figure 4. Frequency distribution of births of *P. formosus* in the three density areas. Vertical axis is % of total births.

Seed samples

Seed samples were taken in February, June and October, which was before, during and after the manipulations of densities of *P. formosus* and the most active period of the pocket mice. Soil samples were taken from the exposed areas and under the canopies of the five most abundant shrubs in Plot C: *Ambrosia dumosa*, *Ephedra nevadensis*, *Krameria parviflora*, *Larrea divaricata* and *Lycium andersonii*. Thirty sampling points were chosen randomly from the grid points, and six points were randomly assigned each shrub species. At each point the nearest suitable shrub was chosen, beginning in the northeastern quadrant. "Suitable" means that the shrub size did not deviate markedly from average and that the edge of its canopy was at least 0.5 m from adjacent shrubs.

Soil samples were taken with a fixed-area sampler, which was forced into the ground up to guide flanges. A 25 x 20 cm scoop that fitted into guides was used to remove the surface litter and upper 2 cm of soil and gravel. Canopy samples were taken under the northeastern portion of the canopy. Exposed samples were centered in the smallest exposed area next to the sampled shrub, provided the sampling point was at least 0.5 m from all shrub canopies. A second exposed sample was taken in a larger exposed area if the shrub-to-sample distance exceeded the first sampling distance by 0.5 m.

The maximum height, length and width of each shrub was measured. Canopy area was estimated as the area of an ellipse: $A = \pi ab$. Shrub volume was estimated as the volume of an ellipsoid cone: $V = 1/3 \pi abh$ for *Larrea*, and $V = 1/2 \pi abh$ for the other species, which have more truncated bases than *Larrea*. The distances between the exposed sample and the canopy edges of the surrounding shrubs were recorded, and the area of the space was calculated as an ellipse.

Each soil sample was sieved for 3 minutes on an automatic shaker through a 112-micron soil sieve (U.S. Standard Sieve #70). Rock and gravel were separated by sieving through a coarse screen of about 1 cm openings and discarded with the fraction that passed through the 112-micron sieve. Trial inspections showed that these fractions contained no seeds. The organic material was separated from the remainder by floating it off in a saturated solution of K_2CO_3 . The organic fraction was decanted onto a monofilament nylon organdy material with 0.15 mm openings, which was loosely fitted into a Buchner funnel, and was washed repeatedly with water. The organic residue was dried within the nylon material at 100 C and then sieved with the #70 sieve. Seeds were hand sorted from the fraction retained by the sieve, in a grid-marked petri dish under a stereoscopic microscope at 12X. Empty seed coats and seeds that collapsed when gently squeezed with forceps were not counted. Seeds were identified by comparison with a reference collection from UCLA Laboratory at Mercury, Nevada. Seed counts and sample parameters constitute data set A3UCC02.

The measurements of seed densities are significantly skewed in their distribution. A closer fit of the data to normal distribution is obtained by a square root transformation. Only transformed data were used in the statistical tests reported.

RESULTS

Changes in numbers of *P. formosus*

The numbers of individuals in the three areas are summarized in Table 1. Mice are categorized by sex and source, i.e. according to whether they are original residents (RS), introduced into the area (INT), or born in the area (B). No mice were deliberately introduced into the medium density area, but some that were put into the northern half of Plot C crossed the barrier fence into the southern half and then remained there. Thus these mice were "self introduced" into the medium density area. (Apparently the fence dividing Plot C did not have enough depth at all points to be a complete barrier, but the circular enclosing fence did.)

The basic manipulation was the reduction of the resident *P. formosus* to 10 mice on March 13 in the medium density area, and the gradual introduction of 65 males and 82 females into the high density area on February 10-20, March 3-9, March 21-26, April 16, and May 10-12. The ratio of RS mice, high density:medium density, averaged 1.78 (Table 2) and the ratio of INT mice averaged 3.23, so the effects of the basic manipulations persisted. However, because of different birth rates in the two populations, the ratio of total numbers declined from a maximum of 4.2 in March to about 1 in early July through October 13. The ratio for total numbers for high:low ranged from 10 to 2, decreasing with time.

Table 2. Densities in the three treatment plots: high, medium and low density, and derived information DSCODE—A3UCC01

Approx. Sampling Time	Density per Hectare			High:Medium density ratios				High:Low
	High	Medium	Low	All Mice	RS Mice	INT Mice	B Mice	All
Mar. 13	9.00	3.25	1.25	2.77	1.90	5.67	----	7.20
Mar. 27	12.50	3.00	1.25	4.17	2.25	8.00	----	10.00
Apr. 11	8.50	3.50	1.13	2.43	2.00	3.33	----	7.56
Apr. 24	7.00	5.50	1.00	1.27	1.86	1.88	----	7.00
May 19	21.50	13.50	2.25	1.59	1.86	3.06	0.07	9.56
Jun. 13	31.75	24.75	----	1.28	1.57	2.16	1.03	-----
Jun. 27	27.75	25.50	3.00	1.09	1.57	2.85	0.77	9.25
Jul. 11	25.75	24.75	----	1.04	1.67	2.43	0.75	-----
Jul. 24	21.00	22.00	4.38	0.95	1.80	2.31	0.64	4.80
Aug. 2	19.75	21.25	----	0.93	1.80	2.42	0.60	-----
Aug. 14	17.75	19.00	5.38	0.93	1.80	2.27	0.62	3.30
Oct. 13	11.50	12.25	5.50	0.94	1.25	2.38	0.60	2.09
						3.23		
Average	17.81	14.85	2.79	1.62	1.78	3.32	0.71	6.75
S.E.	2.36	2.64	0.619	0.291	0.072	0.520	0.051	0.936

Incidence and duration of sexual activity

Figure 5 shows the sexual activity of the resident mice, most of which were present throughout the sampling period. "Sexually active" means, for females: swollen vulva, pregnant, or lactating; for males: scrotal testes. The mice in the low density area had a longer breeding season; the males in the high density area became active later and more gradually than in other areas. The areas under the curves for RS mice (Figure 5) and for (RS + INT) mice (not illustrated) are significantly different by Chi-square test; there is a consistent inverse relationship between the relative amount of sexual activity and density.

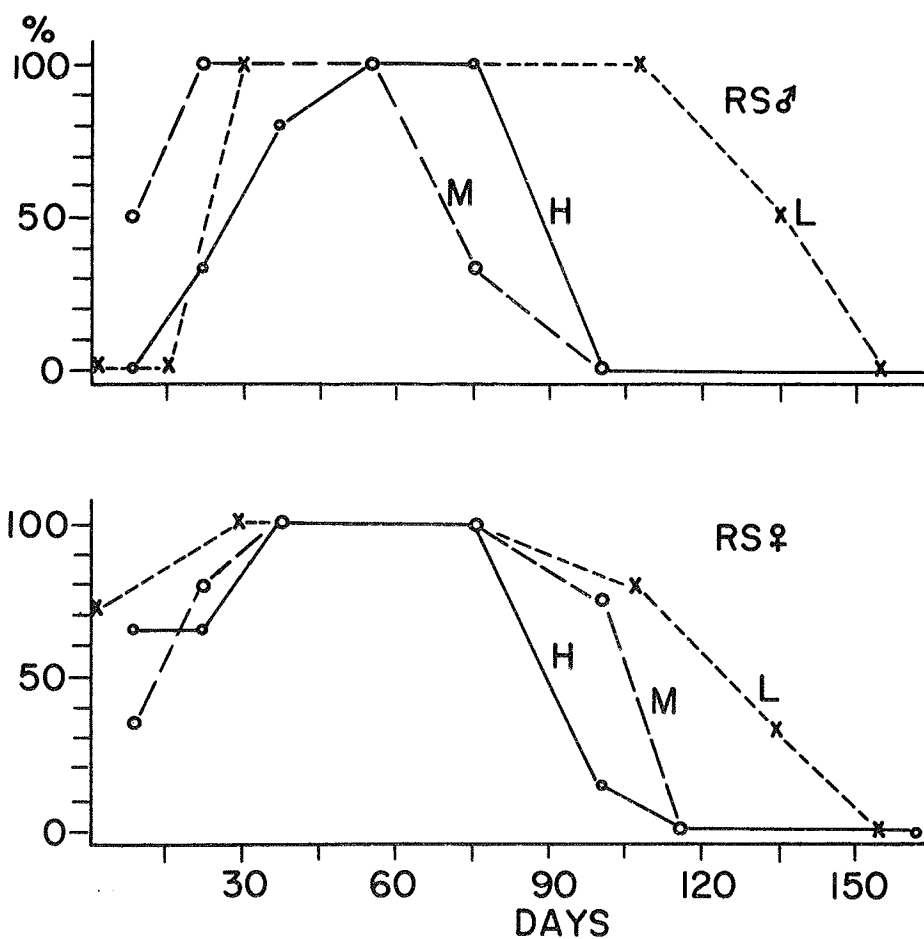


Figure 5. Frequency and duration of sexual activity in resident *P. formosus* in the three treatment areas, high (H), medium (M) and low (L) density. Day 1 = March 6, 1972. Vertical axis is % of RS mice that are sexually active. (Derived from DSCODE A3UCC01).

The frequency of pregnancy and number of weaned young are summarized in Table 3. All RS females that survived until April became pregnant. At high and medium densities, 33% of females were pregnant twice, and at low density, 14%. INT females were more successful in completing reproduction in the medium density area than in high. Only in the medium density area did young of the year breed successfully. The number of weaned young per successful pregnancy is inversely related to density, but the ratios are not significantly different by Chi-square test. No young of year males became sexually active.

Table 3. Incidence of pregnancy and weaning of young in the three treatment areas (derived from DSCODE—A3UCC01)

	High Density				Medium Density				Low Density		
	RS	INT	B	All	RS	INT	B	All	RS	B	All
No. animals	13 ^b	40 ^a	32	85	6 ^b	13 ^a	43	62	7	24	31
No. pregnant	9 ^b	13	2	24	4 ^b	6	9	19	7	0	7
No. pregnancies	12	14	2	28	5	8	9	22	8	0	8
% double pregnancies	33	8	0	17	20	33	0	16	14	0	14
No. successful pregnancies ^c	11	8	0	19	5	8	3	16	8	0	8
% successful	92	57	0	68	100	100	33	73	100		100
No. weaned				73				84			45
Weaned/successful pregnancy				3.84				5.25			5.63
Weaned/pregnancy				2.61				3.82			5.63

a/ counting only those females that were captured in at least two sampling periods after being introduced into the area

b/ the only females that did not become pregnant were those captured in only the 1st and 2nd periods, dying after that

c/ success means that the female was present in the area and lactating after having been observed pregnant

Growth and development

Growth rates are summarized in Table 4. Because of the variability of the individual, there is no significant difference between sexes or density treatment within weight classes. However, it seems clear that mice in the medium density area grew faster than those in the high density, and in general, males grew faster than females. The differences are cumulative through time. As estimated from table 4, growth from 14 to 18 g took 73 days for males in the high density plot versus 56 days in medium density; for females it was 81 days versus 62 days. Growth from 11 to 18 g is estimated as 115 days for females in high density and 78 days in medium density. This latter difference is significant ($\chi^2 = 7.16$). Analysis of variance shows that growth rates for mice in weight classes 14 through 18 g did not vary significantly with density ($F = 2.06$, d.f. 1, 172), but did vary significantly with sex ($F = 12.31$) and weight class ($F = 11.66$, d.f. 5, 172). There was also a significant sex X weight class interaction ($F = 7.93$, d.f. 5, 172).

Table 4. Average growth rates of young of year (derived from DSCODE—A3UCC01)

Weight Class gm	Average growth rate, $K \times 10^5 \pm$ S.E.				Low Density Both Sexes
	High Density		Medium Density		
	Males	Females	Males	Females	
8-8.9	---	---	3430 ₍₁₎ *	---	---
9-9.9	---	3310	2290 ₍₂₎ ⁺ 505	2316 ₍₂₎ ⁺ 1001	---
10-10.9	---	---	---	1699 ₍₁₎	
11-11.9	2700 ₍₂₎ ⁺ 630	1865 ₍₂₎ ⁺ 503	913 ₍₂₎ ⁺ 268	2015 ₍₁₎	1684 ₍₂₎ ⁺ 475
12-12.9	---	1108 ₍₃₎ ⁺ 258	1070 ₍₅₎ ⁺ 148	1282 ₍₄₎ ⁺ 240	1043 ₍₁₃₎ ⁺ 65
13-13.9	---	331 ₍₂₎ ⁺ 134	1080 ₍₅₎ ⁺ 238	1395 ₍₇₎ ⁺ 528	733 ₍₁₎
14-14.9	513 ₍₇₎ ⁺ 89	629 ₍₆₎ ⁺ 103	661 ₍₁₀₎ ⁺ 113	660 ₍₁₃₎ ⁺ 152	288 ₍₆₎ ⁺ 83
15-15.9	320 ₍₁₄₎ ⁺ 48	336 ₍₁₁₎ ⁺ 215	400 ₍₁₂₎ ⁺ 30	452 ₍₁₂₎ ⁺ 71	369 ₍₅₎ ⁺ 48
16-16.9	347 ₍₁₁₎ ⁺ 93	364 ₍₁₀₎ ⁺ 71	500 ₍₁₆₎ ⁺ 76	364 ₍₁₂₎ ⁺ 92	71 ₍₅₎ ⁺ 242
17-17.9	264 ₍₅₎ ⁺ 132	167 ₍₆₎ ⁺ 76	325 ₍₁₀₎ ⁺ 78	274 ₍₅₎ ⁺ 67	139 ₍₈₎ ⁺ 71
18-18.9	208 ₍₉₎ ⁺ 105	171 ₍₉₎ ⁺ 141	340 ₍₆₎ ⁺ 114	49 ₍₆₎ ⁺ 106	---

*Number of cases in parentheses

2.3.2.1.-16

Because of the missing weight classes and small classes in Table 4, we pooled all data for a general growth curve (Table 5). The smallest mice captured ranged from 8.0 to 9.5 g; French et al. (1973) never captured animals less than 11 g. We think it is reasonable to assume an age of 20 days for 9.5 g *P. formosus*, based on the known ages of weaning for *P. longimembris*, *P. californicus* and *Dipodomys merriami* (14-18, 22-24, and 19-22 days, respectively) as reported by Hayden and Gambino (1966) and Eisenberg and Isaac (1963). The growth curve of Figure 6 is begun at 20 days and 9.5 g and developed further using the information of Table 5.

Table 5. Growth of *P. formosus* young of year, by weight classes

Weight Class	n	$K \times 10^5 \pm S.E.$	Plotted Weight, g	Age at that Weight, Days
8-10.9	8	2852 ± 253	9.5	20
11-11.9	9	1815 ± 268	11.5	26.7
12-12.9	24	1103 ± 65	12.5	31.0
13-13.9	11	745 ± 196	13.5	38.3
14-14.9	33	588 ± 68	14.5	47.9
15-16.9	84	447 ± 33	16	64.6
17-18.9	41	202 ± 31	18	90.0
			20	143.1

Note: Data pooled for sexes and treatments.

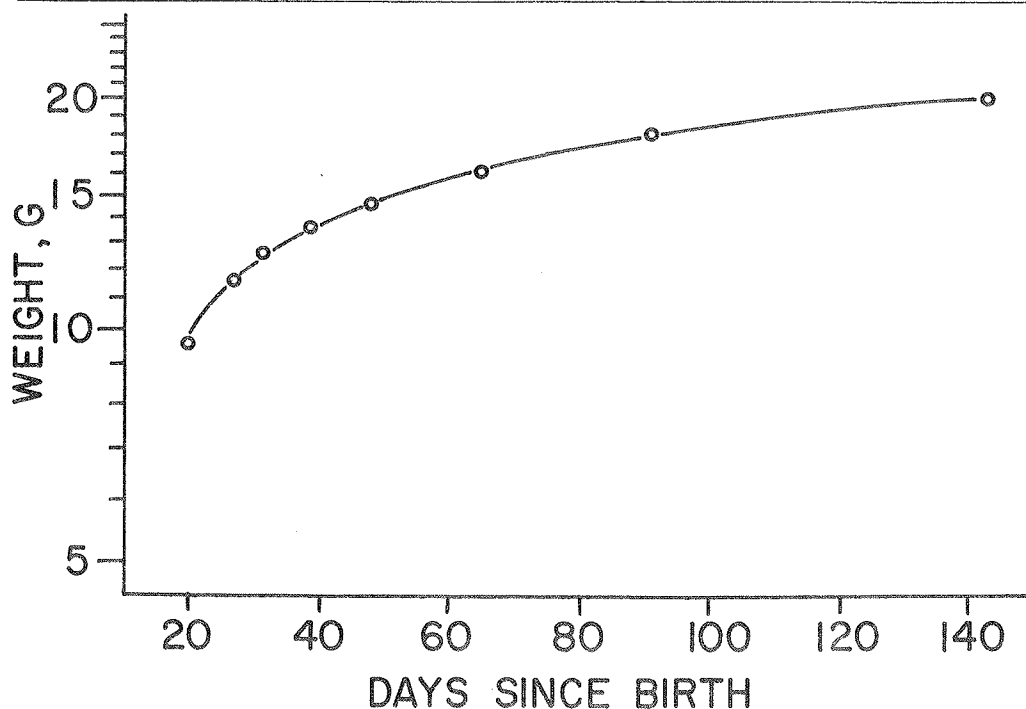


Figure 6. Growth of *P. formosus* in Plots A and C based on growth rates pooled for sexes and all treatment areas (Table 5).

Figure 6 was used to estimate the birth dates of animals from their weight at first capture. Figure 4 shows the frequency distribution of the births. The distribution is probably not different in high and medium density areas, with median dates of April 6 and 18. Births occurred later in the low density area, having a median of May 19.

Table 6 gives the average weights of *P. formosus* when they were first observed in the adult pelage. There is no significant difference among categories.

Table 6. Average weight of *P. formosus* when they were first observed in adult pelage (derived from DSCODE--A3UCC01)

Area	Average weight, g \pm S.E. (n)	
	Males	Females
High density	17.81 \pm 0.292 (24)	16.91 \pm 0.292 (22)
Medium density	18.63 \pm 0.267 (31)	18.04 \pm 0.315 (31)
Low density	18.00 \pm 1.150 (3)	17.04 \pm 0.467 (11)

Survival

The *P. formosus* in Plot C in August 1971 had a survival over winter of $18/37 = 0.49$ for females and $14/28 = 0.50$ for males. In March 1972 most of the residents in Plots A and C were 2 years old (31/36); the other 5 mice ranged from 0.7 to 3.8 years old. The percentage survival of these RS is shown in Figure 1. Survival was inversely related to density, but the differences among areas developed mostly after July. The areas under the curves are not significantly different if the period to October 13 is included ($\chi^2 = 16.8$).

The survival of introduced mice differed among areas. Mice put into the high density area in February, March and April had low survival, but the May cohort had high survival (Table 7). However, INT mice that moved from the high density to the medium density area had high survival regardless of month of introduction. The INT mice in medium density had the same survival as the RS; both had significantly higher survival than INT mice in the high density area, as shown in Figure 2 ($\chi^2 = 31.8$ for the difference between high and medium).

The survival of the first cohort of young animals (first captured May 17-19) was the same as the RS mice, but survival was less in later cohorts. The survival of later cohorts was inversely related to density (Figure 3); the curves are significantly different. The nearly linear sections of the semilogarithmic plots of Figure 3 show that in some cases survivorship is exponential.

Table 7. Survival of *P. formosus* introduced into high and medium density area, for 150 days after introduction

Cohort Introduced	% Surviving 150 days		
	High Density Males	Females	Medium density Females
February 10-17	0	0	50
March 6	0	11.1	100
March 23-26	6.3	7.2	100
April 11-16	0	-----	100
May 11	47.7	44.4	71.4
All cohorts	16.0	23.4	76.9

Home range

Table 8 summarizes information on the 2-sigma home ranges of RS, INT and B mice. Except for one case, males have a larger home range than females. The sexual difference is significant for RS and INT groups but not for B. With one exception, home range is inversely related to density. Home range varies significantly with density in all categories.

Table 8. Summary of home range information (derived from DSCODE—A3UCC01)

Category	Density	Sex	Ave. sigma, m \pm S.E.	n	2-sigma range	
					m	m ²
RS	High	m	19.38 \pm 1.81	5	38.76	4720
	High	f	14.43 \pm 0.82	8	28.84	2613
	Medium	m	19.08 \pm 3.46	3	38.16	4574
	Medium	f	16.73 \pm 4.08	4	33.46	3517
	Low	m	55.98 \pm 15.1	2	111.96	39380
	Low	f	19.59 \pm 2.02	6	39.18	4822
INT	High	m	14.94 \pm 2.48	10	29.88	2804
	High	f	11.94 \pm 0.70	21	23.88	1792
	Medium	m	34.63 \pm 23.8	2	69.26	15070
	Medium	f	12.80 \pm 1.53	10	25.60	2059
B	High	m	13.07 \pm 1.91	23	26.14	2147
	High	f	12.83 \pm 0.86	18	25.66	2069
	Medium	m	11.31 \pm 0.58	29	22.62	1607
	Medium	f	10.82 \pm 0.51	30	21.64	1471
	Low	m	17.48 \pm 2.08	5	34.96	3840
	Low	f	22.18 \pm 0.39	13	44.36	6182

Analysis of Variance, F Values

Source of Variation	RS Mice	INT Mice	B Mice
Area	F = 22.95 (2,22)	F = 10.48 (2,39)	F = 8.25 (2,106)
Sex	F = 22.98 (1,22)	F = 15.30 (1,39)	not sig.
Area x sex	F = 16.46 (2,22)	F = 8.80 (2,39)	not sig.

Other species

Similar data are available on the other species in the study plots, but numbers of individuals are much smaller. These data have not been analyzed, except for initial numbers and biomass; details are in data set A3UCC01.

Seed density and distribution

Tables 9 and 10 give the densities and distributions of seeds among the strata sampled in February 1972. The other two collections have not been completely analyzed. Total seed density and densities of seeds of perennials and of annuals separately are all significantly higher under shrubs than in the open ($P < 0.01$) (Table 10). When the distributions of seeds of individual species are examined, only 5 of 35 species have significantly higher seed densities ($P < 0.05$) under shrubs than in the open: *Bromus rubens*, *Festuca octoflora*, *Gilia* sp., *Pectocarya* sp. A and *Pectocarya* sp. B (Table 10). No species has a significantly higher density in the open.

The species of shrub under which the samples were taken had no significant effect on the variation of the total number of seeds. But, the numbers of five species of seeds did vary significantly with canopy species (Table 9). *Ambrosia dumosa*, *Larrea divaricata*, and *Lycium andersonii*, each each had its highest seed density under its own canopies. The most abundant seed, *F. octoflora*, was densest under *L. divaricata*; seeds of Unknown sp. A were most abundant under *L. andersonii*.

Table 11 summarizes the significant correlations of seed densities with the sampling attributes. Total seed density under shrubs is positively correlated with canopy area (Figure 7) and volume. Seed density in open areas is inversely related to distance from shrub canopies (Figure 8) and area of the open space. Density of seeds of annuals is significantly correlated with canopy area and volume, distance from canopy and area of open space. Density of perennials has no significant correlation. *F. octoflora* is the only species that has any significant correlation (Table 11).

Table 9. Mean seed densities for canopy samples of February 1972

Seed Taxon†	Canopy species				
	<i>Ambrosia</i>	<i>Ephedra</i>	<i>Krameria</i>	<i>Larrea</i>	<i>Lycium</i>
	Seeds/m ² ± S.E.				
<i>Ambrosia dumosa</i> F = 7.22 (4,25)**	80.0 ± 35.0	0	3.3 ± 3.33	0	6.7 ± 6.67
<i>Larrea tridentata</i> F = 3.92 (4,25)*	0	0	3.3 ± 3.33	30.0 ± 14.4	0
<i>Lycium andersonii</i> F = 3.46 (4,25)*	6.7 ± 6.67	30.0 ± 16.1	10.0 ± 10.0	6.7 ± 4.22	157 ± 67.0
<i>Festuca octoflora</i> F = 4.18 (4,25)*	1200 ± 245	793 ± 172	1690 ± 412	3078 ± 615	1277 ± 383
Unknown sp. A F = 3.67 (4,25)*	6.7 ± 6.67	30.0 ± 16.9	36.7 ± 32.8	4.33 ± 21.6	1767 ± 1138
All perennials	86.7 ± 32.5	30.0 ± 16.1	16.7 ± 9.55	36.7 ± 15.9	163 ± 70.5
All annuals	2153 ± 455	1000 ± 183	2720 ± 680	3990 ± 662	3997 ± 1679
All seeds	2240 ± 465	1030 ± 196	2737 ± 679	4027 ± 661	4160 ± 1702

Note: F value for variation between canopy classes is given under each taxon (d.f.), significance as ** (P < 0.01), * (P < 0.05)

† The species listed are the only ones that showed significant variation between canopy species on analysis of variance of square-root transformed data. Details are in DSCODE—A3UCC02.

Table 10. Mean seed densities for canopy and exposed samples of February 1972
(data derived from DSCODE—A3UCC02)

Seed Species	Seeds/m ² ± S.E.	
	Canopy	Exposed
<i>Ambrosia dumosa</i>	18.0 ± 8.81	1.7 ± 0.96
<i>Ephedra nevadensis</i>	0	0.6 ± 0.57
<i>Krameria parvifolia</i>	0	0
<i>Larrea tridentata</i>	6.7 ± 3.50	0.6 ± 0.57
<i>Lycium andersonii</i>	42.0 ± 16.99	10.3 ± 4.74
<i>Bromus rubens</i>	131 ± 32.36	8.6 ± 2.36**
<i>Chaenactis</i> spp.	17.3 ± 6.34	8.6 ± 2.99
<i>Caulanthus cooperi</i>	6.0 ± 6.00	0
<i>Chorizanthe brevicornu</i>	14.7 ± 6.06	4.0 ± 1.60
<i>C. rigida</i>	28.0 ± 12.56	14.3 ± 5.09
<i>Cryptantha</i> sp.	9.3 ± 5.35	4.0 ± 1.80
<i>Eriogonum</i> spp.	1.3 ± 0.93	1.7 ± 1.26
<i>Erodium</i> sp.	0	0.6 ± 0.57
<i>Eschscholzia glyptosperma</i>	2.7 ± 2.68	0
<i>Euphorbia micromera</i>	11.3 ± 5.07	9.7 ± 3.96
<i>Festuca octoflora</i>	1609 ± 221	236 ± 44.39**
<i>Gilia</i> sp.	36.0 ± 18.63	0.6 ± 0.57*
<i>Ipomopsis polycladon</i>	31.3 ± 13.00	28.0 ± 6.92
<i>Langloisia</i> sp.	25.3 ± 6.17	21.7 ± 7.12
<i>Mentzelia veatchiana</i>	16.0 ± 9.06	0
<i>Mirabilis pudica</i>	0.7 ± 0.67	0.6 ± 0.57
<i>Nama</i> sp.	0	1.7 ± 1.71
<i>Oryzopsis hymenoides</i>	1.3 ± 0.93	0.6 ± 0.57
<i>Pectocarya</i> sp. A	212 ± 31.90	9.7 ± 2.76**
<i>Pectocarya</i> sp. B	108 ± 44.90	8.6 ± 2.88**
<i>Phacelia fremontii</i>	17.3 ± 11.41	1.7 ± 0.57
<i>P. vallis-mortae</i>	14.7 ± 8.93	0.6 ± 0.96
<i>Stephanomeria exigua</i>	2.6 ± 1.48	0
<i>Streptanthella longirostris</i>	2.0 ± 2.01	0
<i>Tridens pulchellus</i>	1.3 ± 0.93	0
Unknown sp. A	377 ± 249	19.4 ± 4.88
Unknown sp. B	11.3 ± 7.45	49.7 ± 28.69
Unknown sp. C	8.7 ± 3.57	12.0 ± 6.82
Unknown sp. D	30.6 ± 12.34	30.9 ± 20.36
Unknowns	30.0	2.3
All perennials	66.7 ± 18.23	13.2 ± 4.70**
All annuals	2772 ± 428	476 ± 63.86**
All seeds	2839 ± 434	489 ± 63.32**

* P < 0.05, Significance as determined by t-test.
** P < 0.01, Significance as determined by t-test.

Table 11. Significant regressions of seed densities on various sample attributes
(derived from DSCODE—A3UCC02)

Dependent Variable (Y)	Independent Variable (X)	a	b	r
$\sqrt{\text{Total seed density}}$	Canopy area	40.5	19.7*	0.403*
$\sqrt{\text{Total seed density}}$	Shrub volume	43.4	61.6*	0.373*
$\sqrt{\text{Total seed density}}$	Minimum distance from canopy	29.1	-6.3**	-0.503**
$\sqrt{\text{Total seed density}}$	Area of exposed area	24.3	-0.46**	-0.528**
$\sqrt{F. octoflora \text{ density}}$	Minimum distance from canopy	21.7	-5.7*	-0.478**
$\sqrt{F. octoflora \text{ density}}$	Area of exposed area	17.3	-0.40*	-0.478**

* $P < 0.05$ ** $P < 0.01$

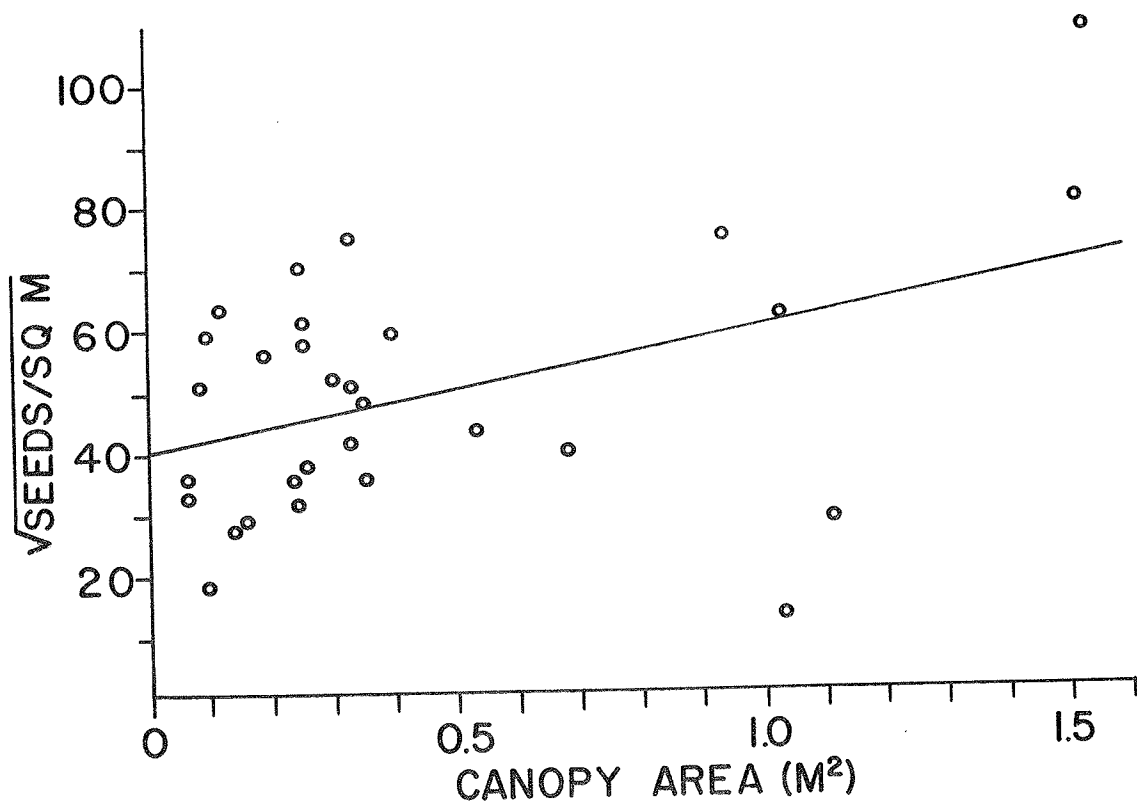


Figure 7. Regression of seed density on area of canopy under which sample was taken.
(Table 11).

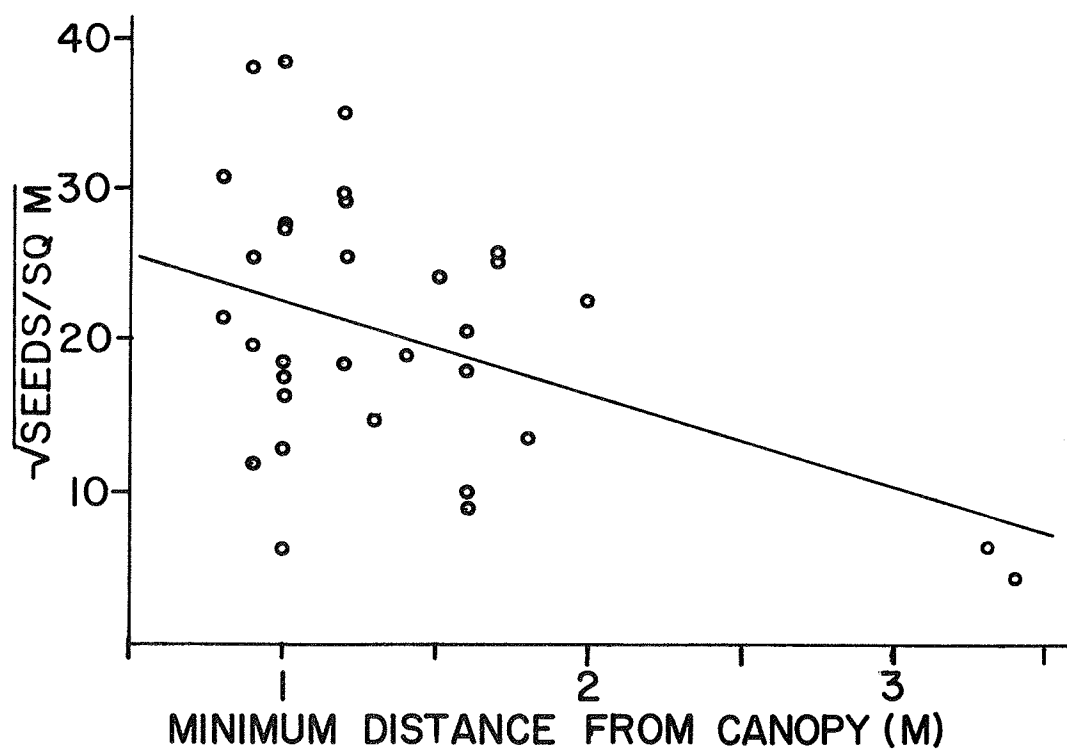


Figure 8. Regression of seed density on minimum distance of sample from shrub canopies. (Table 11).

DISCUSSION

Changes in population size

The degree of "success" of the *P. formosus* populations in the study plots in 1972 was unexpected for several reasons. Total dry matter production of annuals was low in 1971 and 1972 (Turner 1972, 1973), and there is good evidence of a correlation between production of annuals and rodents (Beatley, 1969). There was good fruiting by perennials, especially *Lycium andersonii*, but not until after reproduction was well under way. French et al. (1973) stated that, "there was virtually no reproduction...during...1970 and 1971", referring to *P. formosus*. In March 1972 the density of *P. formosus* in Plot A (1.14/ha) was lower than ever recorded in the period 1962-1968 (French et al., 1973). Density in the southern half of Plot C after the removal of half the RS was almost as low (2.95/ha) as that previously recorded (2.18/ha, October 1963). However, births began in Plot C in late January and continued through May; in Plot A births occurred from March through July at least. The peak density in the high density area (28.9/ha) exceeded the highest natural peak recorded for Plot C (27.8/ha, May-July 1966). The peak in the medium density plot (25.2/ha) was exceeded only by the 1966 peak. There is a gap in our understanding of the conditions that result in good reproduction by *P. formosus*; this may be filled by the information on plant and abiotic conditions in the 1972 season.

There are two patterns of numbers change in the study plots. In plot C numbers reached a peak in June and then declined to 36% (high density area) and 48% (medium density) of the peak. Numbers increased steadily in Plot A from March through October. Previous data from these plots show a lack of consistency in the time of maximum numbers from year to year. The factors affecting population size must be too erratic for any consistent annual pattern. The data suggest that the density at the beginning of the year is also a factor determining when the peak occurs. The population beginning with 1.14/ha grew continuously without reaching carrying capacity; the populations beginning with 2.95/ha and 8.18/ha exceeded carrying capacity and declined.

The general impression from the changes in abundance is that the artificially high density could not be sustained because there were no unexploited resources to support the increase. The artificially-reduced population in the medium density area had sufficient reproductive potential to quickly "take up the slack" of unused resources and closely followed the opportunities of the system. In the low density plot the initial density was near the extinction threshold. In spite of maximum performance per pregnancy this population could not grow fast enough to take full advantage of the resources in 1972, because of delay in the beginning of reproduction.

Reproduction

Density clearly affected reproductive behavior, particularly the success of pregnancies and the timing of breeding (Table 3). The resident mice were not as old as predicted by French et al. (1973). As we judged from the cumulative trapping records for Rock Valley, the RS mice had a median age of 2 years at the beginning of March 1972, rather than 3 years. There was no difference in the survival of residents ranging from 0.7 to 3.8 years of age, and all females that survived through March became pregnant at least once. The RS females accounted for the majority of reproduction.

Introduced mice did not have as high an incidence of pregnancy as RS, which is expected for several reasons. The introduced animals had to establish a home range and had no food caches of their own to begin the breeding season; some had already bred before they were introduced; and others were juveniles. The majority of successful introductions were of the cohort of May 10-12, when breeding was declining in Plot C (last pregnancy observed May 19). In our plan the function of the INT mice was to provide "density pressure" rather than reproductive potential. The pressure of density on the ability of an INT mouse to breed is seen in the difference between the mice that were self-introduced into the medium density area and those that remained in the high density plot. Of the former, 6 of 13 became pregnant, and of the latter, 13 of 41; there were 8 successful pregnancies in each group.

Two young of the year in the high density plot and 7 in the medium became pregnant. Eight of these were pregnant when first captured May 19, in juvenile pelage and with body weights of 16.8 to 23.9 g. If the weights of these mice are reduced by 2.7 g (for fetal tissues), their birth dates as estimated from Figure 6 range from January 24 to March 31, with a median of March 1. This would make them 1.5 to 4.0 months old at the time of their pregnancy. Such extrapolations of birth date are uncertain, but it is probable these mice were of an early cohort. They thus had time to grow and mature sufficiently and still be within the breeding period. Reproduction by *P. formosus* young of the year is uncommon. French et al. (1973) recorded this once in 5 years, in June 1966 by females that were 2-3 months old. Only 3 of the young, all in the medium density area, were successful in their pregnancy, so they contributed no more than 3/16 (19%) of the reproduction by this population.

The success of reproduction is clearly related to density as shown in Figure 9. The only significant correlation is the number of young weaned per successful pregnancy with density ($r = 0.991$, $P < 0.05$). The number weaned per pregnancy in the low density population (in which all pregnancies were successful) was 5.63; this is the same as the average litter size (6) reported by French et al. (1973).

The information for Plot A suggests to us that breeding was delayed by low density. In April there were only 2 males and 7 females in 8.8 ha. Even with the large home ranges of

these males (6.3 and 2.1 ha), the incidence of meeting and successful mating must have been less than in the other plots. The first young were born about March 19, about 50 days after the first births in Plot C. These young may have reached breeding size too late to become pregnant. The field data suggest there are two kinds of determinants of length of breeding season. The continuation of sexual activity in Plot A for at least a month after Plot C suggests a density-dependent effect (behavioral and/or food) in the high and medium density populations. The failure of young to breed in Plot A, where they were born late, suggests a weather effect (directly or via an effect on vegetation) or a seasonal effect (photoperiod).

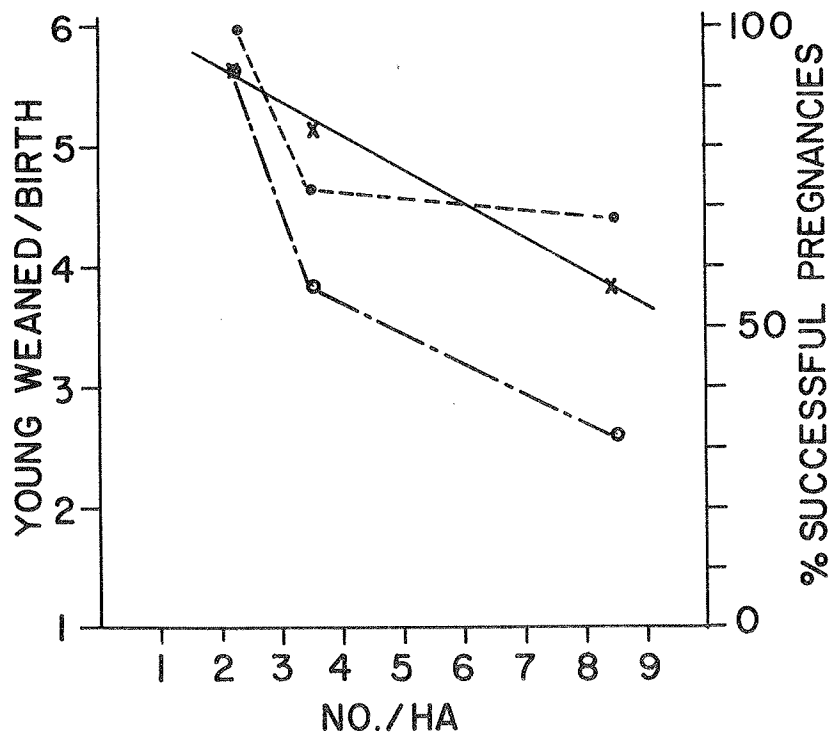


Figure 9. Relationship of three dependent variables to density: young weaned/successful pregnancy (solid line plotted as regression), young weaned/pregnancy (broken line), and % successful pregnancies (dashed line). Regression: weaned/successful birth (Y) = $6.25 - 0.310 (X)$, where X is the density at the median time in the frequency distribution of births.

Growth

It was expected that body weight, particularly of young growing mice, would be a good indicator of the environmental effects. Body weight has been used in this way in other studies of rodents (Joule and Jameson, 1972, and citations therein). However, body weight of growing animals may be too sensitive an indicator. Each animal may be so sensitive to its own particular circumstances, and the circumstances may be so heterogeneous, that the variability of response in any area confounds statistical analysis. As expected, growth does seem to be slower in the high density area than the medium density area, but growth in the low density plot was even slower. The weight and growth rate data need a more complicated analysis than has been done thus far.

Survival

The patterns of survival (Figures 1,2,3) suggest the influence of several factors on pocket mice: (1) Experience. After 2 years a resident animal should have a well-established home range within which it is familiar with food resources and as secure as possible from predation. Of the RS mice, 87% showed no shift of the center of their activity between their 1968-1971 range and their 1972 range. Familiarity with an area does convey protection from predation (Ambrose, 1972, and citations therein). Consistent with these expectations, we observed little or no effect of density on survival of resident mice. (2) Dispersal to a new area. Animals face exceptional hazards when they enter a foreign area. Presumably the lack of an established home range and food caches would be particularly deleterious when the weather is cold. This may be the explanation for the very low survival of *P. formosus* put into the high density plot in March and April (mean air temperatures 19.3 and 16.1 C) as compared to the good survival in May (20.8 C). (3) Density. The higher survival of mice introduced into the medium density area in March and April shows that cold and lack of caches is an impossible stress only when shelter and seed reserves must be competed for with residents that already "saturate" the area with their activity. In general, mice introduced into the high density area and meeting this competition died quickly; conversely, mice entering the medium density, which had fewer residents, generally survived. (4) Age. The high survival of the "inexperienced" young of the first cohort, equalling that of the "experienced" parents, probably illustrates the benefit of youth over middle and old age. The lower survival of later cohorts is a result of density interaction.

Home range

Home range obviously should show a density dependence, but the effects of density could easily be obscured. As it is measured in this study, the 2-sigma home range is a datum assembled through time, while the individual pocket mouse is experiencing changes

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of weather, food, traps, bait, and disturbance by ecologists, in addition to differences in density. However, we did find that home range is inversely related to density. White (1964) found that home range of *Peromyscus* was inversely related to density.

Since males are so wide ranging (Table 8), it is the "conservative" females and the asexual young that are the best indicators of density effects on home range. Table 12 gives the correlations of home range area and density for the comparisons that are possible. Home ranges of female *P. formosus* are significantly correlated with density.

Our range values are similar to those of Maza et al. (1973). They found a 2-sigma range of 31 meters for 1443 *P. formosus* with 39,200 captures over 7 years in three enclosures and one unenclosed trapping grid. The average 2-sigma range varied from 28.2 to 37.2 m for the four areas. The average range for all our animals (Table 8) is 28.8 m, varying from 21.6 to 112.0 m for different categories of mice.

A summation of individual home ranges for each density treatment area (Table 13) shows that the sum of 2-sigma ranges exceeds the 4.4 ha size of the study plot in all but two cases. If summation is done in terms of a 1-sigma range, the sum still exceeds plot size in 6 of 11 periods in the high density area and 3 of 11 in medium density, but never in the low density area. The total "excess" is proportional to density (Table 13).

How *P. formosus* interact in the field is not known, but we can extrapolate from the laboratory observations of Eisenberg (1963). The 2-sigma ranges must overlap extensively (Table 13), so this range is not an area of exclusive use. The home range of each mouse must be temporally interdigitated with the areas of other individuals. In the laboratory when two pocket mice perceive each other, the "intruder" is defensive and exhibits flight and escape patterns. Tail-flagging, drumming, chattering and growling usually keep the mice from physical contact. A "resident" mouse may establish its preeminence simply by greater use of the area around its center of activity and hence greater tagging of the area with its odors. In the laboratory an intruder pocket mouse investigates urination spots and areas of perineal dragging of the resident. Pocket mice tend to sand bathe at the same spot as a previous mouse. These areas may provide information on what individuals are present and their sexual condition.

These kinds of interactions could affect home range size. The extreme ranges (2-sigma greater than 150 m) are predominantly in the low density area, where they make up 5 of 26 cases, as compared to 4 of 78 in the medium density area, and 2 of 85 in high density. The space between "digits" of a home range obviously decreases towards the center of activity of the range. The extent of overlap of 1-sigma areas, the central 1/4th of a 2-sigma home range, illustrates the packing problem of the populations in the high and medium density areas.

It is not known how meetings between pocket mice affect their reproductive success, survival and growth. The energy used in inter-individual interactions may be a significant diversion of energy from reproduction, maintenance or growth. Interactions may inhibit feeding, or within overlapping ranges animals may steal each other's food caches. There might be pheromone inhibition of development of fetuses, as is known for *Mus musculus*, or an endocrine stress syndrome. We do hypothesize that behavioral interactions are the limiting factor on the size of *P. formosus* populations under the conditions in our enclosures.

Table 12. Regression of 2-sigma home range (Table 9) on density, where density is the value at the midpoint in the sequence of captures that went into calculating the home range

Category	Regression	r
RS males	$Y = 39,576 - 2050 X$	-0.909 n.s.
RS females	$Y = 5073 - 124.9 X$	-0.9999 *
B males	$Y = 4432 - 127.2 X$	-0.992 n.s.
B females	$Y = 7230 - 255.9 X$	-0.997 *

Y = home range (m²)

X = no./ha

* P = < 0.05

Seed distribution and density

The distribution of seeds is a function of several factors: distribution of the parent plants, transport by wind and water, caching by rodents. Litter at the bases of shrubs and topographic features such as washes may retard or direct the movement of seeds. Characteristics of the seed such as shape and mass and palatability could influence their distribution.

The higher density of seeds under shrubs and the decrease of density with distance from shrubs is probably due to a higher production of seeds by annuals under shrubs. Turner, Medica and Smith (1973) found, "the vast majority of annuals occurred beneath shrubs rather than in open areas" in their irrigated and control plots near Mercury. Our cursory observation was that the few annual seedlings that were present in February and October were only under shrubs. On the validation site the soil is deeper and has a different profile and higher moisture content under shrubs than in bare areas (Turner, 1972).

The association of perennial seeds with their own canopies is not surprising. The fact that only three annuals showed significantly higher seed densities under shrubs than in the open may be a result of a large sampling error. The fixed-area sampler extended beyond the canopy when smaller shrubs were sampled, and a variable amount of bare space was thus contaminating the "under canopy" sample. In June and October four smaller samples were collected under each shrub in place of the single 0.05^2 sample taken in February.

Our seed density values for February 1972 are consistent with other information. Of the 10 most abundant annual seeds (Table 10), 7 species are among the 10 annuals most abundant on the validation site in 1971 (Turner, 1972). Three of the top 10 seed species in our list are among the 10 most abundant seeds in stomach contents of *P. formosus* (French et al., 1973).

French et al. (1973) estimated shrub coverages in the plots as 14.6% (bare space thus = 85.4%). Our average seed densities (Table 10) and this coverage estimate give a seed density for the study plots of: $10,000 \times ((489 \times 0.854) + (2839 \times 0.146)) = 8,320,000$ seeds/ha. Assuming a dry weight of 0.5 mg per seed, this is equivalent to a biomass of 4.16 kg/ha. French et al., (1973) found seed productions by shrubs and annuals ranging from 5.31 to 80.92 kg ha⁻¹ year⁻¹ for Plots A and C, 1966-1968. Thus, the accumulated reserves of seeds in the upper 2 cm of soil in February is equal to about annual seed production.

Our trap-baiting procedures left 0.43 kg of oats per ha in Plot A, 1.45 kg/ha in Plot C from March through August; these artificial inputs of seed are 10.6% and 34.9% of the natural seed reserve present in February. The larger input of oats into Plot C was due to the greater incidence of captures in this plot.

EXPECTATIONS

We hypothesize from the 1972 results that the carrying capacity of a Mohave Desert ecosystem for *Perognathus formosus* is limited by density acting through behavioral interactions. If this interaction can be reduced by reducing the sensory perception of pocket mice of each other, then an area should be able to support a higher density. To test this hypothesis experimentally, in 1973 one plot will be supplied with 1000 m of 31.5 cm high sheet metal baffles in 16 m lengths, on a repetitive pattern based on the 1-sigma home range of mice in 1972. Animals will be introduced into this experimental area (northern side of Plot C) and into the unbaffled southern side of Plot C, up to densities of 30/ha. The dynamics of the two *P. formosus* populations will test

the hypothesis. If the hypothesis is correct, a higher density will persist on the side with the sheet metal baffles.

It is also possible that competition for food is a limiting factor. To test this, a contiguous 1/3 of Plot A (about 2.9 ha) will be supplemented with seeds put out at 15 m intervals. We will observe the dynamics of the population in Plot A for different responses in the two unfenced halves of the plot.

ACKNOWLEDGEMENTS

Peter August and Ward Cockrum did the live trapping in Rock Valley. Peter August made preliminary analyses of data as they accumulated. Bernardo Maza helped with the trapping and supervised and trained other field personnel. Arthur Vollmer also helped with the trapping. James Nelson supervised and participated in the seed sampling program, processed the soil samples and analyzed the seed information. Mary Willenborg assisted in taking soil samples.

We thank Norman French and Bernardo Maza for the opportunity to have advance copies of their in-press manuscripts.

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1972 PROGRESS REPORT

NATURAL ACTIVITY PATTERNS AND THERMAL EXPERIENCE

IN *Dipodomys merriami*

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Research Memorandum, RM 73-19

MAY 1973

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Report Volume 3

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A B S T R A C T

Objectives of this study were to document by biotelemetric techniques the natural activity patterns and thermal experience of *Dipodomys merriami* on the western Sonoran desert. Technical difficulties prevented us from obtaining functional telemetric equipment. One year's demographic data on *D. merriami* and associated nocturnal rodents were obtained, along with temperature measurements of burrow, surface, and air. Activity patterns of *D. merriami* under simulated desert summer and winter conditions were examined in the laboratory.

Perognathus formosus was the most abundant nocturnal rodent in every month except December. Highest densities of *Dipodomys merriami* occurred from April through June. *Perognathus spinatus*, *P. fallax*, and *Peromyscus eremicus* were found in low numbers throughout the year. Biomass of *D. merriami* varied from 151 g/ha in April to 29.1 g/ha in January, while that for *P. formosus* varied from 196 g/ha in July to 21 g/ha in December. *D. merriami* was reproductively active from late February through September, and *P. formosus* and *P. spinatus* from late April through August. The study area was coldest, both above and below ground, from November through February. Burrow temperatures of 34-39.5 C were recorded from June through September, but we suspect *D. merriami* move to burrows deeper than 30 cm in these months. Captive *D. merriami* were active an average of 5.02 (± 0.38) hours during cooler months and 5.89 (± 0.51) hours during summer months. 68% of all activity was before midnight during winter while only 57% of summer activity was before this time. Captives thus seem to avoid the coldest part of winter nights, but space activity evenly over summer nights.

INTRODUCTION

The purpose of this study was to define the natural activity patterns of *Dipodomys merriami* on the western Sonoran desert, and to document the thermal experience of this species as a result of activity patterns. Knowledge of activity patterns is of prime importance in estimating energy flow as these patterns determine the regimes of temperature that the individual encounters. Thermal experience largely determines rate of energy flow, since most energy flow of endotherms is a function of temperature regulation and food gathering to satisfy the energy requirement for this regulation. No estimate of energy flow can be made until demographic and reproductive parameters are known for the species. These values, coupled with estimates of metabolic rates at different ambient temperatures, permit calculation of energy flow through the species by the equations proposed by Chew and Chew (1970).

The study of natural activity patterns in the past has been complicated by the techniques, such as repeated trapping, used to determine these patterns. Important to this study was the development of biotelemetric techniques for monitoring activity patterns and thermal experience. Early in 1970 the project leader began working with General Dynamics, Pomona, on the design of biotelemetric equipment for the project. and by late 1971 functional models were breadboarded. In spite of this progress we have experienced an inordinate delay in receipt of the finished system, and no transmitters were made available to the project in 1972. Our work this year was therefore devoted to obtaining necessary demographic and micro-temperature data. A laboratory environmental chamber has been used to collect data on activity patterns of *D. merriami* exposed to simulated desert temperature regimes.

In December 1972 we began work on an alternate telemetry system recently described in the literature (Osgood and Weigl, 1972) which shows promise for this type of study. Efforts in early 1973 will be directed toward use of this system to obtain the needed information on natural activity patterns and thermal experience.

OBJECTIVES

1. To determine the species of nocturnal rodents utilizing the study area in addition to *D. merriami*, and to determine the population dynamics and reproductive phenology of all species.
2. To determine the pattern of microtemperatures to which *D. merriami* is exposed, both in its burrow system and above ground, in the course of one calendar year.
3. To estimate the amount of time spent outside the burrow each night in the field, determine the times of activity in both warm and cold months, under simulated natural conditions in the laboratory.

METHODS

Study area

All studies were conducted at the Philip L. Boyd Deep Canyon Desert Research Center in Riverside County, California, operated by the University of California at Riverside. Deep Canyon extends in a north-south axis approximately 13 km from the northern face of Santa Rosa Mountain in the Santa Rosa range to its mouth on the desert slopes below to the north. The study area was located on an alluvial fan in Sheep Canyon at 275 m elevation, just south of where this smaller canyon drains into Deep Canyon.

The climate of this region is characterized by scant, erratic rainfall, high summer temperature, and cold winter nights. Based on ten-year averages, rainfall is heaviest in March and November-December, while April through June are the driest months. In the larger canyons sufficient ground water seeps along the drainage to support those desert plants requiring greater soil moisture, such as palo verde and smoke tree. High winds, often exceeding 48 km/hr are most prevalent during the spring months.

The study area lies entirely within the lower Sonoran life zone, and can be characterized as creosote-palo verde habitat. Creosote bush, *Larrea tridentata*, and palo verde, *Cercidium floridum*, are scattered throughout the wash in which the area is located. Other perennial shrubs, such as burro bush, *Fraseria dumosa*, indigo bush, *Dalea schottii*, smoke tree, *Dalea spinosa*, desert lavender, *Hyptis emoryi*, and cheesebush, *Hymenoclea salsola*, are also present. Frequency of occurrence and percentage cover for common shrub and tree species, as well as dominant soil types, are presented in Table 1. The only herbaceous plant found in the open sandy areas is a spurge, *Euphorbia* sp.

Population dynamics/reproductive phenology

In January 1972 we began mark and release studies (DSCODE A3UWW01) on an 8.9 ha study area in Deep Canyon previously utilized by the project leader for other studies. In April 1972 studies were shifted to a new 3.9 ha grid 0.5 km to the east in Sheep Wash in an area with a higher density of *D. merriami*. Stations in both of these areas were on a 15 m grid, with one trap per station. At initial capture each animal was marked by toe-clipping. For each capture we recorded sex, weight to the nearest 0.1 gm, and station of capture. The cheek pouches of heteromyid rodents were emptied prior to weighing. Reproductive condition was noted as follows: for males -- testes

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undeveloped or developed (with tubules of cauda epididimides distended by mature sperm); for females -- teats undeveloped or developed, parous (teats showing evidence of previous lactation) or nulliparous, vulva perforate or imperforate, lactating, pregnant, number of embryos as determined by palpation.

Table 1. Frequency of occurrence and percentage cover for common shrub and tree species, and dominant soil types, on Sheep Wash study area

Species	% Frequency	% Cover
<i>Larrea divaricata</i>	6.94	1.98
<i>Cercidium floridum</i>	6.54	3.68
<i>Hymenoclea salsola</i>	11.80	2.27
<i>Hyptis emoryi</i>	4.16	1.57
<i>Beloperone californica</i>	6.94	2.19
<i>Krameria grayi</i>	1.73	0.21
<i>Dalea schottii</i>	2.77	1.03
<i>Dalea spinosa</i>	0.69	0.23
<i>Bebbia juncea</i>	2.43	0.27
<i>Encelia farinosa</i>	0.69	0.08
<i>Franseria dumosa</i>	3.47	0.41
<i>Acacia greggii</i>	1.38	0.47
<i>Opuntia bigelovii</i>	7.29	0.43
<i>Opuntia ramosissima</i>	6.59	0.78
<i>Opuntia acanthocarpa</i>	1.38	0.12
<i>Opuntia basilaris</i>	2.08	0.19
<i>Mammillaria microcarpa</i>	0.69	0.02
<i>Echinocactus acanthodes</i>	0.69	0.04
<i>Echinocereus englemanni</i>	0.34	0.01
Total Plant Material		15.98
Dead Material	31.25	6.51
Sandy Soil	64.45	57.27
Medium Rocky Soil	35.55	20.24
		100.00

Densities were estimated by use of the Hayne (1949) equation. The area sampled for each species was estimated by adding the mean distance traveled between captures for each species as a zone around the boundary of the study grid.

Microtemperature

For this aspect of the study temperatures were monitored at the following locations: 10 cm above ground in an instrument shelter, thermal element lying on the surface, thus measuring absorbed and radiated heat, and in two *D. merriami* burrows at approximately 30 cm depth (DSCODE A3UWW02). Recording instruments for burrow and surface were not available until May 1972, and readings earlier in the year were taken manually with a Yellow Springs telethermometer, which failed at the end of February and was not repaired until April. The surface recording instrument was destroyed by a flash flood in the middle of September.

Activity patterns under simulated desert conditions

A 14.15 m³ chamber equipped with temperature and light control was used to study activity patterns under simulated conditions (DSCODE A3UWW03). Temperature controls permitted replicable diel fluctuation of ambient temperature within the range of an early afternoon high and a night low set by the experimenter to conform with the desert conditions desired. Activity was indicated by movement through the burrow entrance or to food and water sources as recorded by mercury microswitches and a Rustrak 8-channel event recorder. Each animal was tested for one to two weeks at each set of environmental conditions, after first allowing the animal to become acclimated to the experimental setup. Warm season (afternoon high 40 C, night low 24 C) and cold season (afternoon high 24 C, night low 7 C) temperature regimes were utilized. Light cycles were held at 12L-12D throughout the entire experiment to standardize this variable. For six months animals that were kept in a constant temperature room (24 C) at 12L-12D were arrhythmic, suggesting that diel temperature fluctuation as experienced in the wild is of more importance than alternation of light and dark in influencing activity patterns in this species.

RESULTS

Population dynamics/reproductive phenology

Five species of nocturnal rodents occurred on the two study areas in Deep Canyon, DSCODE A3UWW01, (Table 2); but only *D. merriami* and *P. formosus* were trapped in significant numbers. Trap success for *D. merriami* varied from 1.60 to 8.47 individuals per 100 trap-nights, while success for *P. formosus* varied from 1.00 to 16.00 (Table 2). Densities of *D. merriami* varied from a high of 3.98 individuals per ha in April to a low of 0.81 per ha in January, while those of *P. formosus* varied from a high of 13.02 per ha in July to a low of 1.32 per ha in December (Table 2, Figure 1b). Mean weights of adults for each species per month are presented in Table 3. Biomass of *D. merriami* varied from 151 g/ha in April to 29 g/ha in January, while that of *P. formosus* varied from 196 g/ha in July to 21 g/ha in December (Table 2, Figure 1a).

Reproductive phenology, as determined by the presence of fertile males, pregnant or lactating females, and immatures in the trapped population, is indicated in Figure 2. No reproductively active female *P. spinatus* were taken, reproductively active female *P. formosus* were taken in only two months, and those of *D. merriami* in only one month. Using the growth data of Chew and Butterworth (1959), approximate ages were obtained for the immature *D. merriami*. These ages are added along the curve for this group in Figure 2.

2.3.2.2.-6

Table 2. Index of density and biomass of nocturnal rodents (A3UWW01)

Density (individuals per ha)						
	JAN	FEB	MAR	APR	MAY	
<i>Dipodomys merriami</i>	0.81	1.11	1.72	3.98	2.77	
<i>Perognathus formosus</i>	3.63	10.62	3.09	4.45	7.09	
<i>Perognathus fallax</i>	0	0	0	0.33	0.33	
<i>Perognathus spinatus</i>	0.81	0.67	1.34	2.80	0.49	
<i>Peromyscus eremicus</i>	0	0.81	0.94	0.82	0	
Biomass (gm per ha)						
	JAN	FEB	MAR	APR	MAY	
<i>Dipodomys merriami</i>	29.06	40.92	62.44	150.56	106.84	
<i>Perognathus formosus</i>	53.87	157.81	45.89	65.77	109.26	
<i>Perognathus fallax</i>	0	0	0	5.00	5.00	
<i>Perognathus spinatus</i>	10.81	8.93	18.50	41.75	6.57	
<i>Peromyscus eremicus</i>	0	12.64	14.78	12.96	0	
JUNE	JULY	AUG	SEPT	OCT	NOV	DEC
3.49	2.29	0.84	0.96	1.81	1.93	1.32
10.05	13.02	3.30	5.93	3.62	2.64	1.32
0.49	0.49	0.16	0	0.16	0.49	0.33
1.15	1.15	0.99	2.64	2.14	1.15	0.16
0.16	0.16	0.16	0	0.33	0.33	0.33
131.96	80.10	31.92	26.07	62.77	67.07	45.42
157.78	195.95	51.98	88.18	52.24	40.15	21.00
6.66	6.12	2.24	0	1.68	5.44	4.46
17.71	15.26	12.18	32.50	27.71	14.66	1.96
2.80	2.08	3.20	0	4.54	4.50	5.44

Microtemperature

Three separate sets of data are available from this portion of the study (DSCODE A3UWW02); ambient temperature taken 10 cm above the ground in a weather station (Figure 3), surface temperature (Figure 4b), and temperature within *D. merriami* burrows at 30 cm depth (Figure 4a). Two such burrows were monitored, but the data gathered did not differ significantly so only one is presented graphically. Surface temperatures for May through September go off the scale during much of the day as the instrument does not read over 50 C, and thus the values in Figure 4b stop and start according to the range of the instrument.

Activity patterns under simulated desert conditions

Sixteen individuals were run for two weeks each under summer conditions during the spring and summer of 1972 and sixteen were similarly run for one week each under winter

conditions during the fall and winter of this year (DSCODE A3UWW03). Mean minutes of activity per quarter hour and mean duration of activity per night in hours is presented in Figure 5 for summer conditions and Figure 6 for winter conditions. Each figure also shows at its head mean minutes of activity per hour for all individuals under that temperature regime. Mean activity per night for winter conditions is 5 ± 0.38 hr at the 95% confidence level, and 5.9 ± 0.51 hr for summer conditions. The means are different at the 0.10 level, but not at the 0.05 level.

Table 3. Mean weight of adults and 95% confidence interval (A3UWW01)

	<i>D. merriani</i>	<i>P. formosus</i>	<i>P. fallax</i>	<i>P. spinatus</i>	<i>P. eremicus</i>
JAN	35.87±1.61	14.84±0.64		13.35±1.67	
N	10	33		7	
FEB	36.86±1.08	14.86±0.57		13.33±2.61	15.61±3.56
N	50	47		6	8
MAR	36.30±1.90	14.85±0.73		13.81±1.19	15.72±2.72
N	20	29		9	9
APR	37.83±0.92	14.78±0.75	15.16±1.16	14.91±0.87	15.80±2.00
N	57	29	3	13	5
MAY	38.57±0.96	15.41±0.47	15.16±1.16	13.40±1.56	
N	56	42	3	5	
JUNE	37.81±0.96	15.70±0.37	13.60±0.52	15.40±1.38	17.50
N	64	86	3	10	1
JULY	34.98±2.46	15.05±0.48	12.50±1.49	13.27±1.21	13.00
N	31	66	3	11	1
AUG	38.00±1.55	15.75±0.52	14.00	12.30±0.67	20.00
N	18	28	1	10	1
SEPT	37.57±1.15	14.87±0.44		12.31±0.57	
N	32	50		22	
OCT	34.68±0.68	14.43±0.43	10.50	12.95±0.51	13.75±1.45
N	57	46	1	35	2
NOV	34.75±0.52	15.21±0.54	11.10±0.95	12.75±1.22	13.62±1.08
N	65	26	5	10	4
DEC	34.41±1.20	15.91±1.77	13.50±4.89	12.00	16.50±0.97
N	30	6	2	1	2

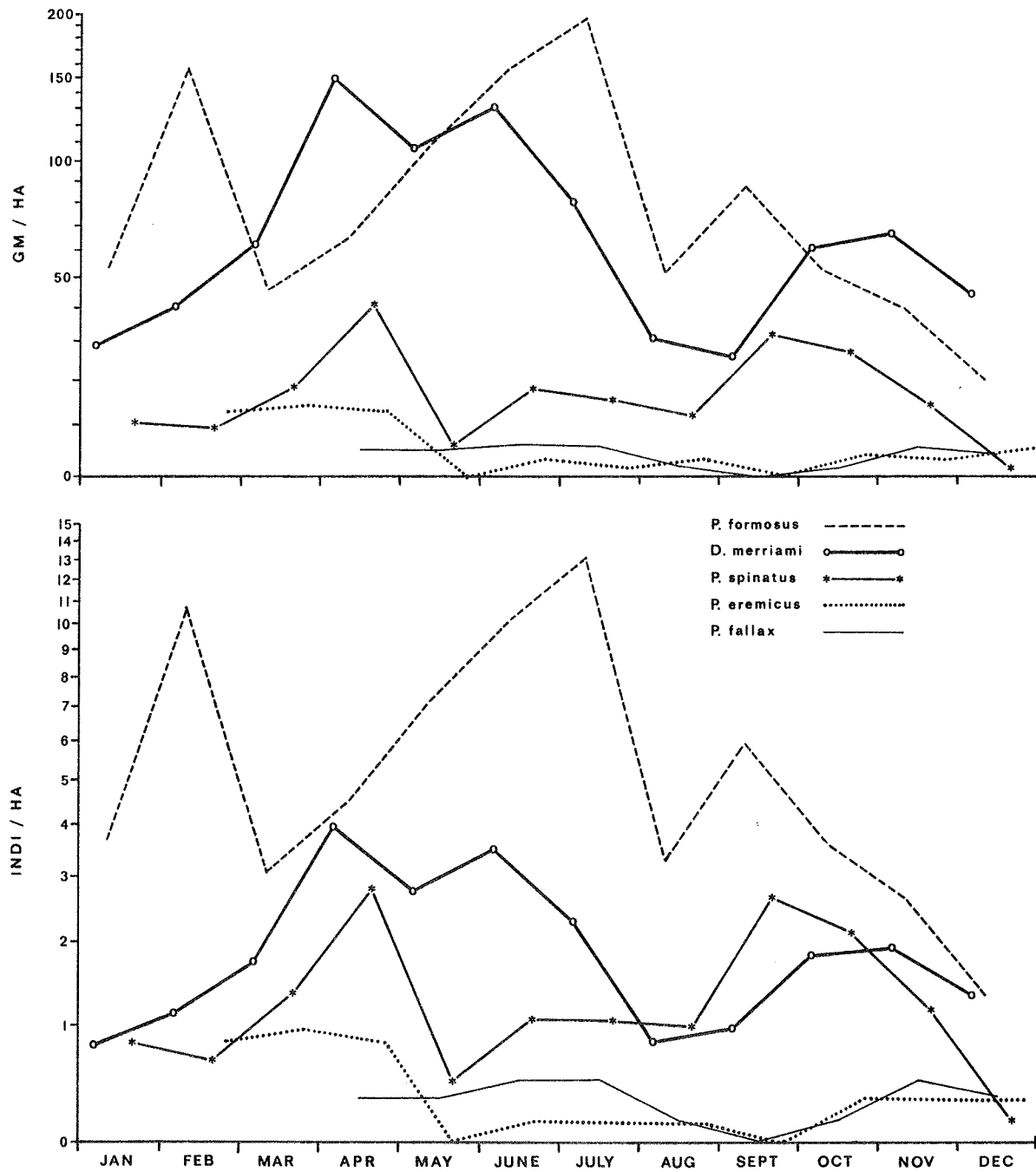


Figure 1. A.(top) semi-log plot of biomass of nocturnal rodents each month (g/ha) A3UWW01.

B.(bottom) semi-log plot of density of nocturnal rodents each month, individuals per ha (A3UWW01).

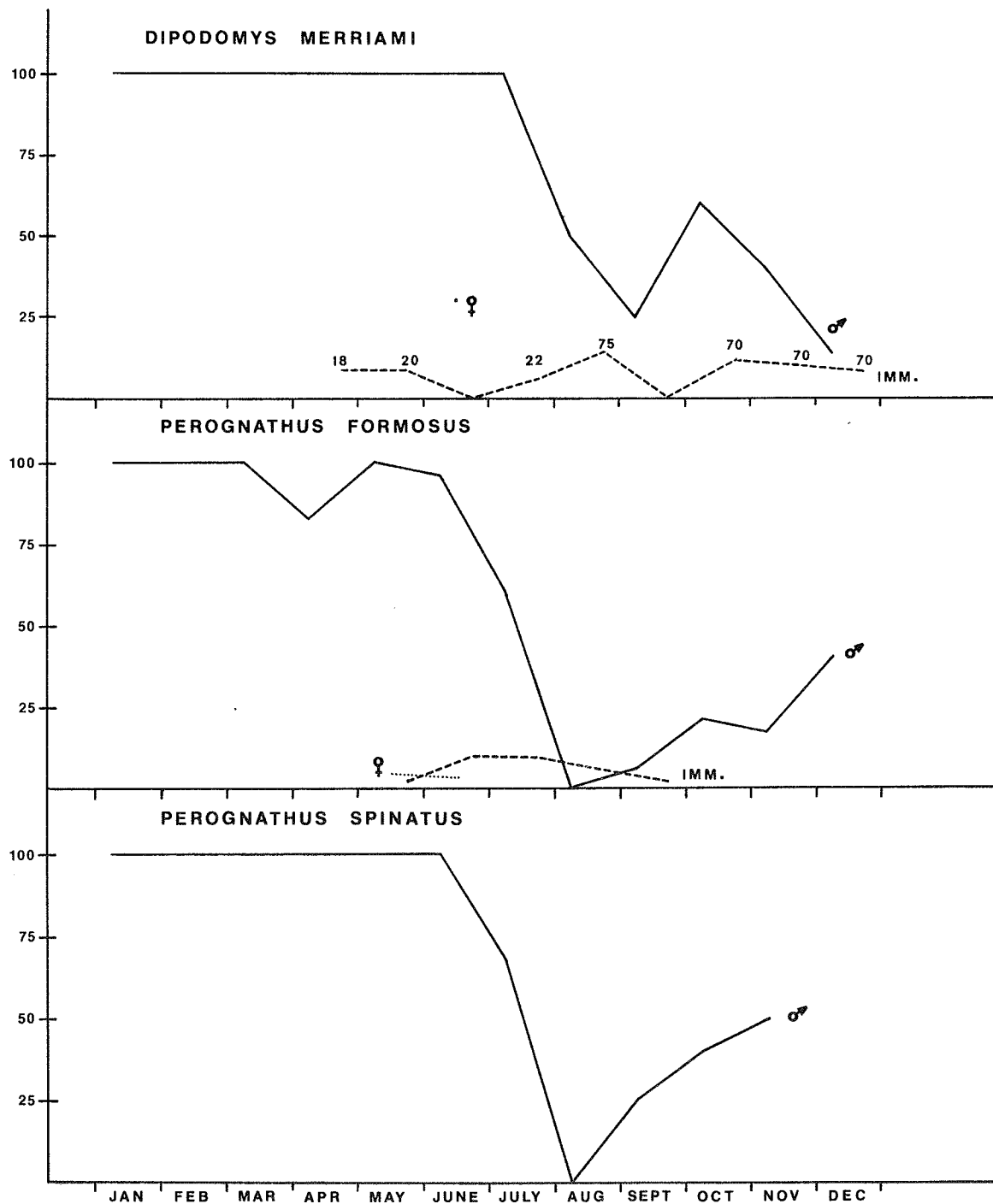


Figure 2. Reproductive phenology. Percent adult males fertile, percent adult females pregnant or lactating, percent of total catch immature, for each month. Numbers on immature line for *D. merriami* are approximate ages of immatures trapped for that month as determined from data of Chew and Butterworth (1959). A3UW01.

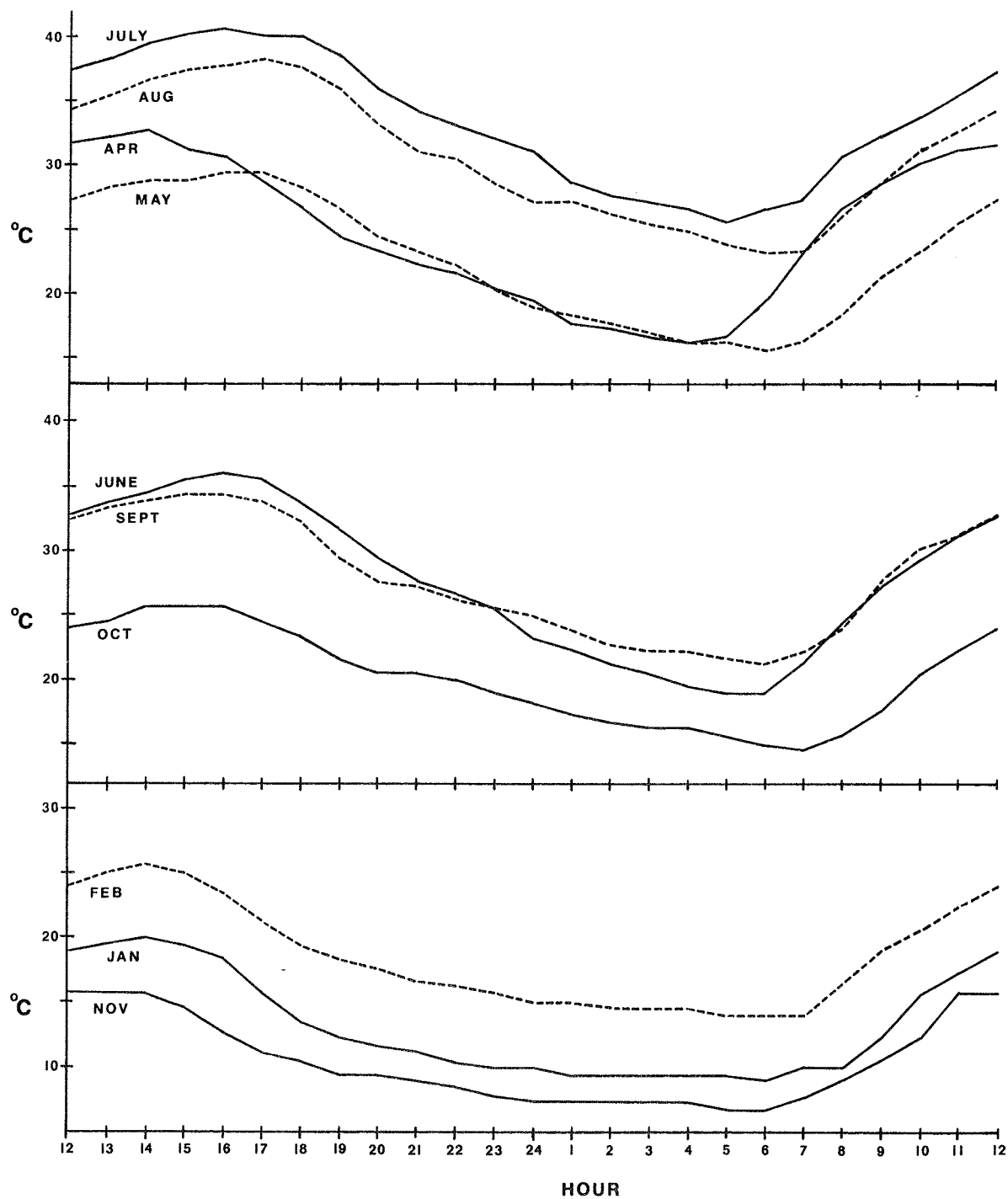


Figure 3. Ambient temperature (C) taken 10 cm above ground in weather station, mean values per hour plotted by month (A3UWW02). See text for explanation of missing data.

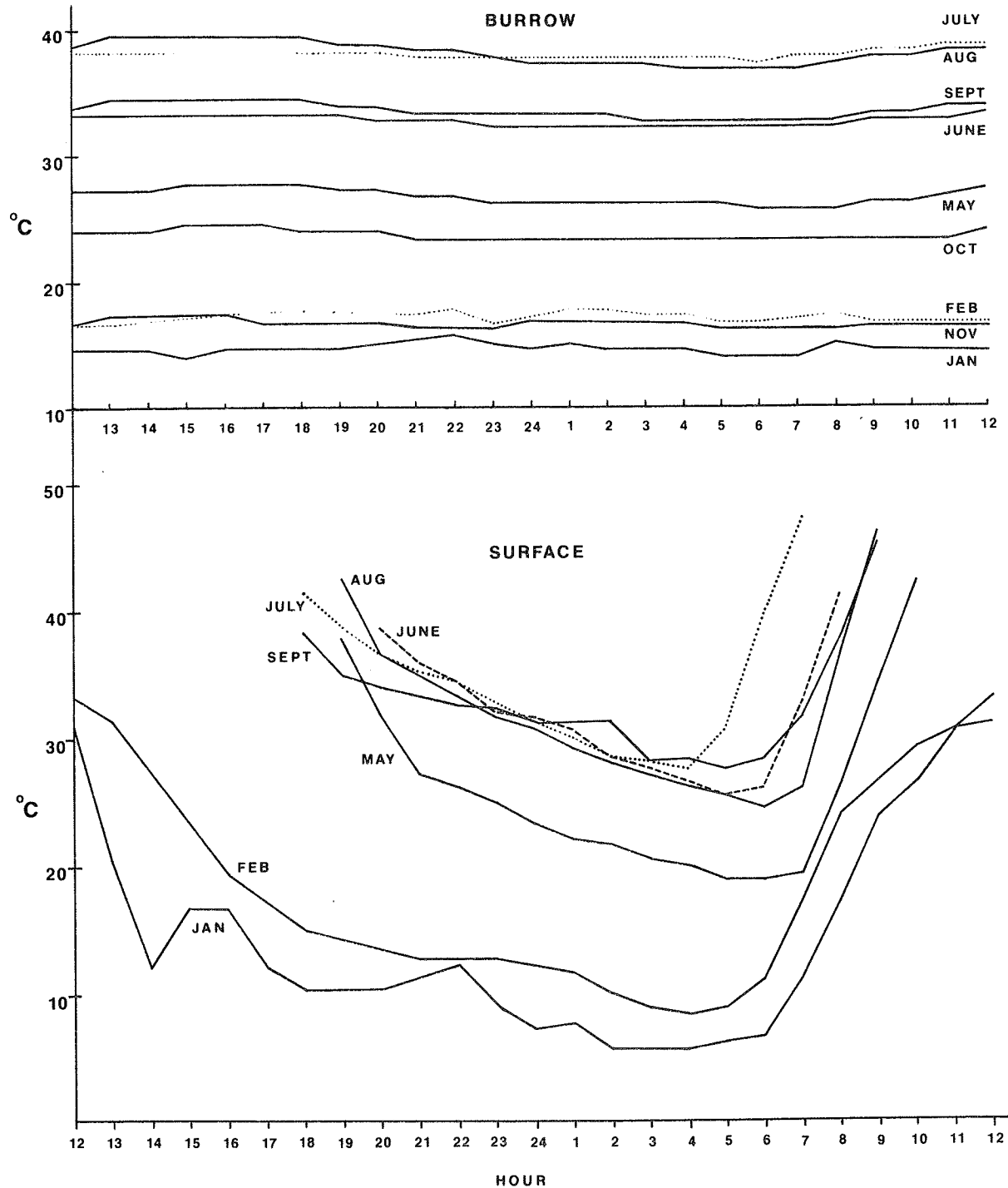


Figure 4. A. (top) Temperature (C) in *D. merriami* burrow at 30 cm depth, mean values per hour plotted by month (A3UWW02). See text for explanation of missing data.

B. (bottom) Surface temperature (C), mean values per hour plotted by month (A3UWW02). See text for explanation of missing data. Surface temperatures from May through September go off instrument scale (> 50 C) during day.

DISCUSSION

Previous data on rodent demography in the creosote-palo verde of Deep Canyon are available only from three trapping periods (29 April-2 May, 1964, 15-18 October 1964, and 12-15 January, 1965) reported by Ryan (1968). Our demographic data on *D. merriami* (Figure 1) show that this species was most abundant in the creosote-palo verde habitat from April through June, though Ryan (1968) found greatest densities in October and January. *Perognathus formosus* was the most abundant nocturnal rodent in every month of the year except December, whereas Ryan (1968) found it only in his October trapping period. *Perognathus spinatus* and *P. fallax* were not recorded in the creosote-palo verde habitat by Ryan (1968). We found small numbers of the latter from April through December; *P. spinatus* numbers were greatest in April and September, and were second only to *P. formosus* from August through October. *Peromyscus eremicus* was not recorded from the creosote-palo verde habitat by Ryan (1968), and was found sporadically by us in low numbers, being most common from February through April. An explanation of the differences in demographic data between this study and that of Ryan (1968) is not immediately forthcoming, but several factors may be significant; seven years separated the collection of the two sets of data. The period preceding and during which Ryan conducted his study were wet (total rainfall for 1963 151.4 mm, for 1964 73.3, for 1965 204.5 mm), while 1971 (35.1 mm) and 1972 (60.5 mm) were considerably drier. Ryan's study area (1.77 ha) was less than half the size of that (3.9 ha) used in the present study. Ryan trapped nine nights in a year; the data of this study are based on six nights of trapping per month. And although the exact location of Ryan's study area is not known to the authors, it is believed to have been further up Deep Canyon in more rocky terrain whereas our study area was in sandy terrain.

Reproductive phenology for *D. merriami*, *P. formosus* and *P. spinatus* may be ascertained by examination of Figure 2. Reproductively active *D. merriami* females were taken only in June, and *P. formosus* females in May and June. Immature weight *D. merriami* were taken from April through December, and immature *P. formosus* from May through September. A decline in percent fertile adult males for all three species in the latter half of the year is interpreted to be due to an increase in the proportion of sexually immature males of adult weight in the catch, rather than a loss of fertility in older males. Our data suggest that the reproductive period for *D. merriami* starts as early as late February and extends into September, and a peak in pregnancies in May and June. Ryan (1968) found reproductively active male *D. merriami* in Deep Canyon from January through April, and lactating females from mid-April to late June, with immatures first appearing in mid-April. We found reproductively active female *P. formosus* only in May and June, but the presence of

immature *Perognathus* in the population suggests that births occurred from late April or early May to August or September. The curve for male *P. spinatus* is similar to that for *P. formosus*.

Temperature data from the study area (Figures 3 and 4) show that the months of November through February are coldest, both above and below ground. Temperature 10 cm above ground in these months (Figure 3) decreases sharply from a high about 1400 hr until 2400 hr, then decreases slowly until a minimum is reached at 0500 or 0600 hr. After dawn temperature again rises sharply toward the 1400 hr peak. The time of daily high changes with season, no doubt influenced considerably by day length. The April and October highs occur at 1400, as in the cooler months, but those from May through September occur from 1500 to 1700 hr. There is no corresponding shift in the time of daily low with season, lowest temperatures occurring between 0400 and 0700. Lowest ambient temperatures in warm months are usually shortly after dawn, but before the sun has reached the bottom of Deep Canyon, whereas in winter months coolest temperatures occur before dawn.

Surface temperatures follow a pattern generally similar to ambient (Figure 4b) with absolute lows occurring from 0200 to 0400 hr in the cooler months and from 0400 to 0600 hr in the warmer months. Surface peaks near 35 C about 1200 in the cooler months, and regularly exceeds 48 C between 0600 and 2000 hr in the warmest months of summer.

In any given month there was little diel variation in burrow temperature (Figure 4a), the greatest being 2.1 C in May and 2.3 C in July. We are suspicious of the burrow temperature data for June through September, as we doubt that any endothermic mammal would select burrow temperatures so high. Yet all temperatures from May through November were recorded from a single probe placed at 30 cm in a burrow which was in use in May when the probe was placed, and there was no significant difference between the two burrows measured. Chew and Chew (1970), measuring burrow temperature at 15 cm in the Chihuahuan desert, recorded means of 28.3 C and 26.8 C for July and August, respectively, while the range noted for those two months during our study was 36.8 C to 39.5 C. It is not known whether *D. merriami* move to deeper burrows during the summer months at Deep Canyon.

As might be expected, great individual variability was observed in mean minutes of activity for *D. merriami* exposed to both winter and summer temperature conditions in the laboratory (Figures 5 and 6), as well as in total time out per night, which varied from 3.20 to 6.51 hours for the winter temperature regime and from 4.36 to 8.30 hr for the summer. Some individuals were active at dusk and just before dawn both summer and winter. However, a significant ($P < 0.05$) difference is seen in the total time active between winter and summer regimes and the spacing of this activity.

2.3.2.2.-14

Mean total activity for winter animals is very close to five hours (5.02 ± 0.38), and 68% of this activity is between dusk and midnight. The tendency then of confined animals is to reduce total activity on simulated winter nights and to concentrate more activity before midnight, thus avoiding the colder hours of early morning. Captives exposed to a simulated summer cycle had nearly one hour more total activity, and showed little tendency to concentrate activity to the hours before midnight.

EXPECTATIONS

Though this project was not funded for 1973, an extension of permanent equipment funds is permitting us to build and test the telemetric system described by Osgood and Weigl (1972). This system will be used to collect activity pattern and thermal experience data throughout 1973. At the same time an increased number of temperature recording instruments made available by Pomona College will permit us to simultaneously monitor several active burrow systems at different depths to check data obtained on two systems in 1972. This information will be added to Biome data banks as it becomes available, along with demographic data collected in the live-trapping phase of this project.

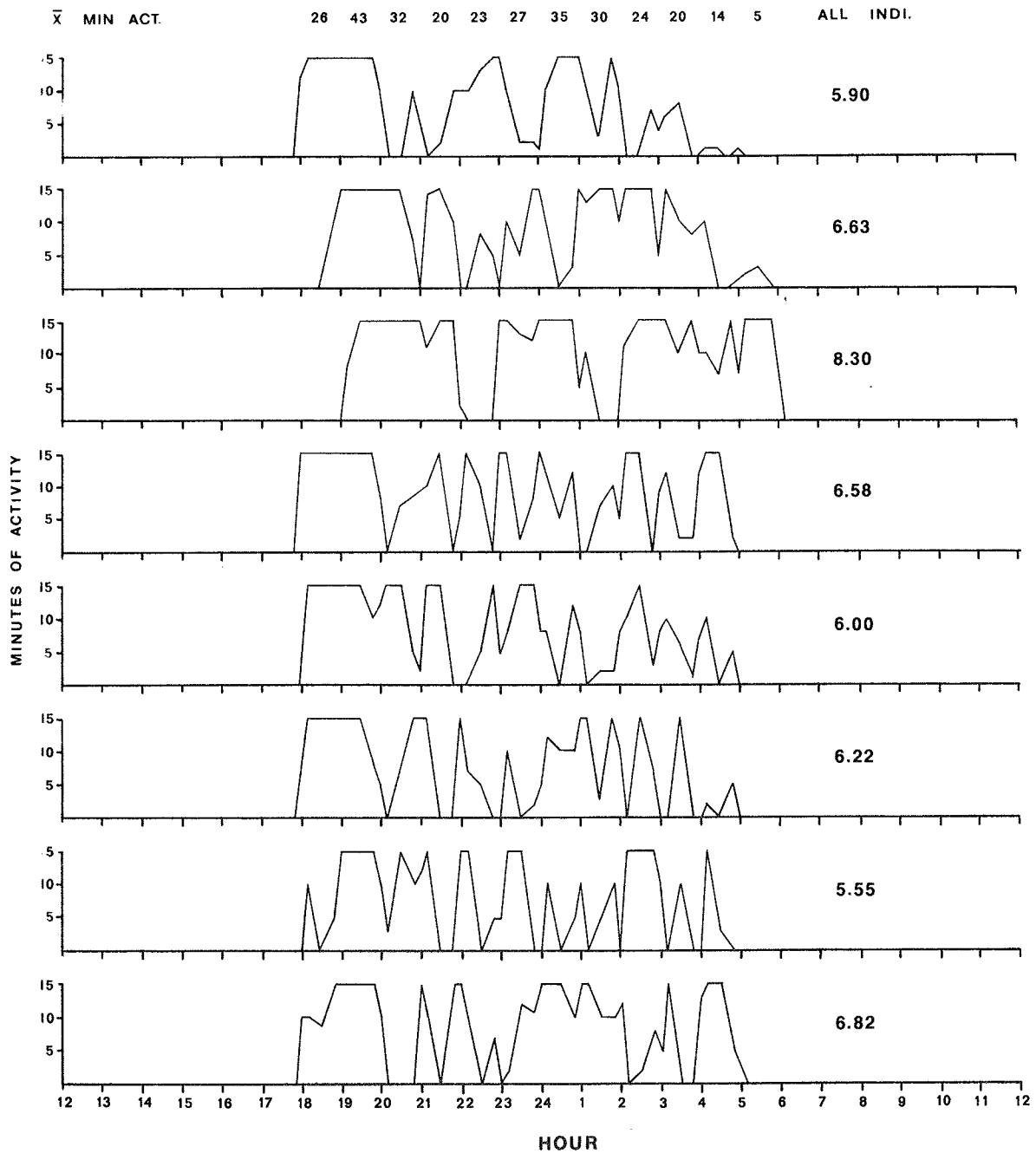


Figure 5. Activity patterns of *D. merriami* exposed to summer temperature conditions in environmental chamber (A3UWW03). Mean total hours of activity per night in bold face to right for each individual. Mean minutes of activity per hour for all individuals at top. (Continued on next page).

2.3.2.2.-16

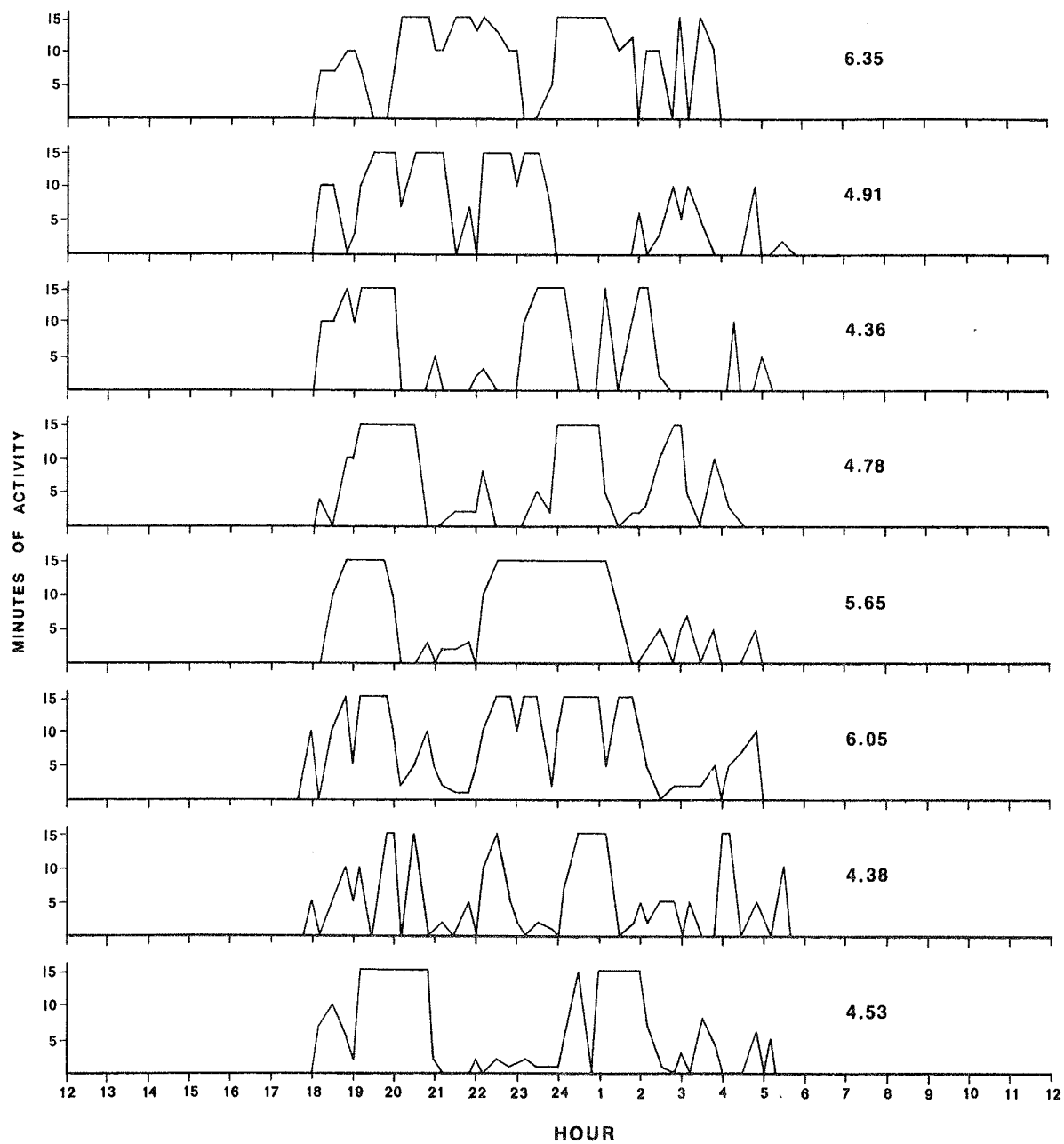


Figure 5. Continued.

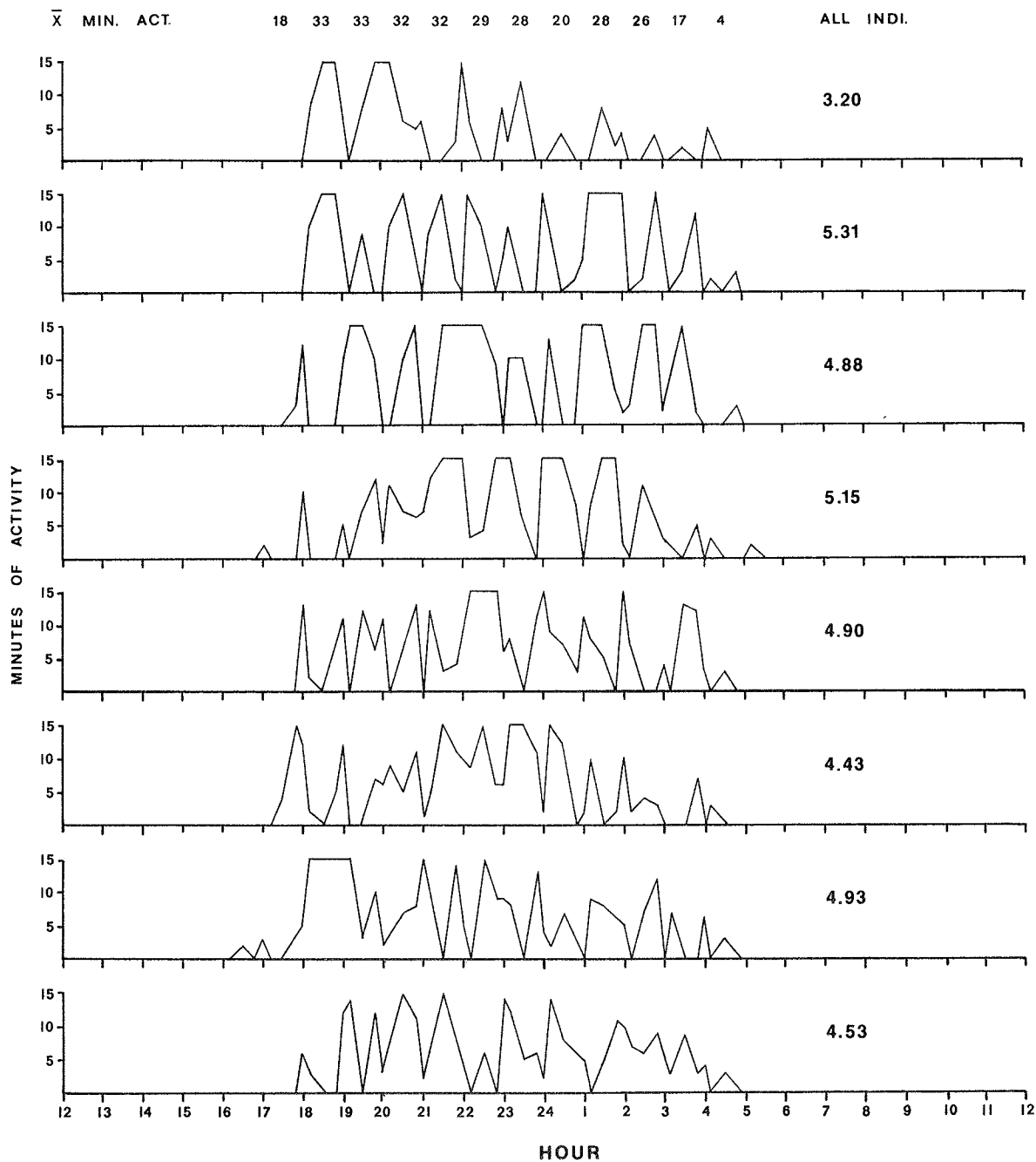


Figure 6. Activity patterns of *D. merriami* exposed to winter temperature conditions in environmental chamber (A3UWW03). Mean total hours of activity per night in bold face to right for each individual. Mean minutes of activity per hour for all individuals at top. Continued on next page.

2.3.2.2.-18

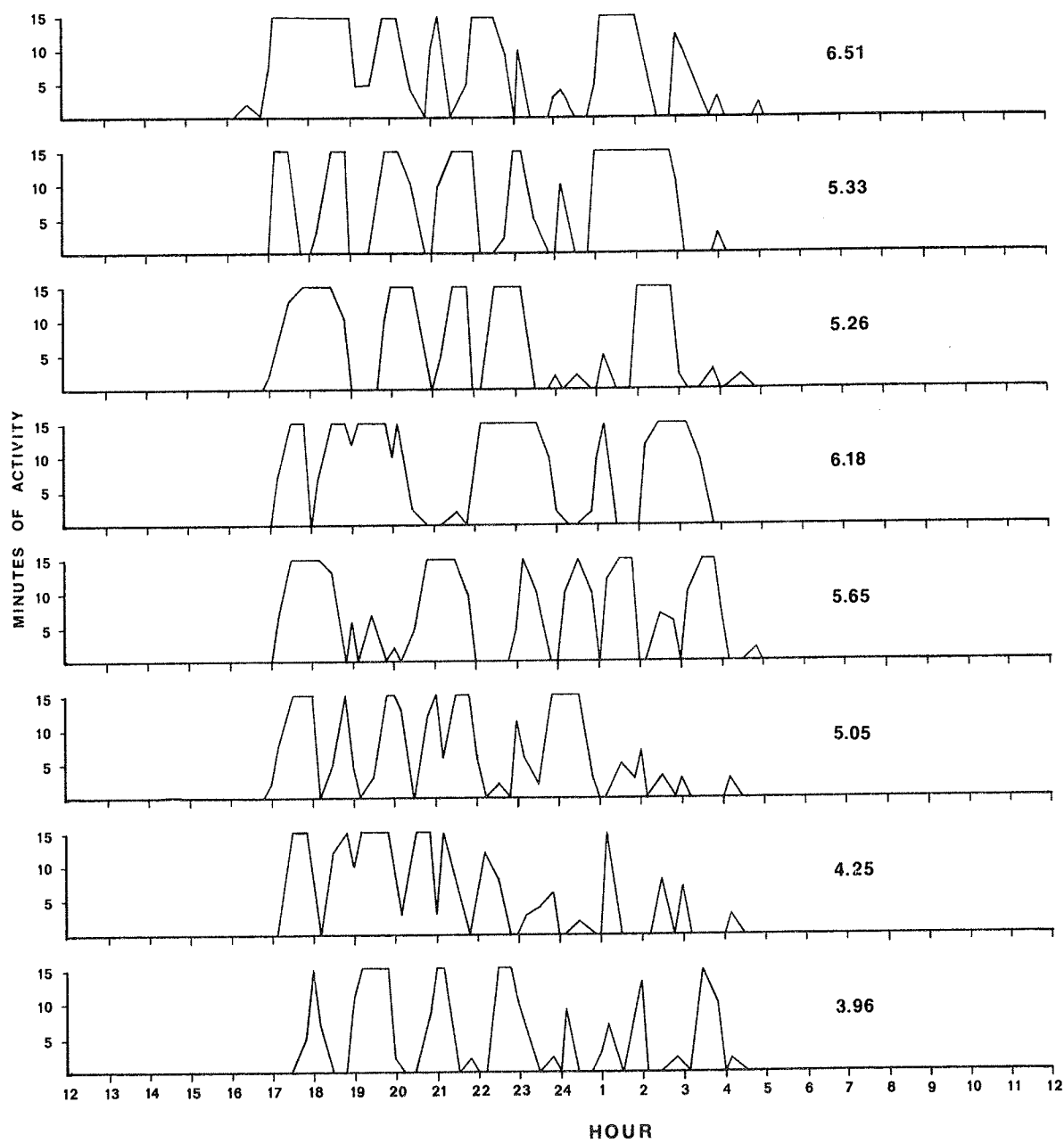


Figure 6. Continued.

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1972 PROGRESS REPORT

DENSITY AND DIETARY HABITS OF POCKET GOPHERS
(*Thomomys bottae centralis*) IN ROCK VALLEY

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Research Memorandum, RM 73-21

MAY 1973

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Report Volume 3

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A B S T R A C T

In July and August, 1972, a field and laboratory project was conducted near Plot C, UCLA/CETO enclosure, Rock Valley, on the AEC test site near Mercury, Nevada. This project was to determine the density of the population of Botta's Pocket Gophers (*Thomomys bottae centralis*) in this region, their daily food consumption and dietary preferences. Density was estimated by live trapping and burrow excavation. Results indicate a density of 3.8 *T. bottae*/ha having a biomass of 270.0 g/ha. Food consumption tests were conducted in the laboratory by measuring amounts of native vegetation (*Ephedra nevadensis*, *Franseria dumosa*, *Lycium andersonii*, *L. pallium*, *Larrea divaricata*, *Coleoyne ramosissima*) cut (cropped), consumed and metabolized per day. Results indicate that a *T. bottae* in Rock Valley cuts 25.4 g/day, consumes 23.9 g/day and metabolizes 20.4 g/day of the above vegetation. This indicates that about 121.5 g/ha/day is cut by *T. bottae*. Food preference was determined by presenting measured amounts of the above plants to captive pocket gophers and comparing species amounts consumed to total amount consumed. The most preferred food plant appears to be *E. nevadensis*, with *F. dumosa* second. Because of small sample size (difficulty of collecting animals because of seasonal inactivity) the above results are considered crude estimates, but they do indicate density, food consumption and preference.

INTRODUCTION

The population dynamics and dietary habits of many desert rodents have been investigated (for example, several projects in the IBP Desert Biome studies are concerned with these parameters), but these studies tend to ignore the strictly fossorial species. At the Rock Valley site, Mercury, Nevada, a two-month study was done to determine if these fossorial mammals, as represented here by Botta's pocket gopher, *Thomomys bottae centralis* (Hall and Kelson, 1959), play a significant role in the ecosystem. More specifically, the study attempted to determine something about the number of individuals of *T. bottae* and their dietary habits in the Mohave Desert at Rock Valley.

OBJECTIVES

1. To determine a means to estimate the density of *T. bottae* in Rock Valley, and to make such an estimate.
2. To estimate the amount of food consumed (as a percent of body weight) per pocket gopher per day.
3. To determine dietary preferences of *T. bottae* in Rock Valley based on the available native vegetation.

METHODS

All aspects of this project were predicated upon the use or capture of live pocket gophers. The traps used to capture the animals were of two types; one a metal box with a spring-loaded door and hardware-cloth floor (Howard, 1952), the other a plastic tube with a metal closure (trap developed by Dr. Robert J. Baker, Texas Tech Univ.). Regardless of the trap used, the method of setting was the same. When a fresh mound was encountered, if possible an excavation was made into a main run (usually from 20 to 30 cm below the surface) where the traps were set. Fresh apple, or apple juice sprayed inside the trap, was used as bait. Metal traps were shaded to prevent death of animals by heat stress. Traps were checked at about 2-hour intervals during the day and left set overnight. Since activity in *T. bottae* appears to be reduced in the hot arid parts of the summer (Howard and Childs, 1959) and since this project ran from July through August, trapping results as related to signs of activity were meager.

In the laboratory, the pocket gophers were housed in glass and metal terraria with screened dirt in the bottom. A small shelter was provided. During the laboratory tests, the terraria were kept in an isolated room maintained at 24 C and a relative humidity of 20 to 25%.

Food material presented to the animals in the food consumption and preference tests consisted, unless otherwise noted, of shoots of the six most prevalent, perennial plants of the study area:

Coleogyne ramosissima

Ephedra nevadensis

Franseria dumosa

Larrea divaricata

Lycium andersonii

Lycium pallidum

Estimation of density

Since pocket gophers reveal their presence by the mounds produced in the course of their burrowing activity, it is easy to find those areas where gophers are active or present. The number of individuals present is not always easy to deduce from the number of mounds. In areas of loose soils and ample vegetation for forage, densities may be quite high and burrow systems so crowded together that it is impossible to tell where one begins and another ends. In less optimal areas, the systems tend to be more discrete, but the problem of separation of systems, from surface evidence, is still difficult.

Two methods were employed in this study to determine the extent of burrow systems (and from this deduce density). One was to set live traps at various points and capture, mark, release, and recapture the occupant or occupants, and from this determine the limits of the burrow of any one pocket gopher. The other method was to excavate the burrow system or systems, determine the limits and measure the extent. Since activity appears to be reduced in the arid summer months, this latter method was the more fruitful.

2.3.2.4.-4

A study area in the form of a grid (26 m x 48 m at 2 m intervals) was established 35 m southwest of Plot C (UCLA/CETO enclosure) in Rock Valley, 19 km west of Mercury, Nevada, on the U.S. Atomic Energy Commission's Nevada Test Site. The vegetation is typical Mohave Desert mixed shrub growing on an alluvial bajada. Selection of this site was based on the discovery of 25 fresh mounds and indication of recent activity by pocket gophers. Live traps were set at selected points and locations of the mounds were plotted, as were the locations of plants of the following species:

Ephedra nevadensis

Krameria parvifolia

Larrea divaricata

Live traps also were set in areas outside the grid wherever recent mounds indicated the presence of pocket gophers. When repetitive captures occurred, distances between points of capture were made to estimate burrow size.

Two burrow systems were excavated: the system within the grid, and another 25 m south of Plot C. An attempt was made to measure the complete system, i.e., laterals, parallels, plugged burrows; any stored food materials were noted.

From the two methods described above, estimates of the areas necessary to support a pocket gopher could be made, in the one case by connecting the outer points of capture, in the other by actual measurement. It must be noted, however, that the burrow systems are spaced and non-contiguous. Therefore, to estimate density, allowance must be made for the distance between burrow systems and as these distances were not measured (only estimated) in this study, estimates of density are very crude. Records were kept on the weights of all pocket gophers captured and from these data the density in grams of biomass per hectare could be calculated.

Food consumption

Data on food consumption were collected by presenting measured amounts of food to captive individuals of *T. bottae* housed in terraria with 8 cm to 10 cm of screened dirt in the bottom. Food was presented at 1830 hours and the unconsumed amount left on the surface of the dirt was removed at 0630 hours of the following day and weighed. This was repeated daily for the duration of the test. During the test water was provided by a drip bottle. At the end of the test, the dirt was screened through 6 mm mesh and 2 mm mesh sieves and all plant material and feces were collected and weighed. Initial and final body weights were recorded for the gopher. From these data, the following estimates were made:

1. Amount of plant material "cut" - this is the plant material put in less the uneaten portion removed and is an approximation of the amount of plant material cropped.

2. Amount of plant material consumed - this is estimated by subtracting the amount of excess (stored) material found buried at the end of the test from the amount of material cut.
3. Amount of plant material metabolized - this is a crude estimate of the amount of plant material (biomass) converted to animal material (biomass) and is calculated by subtracting the weight of the feces from the amount consumed.

Food preference

Food preferences and alternate food sources for *T. bottae* in Rock Valley were determined by presenting measured amounts of the six most prevalent, perennial plants in the study area to captive pocket gophers housed as in the food consumption tests (in fact, both food consumption and preferences were run simultaneously in some cases). Presentation was made at 1830 hours on one day and uneaten plant material was removed, identified as to species and weighed at 1600 hours the following day. This regime was repeated for the course of the experiment. Since *E. nevadensis* appears to be the preferred food (as indicated by field observations and the laboratory tests), the second day the amount of *E. nevadensis* was reduced and after the second day none was included in the diet. After the third day, the amount of *F. dumosa* in the diet was reduced. Daily weight records were kept on the animal. At the termination of the test, the same procedure as in the food consumption test was followed. In two of the tests, on the fifth day roots of the plants were presented using the same procedure as for shoots. Results of these tests were combined (3 tests were run) and from these data were calculated the percent of total, daily input per species of plant and the percent of total, daily consumption per species of plant.

RESULTS

The results of the trapping are summarized in Table 2. From this it can be seen that recaptures were not common, nor was overall success for that matter.

Estimation of density

As mentioned, this estimate is very crude. Comparison of the parameters measured and estimated values is shown in Table 1. From field observation and estimate, there is assumed a 30 m distance (buffer zone) between the perimeters of adjacent systems.

Howard and Childs (1959) found a much higher density than this study (37.6 gophers/ha as compared with 3.8 gophers/ha), but soils and vegetation are far less suitable in Rock Valley than in the area of the other study. An estimate of biomass of *T. bottae* per hectare can be made (combining data from Tables 1 and 2):

$$T. bottae, \text{ biomass/ha} = (3.8 \text{ gophers/ha}) (71.1 \text{ g/gopher}) = 270.1 \text{ g/ha}$$

2.3.2.4.-6

Table 1. Lengths of burrow systems, areas of burrow systems, areas of burrow systems plus buffer zones, density (individuals/ha)

Pocket Gopher No.	No. of Captures	Distance Between Captures	Length of Burrow	Area of System*	Area of System and Buffer*
0001	1	-	39 m	-	-
0002	1	-	71 m	270 m ²	3276 m ²
0004	4	15 m	-	58 m ²	1960 m ²
		13 m			
		9 m			

AV. AREA OF BURROW SYSTEM = 164 m²

AV. AREA OF BURROW SYSTEM AND BUFFER = 2618 m²

NO. OF BURROW SYSTEMS (INDIVIDUALS) PER HECTARE = 3.8

* Areas of burrow systems and burrow systems plus buffer zones are the areas of triangles formed by connecting the extremes (3 most distant mounds) of the system.

Table 2. Results of trapping

Pocket Gopher No.	Sex	Weight	Date and Time of Capture	Location	Tests
0001	male adult	91.5 g	1. 7/10/72 1825 hr	1. 25 m. S. Plot C	Cons.
			2. 7/25/72 0600 hr	2. same	
0002	female adult	--	1. 7/14/72 1300 hr	Grid	Dead in trap
0003	female adult	73.5 g	1. 7/17/72 1300 hr	40 m. S. Plot C	Cons.
0004	female adult	57.4 g	1. 7/28/72 1600 hr	1. 15 m. W. Plot C	Cons. and Pref.
			2. 8/14/72 1230 hr	2. same	

Table 2. (Continued)

Pocket Gopher No.	Sex	Weight	Date and Time of Capture	Location	Tests
			3. 8/15/72 1500 hr	3. same	
			4. 8/20/72 1300 hr	4. same	
0005	female adult	51.8 g	1. 7/28/72	1. W. end Plot C	Pref.
0010	male adult	81.1 g	1. 8/15/72 1030 hr	1. 30 m W. Plot C.	Cons. and Pref.

Mean weight of gophers caught = 71.1 ± 14.7 g

All animals were sexually inactive

Food consumption

Tables 3 and 4 summarize the data on food consumption. From these, it is noted that *T. bottae* in Rock Valley is cutting (cropping) approximately 36% of its body weight per day (under laboratory conditions), or approximately 97.2 g/ha/day of vegetation is being cut.

Table 3. Per diem weights of vegetation cut (cropped), consumed, and metabolized by *T. bottae*

	g/day	g/g body wt/day
Cut	25.5 ± 6.1	0.36
Consumed	24.0 ± 6.3	0.34
Metabolized	20.4 ± 6.7	0.29

Data derived from means of difference values in Table 4 and mean weight in Table 2.

Food preference

Although no statistical analysis was run on these data, it can be seen from Table 5 and Figure 1 that *E. nevadensis* shoots is the preferred food, which concurs with observations in the field. The plants in the area of a burrow system were checked frequently for signs of feeding activity by gophers. The most common plant damaged by gophers was *E. nevadensis* (in the shoot portion, roots were not investigated on all plants). In a

2.3.2.4.-8

Table 4. Food consumption tests

Gopher			Wet weights (g) of feed and feces					
	Body wt (g)		1	2	3	4	5	TOTAL
No. 0005 (a)		in	75.0	50.0	65.0	50.0	50.0	290.0
Body wt in	51.8	out	47.8	28.6	41.7	24.1	24.5	166.7
Body wt out	50.0	diff	27.2	21.4	23.3	25.9	25.5	123.3
diff	-1.8				wt of stored plant material			4.2
					wt of feces			32.2
No. 0004 (a)		in	60.0	65.0	65.0	50.0	50.0	290.0
Body wt in	53.0	out	35.9	38.7	28.0	19.2	29.3	151.1
Body wt out	49.6	diff	24.1	26.3	37.0	30.8	20.7	138.9
diff	-3.4				wt of stored plant material			6.2
					wt of feces			10.8
No. 0010 (b)		in	90.0	80.0	80.0	65.0	--	315.0
Body wt in	81.1	out	77.7	54.9	51.8	39.9	--	214.3
Body wt out	59.0	diff	22.3	25.1	28.2	25.1	--	100.7
diff	-22.1				wt of stored plant material			8.3
					wt of feces			6.6
No. 0004 (c)		in	34.4	48.1	32.7	--	--	115.2
Body wt in	53.9	out	26.2	12.0	6.2	--	--	44.4
Body wt out	56.0	diff	8.2	36.1	26.5	--	--	70.8
diff	+2.1				wt of stored plant material			8.2
					wt of feces			10.8

(a) Mixed diet (*E. nevadensis*, *F. dumosa*, *L. andersonii*, *L. pallidum*, *Larrea divaricata*).
 (b) Mixed diet as above but with *C. ramosissima* in addition.
 (c) Diet of *E. nevadensis* only.

few instances, *F. dumosa*, *L. andersonii* and *C. ramosissima* also were found to be cut. In addition, the map made of mounds and plants on the grid used for the density study showed that for approximately 2/3 of the burrow system the mounds follow the distribution of *E. nevadensis* in the area.

A ranking of the presented vegetation (shoots only) in order of decreasing preference would be as follows:

- | | |
|-------------------------|--------------------------|
| 1. <i>E. nevadensis</i> | 4. <i>L. divaricata</i> |
| 2. <i>F. dumosa</i> | 5. <i>L. pallidum</i> |
| 3. <i>L. andersonii</i> | 6. <i>C. ramosissima</i> |

No real conclusion can be drawn from the root test because of such a small sample, but it is of interest that, as with shoots, *E. nevadensis* was the most preferred root (see Table 6). Howard and Childs (1959) indicate no preference for specific vegetation in their study on *T. b. mewa*, but this does not seem to be the case for the population of *T. bottae* in Rock Valley.

Table 5. Food preference test, shoots, combined totals of three tests

Plant	Wet weights of food (g)					
		DAY				
		1	2	3	4	TOTAL
<i>E. nevadensis</i>	in	45.0	15.0	--	--	60.0
	out	15.2	7.0	--	--	22.2
	diff	29.8	8.0	--	--	37.8
<i>F. dumosa</i>	in	45.0	45.0	60.0	15.0	165.0
	out	22.6	12.0	18.6	2.4	55.6
	diff	22.4	33.0	41.4	12.6	109.4
<i>L. andersonii</i>	in	45.0	45.0	45.0	45.0	180.0
	out	38.4	31.9	27.1	11.9	109.3
	diff	6.6	13.1	17.9	33.1	70.7
<i>L. pallidum</i>	in	30.0	30.0	45.0	45.0	150.0
	out	27.4	25.0	35.4	31.0	118.8
	diff	2.6	5.0	9.6	14.0	31.2
<i>L. divaricata</i>	in	45.0	45.0	45.0	45.0	180.0
	out	37.1	35.7	27.7	26.3	126.8
	diff	7.9	9.3	17.3	18.7	53.2
<i>C. ramosissima</i>	in	15.0	15.0	15.0	15.0	60.0
	out	10.7	10.6	12.7	11.6	45.6
	diff	4.3	4.4	2.3	3.4	14.4
TOTAL DIFFERENCE		73.6	72.8	88.5	81.8	316.7

Table 6. Food preference, roots

Plant Species	Wet weight (g)			% of total consumed
	In	Out	Diff	
<i>E. nevadensis</i>	20.0	7.5	12.5	27.1
<i>F. dumosa</i>	20.0	11.8	8.2	17.7
<i>L. andersonii</i>	20.0	12.9	7.1	15.3
<i>L. pallidum</i>	20.0	11.6	8.4	18.2
<i>L. divaricata</i>	20.0	10.0	10.0	21.6
TOTAL	100.0	53.8	56.2	

2.3.2.4.-10

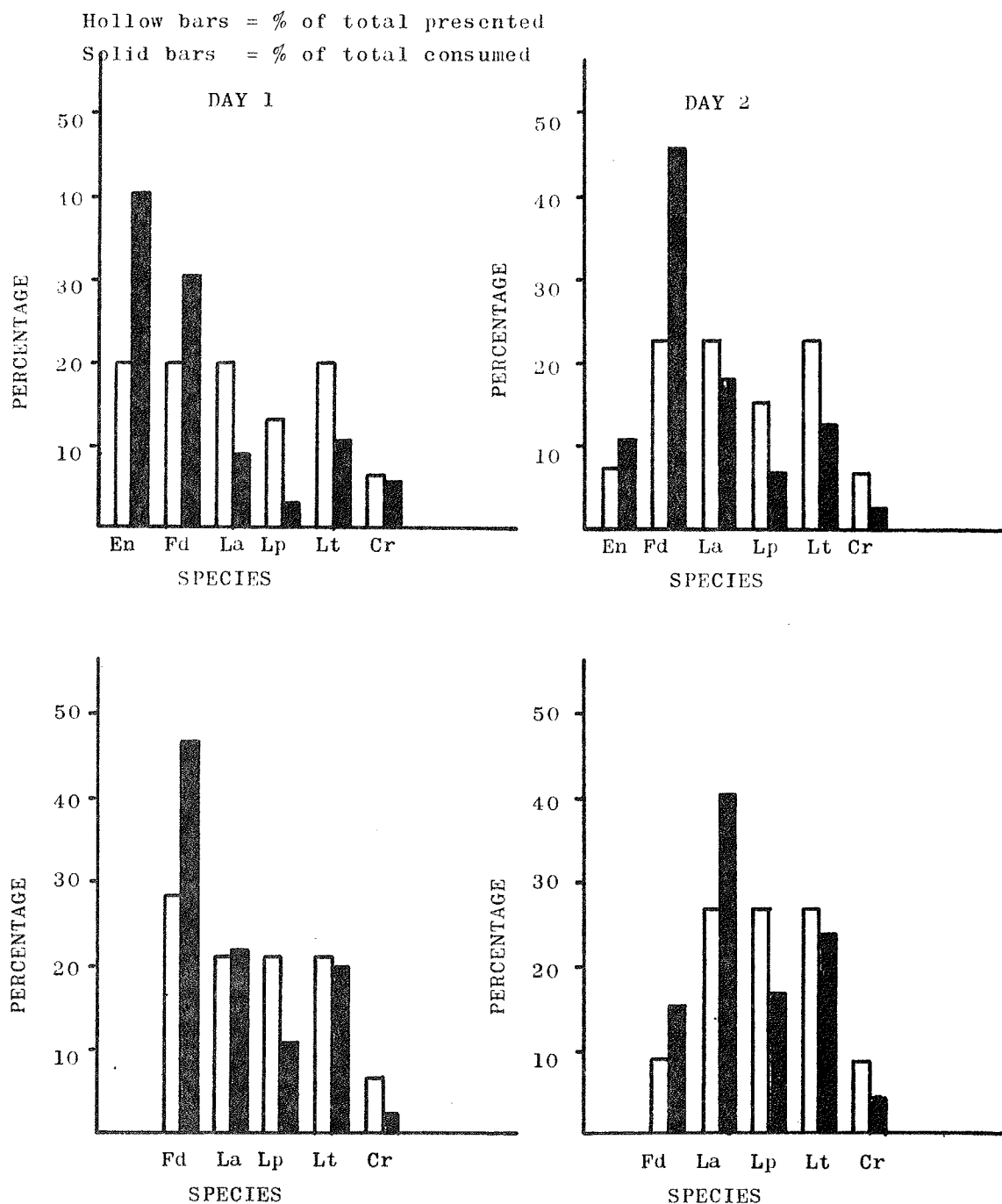


Figure 1. Food preference. Comparison of percentage of total presentation (per day) to percentage of total consumption (per day).

DISCUSSION

In a short project such as this, little more than a survey and some crude estimates can be made. The greatest difficulty was encountered in collecting animals because of the summer season, as mentioned previously. It was of interest that although in Rock Valley the activity pattern of *T. bottae* is similar to that reported by Howard and Childs (1959), it is contrary to the experience of one of us (Dingman) in trapping along the lower Colorado River during the summer.

In estimating densities of animals such as pocket gophers, one must realize that these fossorial mammals are closely tied to the nature of the soil and distribution of edible vegetation in relation to soils suitable for burrowing. In giving a value for density in number of individuals/ha or grams of biomass/ha, without a complete census, only the crudest of estimates can be made. Local concentrations of *T. bottae* in certain areas within Plot C of the UCLA/CETO enclosures, may exceed the estimates given, but other areas of the valley are devoid of these animals. In addition, from the pattern of old and new mounds, it appears that the burrow system of any one animal may shift considerably from season to season.

Food consumption and preference tests were conducted in the laboratory and can only be construed as indications of these parameters in the field. Dry weight values would have been more valid, but the unavailability of an oven precluded this. The values determined for cutting, consumption and metabolizing of food seem to be reasonable. The method of determining the amount of vegetative material metabolized is suitable for a very crude estimate only, but it gives an indication of how much plant material is being converted into pocket gopher. The values for cutting and consumption estimate how much of the vegetation is cut, but perhaps do not indicate the full impact of the animal on the plant community, since many of the preferred plants, *E. nevadensis* in particular, are cut to a stump and destroyed.

From the data collected to date it would appear that *T. bottae* is an important vertebrate in those areas of Rock Valley where it is found, in regards to numbers of individuals and biomass. Chew (pers. comm.) stated that in March, 1972, in enclosure C the density of *Perognathus formosus*, the most common species, was 3.5/ha. In August of the same year, the density of *P. formosus* rose to 16.7/ha. In either case *T. bottae* with a density of 3.8/ha was a major portion of the mammalian fauna. In March, pocket gopher biomass was in excess of *P. formosus* biomass as follows:

Biomass of <i>T. bottae</i> , March	= 270.2 g/ha
Biomass of <i>P. formosus</i> , March	= 68.9 g/ha
(3.5 <i>P. formosus</i> /ha; 19.7 g/ <i>P. formosus</i>)	
In August, the figures are:	
Biomass of <i>T. bottae</i> , August	= 270.2 g/ha
Biomass of <i>P. formosus</i> , August	= 329.0 g/ha
(16.7 <i>P. formosus</i> /ha; 19.7 g/ <i>P. formosus</i>)	

2.3.2.4.-12

Table 3 showed a food cropping rate of 25.5 gms wet wt/gopher/day, which would give an annual cropping rate of 9.3 kg wet wt/gopher/year. Assuming 3.8 gophers/ha (Table 1), a total of 35.3 kg wet weight are cropped by gophers/ha/year. The above figures are based on laboratory testing using shoots, with data taken in wet weights, which of course are larger than dry weight values. Data on cutting of roots is not conclusive. Bamberg (pers. comm.) stated that in 1971 the amount of new stem production by the seven major plants in Zone 20 (an area near our study site) was equal to 22 kg dry wt/ha/year, with a total plant biomass of 2477 kg/ha/year (dry weight). Although our figures are wet weights, they do show that gophers may crop a sizable portion of the biomass. The amount of damage done by cropping of new stems or annuals is not known, but could also be of significance to the total structure of the ecosystem.

EXPECTATIONS

If continuing work in this area should be funded, it is proposed to concentrate on determining the impact of *T. bottae* on the plant community, particularly *E. nevadensis*, and also the role of *E. nevadensis* in determining the distribution of *T. bottae* in Rock Valley. In addition, it is hoped that a continuation of the current studies reported in this paper will produce more valid data on density, food consumption and preference.

ACKNOWLEDGEMENTS

We wish to thank Bernado Maza for his assistance in making this work possible, both in calling the problem to our attention and in his advice and help during the project.

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1972 PROGRESS REPORT

ANNUAL NUTRIENT AND ENERGY INTAKE OF THE DESERT COTTONTAIL,
Sylvilagus auduboni, UNDER NATURAL CONDITIONS

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Research Memorandum, RM 73-25

MAY 1973

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Report Volume 3

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ABSTRACT

Annual nutrient and energy intake of *Sylvilagus auduboni* were studied under natural conditions for the initial 7 months of the 16-month study. Diets were determined by stomach analysis for three vegetative growth periods from March through September, 1972. Pace transects were used to estimate relative abundance of plant species on the study location, an area equivalent to the Silverbell Validation Site of the Desert Biome. Protein, crude fiber, calcium, phosphorus, and net energy were determined for important plant species.

Twenty-four plant species were identified in the diet. Eight species accounted for 75% of the dry weight consumed: *Eragrostis superba*, *Opuntia* spp., *Plantago purshii*, *Tridens pulchellus*, *Boerhaavia* sp., *Acacia* spp., *Eriogonum* sp., and *Erodium cicutarium*. There were definite changes in the composition of the diet and in preferred species through three sampling periods: March-April, May-June and July-September. Completion of the 16-month span of the study will complete the annual sequence, and thus indicate how desert cottontail dietary requirements are adjusted to seasons of low rainfall.

INTRODUCTION

Desert ecosystems are open systems with ample energy (sunlight) input for their operation. The diversity and abundance of animals depends upon adaptation to a highly variable plant food supply, which is related to rainfall. The desert cottontail, *Sylvilagus auduboni*, a well-adapted primary consumer, is important in some ecosystems because of its relatively large biomass contributions to several secondary consumers (mammalian, avian and reptilian). Quantification of the relation of this important game species to forage plants in terms of energy and important minerals should provide some important ecological insights.

Food habits reports for the desert cottontail are at present limited to general observations. Bailey (1931) commented that cottontails in New Mexico ate a great variety of vegetation, but he did not identify any specific plants. Orr (1940) also made general observations for cottontails in California. Fitch (1947) concluded that the food of cottontails consisted almost entirely of annual grasses and broad-leaf herbs of the Mediterranean-annual type in the Sierra Nevada foothills of southern California. Ingles (1941) observed some of the plant items selected by desert cottontails in an intensively farmed area in the Sacramento Valley, California. These studies are either not quantitative or not within the desert biome.

In this study we hope to combine quantitative information on food consumption with that on population dynamics in order to estimate chemical cycling and energy degradation for desert cottontails within a desert ecosystem. This report covers the results of the first 7 months of the study, which include three growing conditions of vegetation. Precipitation for the first 4 months of the study period was unusually low and the study extension will allow for more complete data collection and thus enhance the validity of the results.

OBJECTIVES

Specific objectives of this study are:

1. To ascertain the kinds of plants consumed by desert cottontails during an annual cycle.
2. To determine the energy, nitrogen, phosphorus and calcium contents of the plant species that form the bulk of the cottontail's diet.
3. To relate plant intake to plant availability.
4. To estimate the energy and nutrient intake of desert cottontails under field conditions.

Only the first three objectives can be reported upon here.

METHODS

The study area

The Sugarloaf Mountain area of the Tonto Forest, 74 km North of Phoenix, is ecologically similar to the Silverbell Validation Site, which lies within what is often termed the palo verde-cacti desert type. *Cercidium microphyllum* is the dominant tree. *Carnegiea gigantea* occurs sparingly. Several species of *Opuntia* are dispersed over the area. The prominent shrub is *Franseria deltoidea*. Other woody plants that give character to the site are *Lycium* spp., *Fouquieria splendens*, *Acacia greggii*, *A. constricta*, and *Encelia farinosa*.

During spring, whenever winter moisture is adequate, numerous annuals are present. Prominent species are *Erodium cicutarium*, *Plantago insularis*, *Schismus barbatus*, *Lupinus* spp., *Lesquerella* spp., *Calochortus* spp. and *Phacelia* spp. During summer, grasses and perennial forbs occupy the intershrub spaces. Abundant annual grasses include *Bouteloua barbata* and *B. aristidoides*. Perennial forbs include *Cucurbita* spp., *Janusia* spp., *Ipomoea* spp., and *Clematis* spp. Tables 1 and 2 list relative abundance of overstory and understory plants on the study area during each sampling period.

Table 1. Overstory plant species -- abundance on Sugarloaf Mountain study area (based on percentage of occurrences in 30-100 pace transects)

Species	Trees and shrubs	% Ground cover
<i>Acacia greggii</i>		2.7
<i>Yucca elata</i>		2.7
<i>Simmondsia chinensis</i>		2.1
<i>Opuntia versicolor</i>		1.9
<i>Haplopappus larcifolius</i>		1.8
<i>Franseria deltoidea</i>		1.6
<i>Cercidium microphyllum</i>		1.6
<i>Opuntia engelmannii</i>		1.4
<i>Thamnosma montana</i>		1.0
<i>Celtis pallida</i>		1.0
<i>Opuntia bigelovii</i>		1.0
<i>Acacia constricta</i>		.9
<i>Krameria parvifolia</i>		.7
<i>Canotia holacantha</i>		.6
<i>Calliandra eriophylla</i>		.5
<i>Condalia lycioides</i>		.3
<i>Lycium pallidum</i>		.2
<i>Prosopis velutina</i>		.2
<i>Larrea divaricata</i>		.1
<i>Lycium velutina</i>		.1
<i>Fouquieria splendens</i>		.1
<i>Encelia farinosa</i>		.1
<i>Carnegiea gigantea</i>		T
<i>Dodonaea viscosa</i>		T
<i>Janusia gracilis</i>		T
<i>Echinocereus</i> sp.		T
Total for shrubs and trees		22.6

2.3.2.8.-4

Table 2. Herb plant species -- seasonal abundance on Sugarloaf Mountain study area (based on percentage of occurrences in 10-100 pace transects per season)

Species	Grasses and forbs		
	March-April	May-June	July-Aug.-Sept.
% Ground cover			
<i>Aristida adscensionis</i> (G)	8.8	1.8	5.0
<i>Plantago purshii</i> (F)	4.4	T	---
<i>Bromus rubens</i> (G)	4.1	1.8	---
<i>Erodium cicutarium</i> (F)	2.6	.3	---
<i>Euphorbia polycarpa</i> (F)	1.3	.7	.3
<i>Lepidium lasiocarpum</i> (F)	1.3	---	---
<i>Lupinus sparsiflorus</i> (F)	.9	T	T
<i>Amsinckia intermedia</i> (F)	.8	---	---
<i>Lotus wrightii</i> (F)	.7	---	---
<i>Pectocarya recurvata</i> (F)	.7	---	---
<i>Gilia</i> sp. (F)	.6	---	---
<i>Mahonia repens</i> (F)	.6	---	---
<i>Tridens pulchellus</i> (G)	.6	.5	.3
<i>Eriogonum wrightii</i> (F)	.5	.4	.1
<i>Baileya multiradiata</i> (F)	.2	---	---
<i>Panicum</i> sp. (G)	.1	---	---
<i>Lesquerella</i> sp. (F)	.1	.2	---
<i>Ambrosia deltoidea</i> (F)	T	---	---
<i>Aristolochia watsonii</i> (F)	T	---	---
<i>Cryptantha</i> sp. (F)	T	T	T
<i>Cryptantha pterocarya</i> (F)	T	---	---
<i>Dyssodia porophylloides</i> (F)	T	---	---
<i>Porophyllum gracile</i> (F)	T	---	---
<i>Rumex hymenosephalus</i> (F)	T	---	---
<i>Senecio monoensis</i> (F)	T	---	---
<i>Cucurbita foetidissima</i> (F)	T	---	---
<i>Proboscidea arenaria</i> (F)	---	---	.1
<i>Bouteloua barbata</i> (G)	---	---	.1
<i>Muhlenbergia porteri</i> (G)	.6	.4	---
<i>Aristida arizonica</i> (G)	---	.6	---
<i>Bouteloua hirsuta</i> (G)	---	---	.4
<i>Bouteloua eriopoda</i> (G)	---	---	.5
<i>Monodora</i> sp. (F)	---	---	.1
<i>Allionia incarnata</i> (F)	T	.1	---
<i>Eragrostis superba</i> (G)	T	T	T
<i>Delphinium</i> sp. (F)	T	---	---
<i>Erysimum capitatum</i> (F)	---	T	T
<i>Solanum jamesii</i> (F)	---	---	T
<i>Berberis repens</i> (F)	T	---	---
Grasses and forbs	28.9	6.8	6.9
Shrubs and trees	22.6	22.6	22.6
Total plant cover	51.5	29.4	29.5

G = grass; F = forb; T = trace amount

Elevation of the study area is 850 m. Annual rainfall since 1895 has averaged 18.3 cm. The soil is coarse, shallow, and composed mainly of decomposed granite. Topography is gently rolling with occasional deep ravines and boulder piles. No permanent water is present except that provided for livestock, which graze the area all year.

Procedures

Cottontails were collected on the Sugarloaf Mountain area with at least 15 individuals referenced to each of the phenological periods of vegetation development (16 specimens for May-June), namely: 1) spring growth period (March and April); 2) summer drought season (May and June); and 3) summer growing season (July, August and September). Specimens were stored frozen. Each cottontail was weighed and sexed prior to removal of the stomach.

Relative abundance of plant species for each collecting period on the study area was determined by 10-pace transects for each collecting period (Costello and Schwan, 1946). At each collecting date, as dictated by changes in vegetation, ten random lines of 100 steps were paced across the study area. Each plant encountered at a point on the toe was recorded by species, thus species composition of the total vegetative ground cover was determined. The adequacy of this method for our study is questionable, since some of the species that were important in the diet of our cottontails were not detected in the transects. The transects themselves may be inadequate, or the cottontails may be feeding in areas other than where the transects were made.

Representative samples were collected of each anticipated major plant species in the cottontail habitat coincident with animal collections. The food items that were important for cottontails were analyzed for gross content of protein (nitrogen), calcium, phosphorus, crude fiber, and energy, according to accepted procedures (Assoc. Off. Agr. Chem., 1965). A commercial laboratory in Phoenix, Arizona, did the plant analyses.

Stomach contents of cottontails were analyzed by the microtechnique method pioneered by Dusi (1949). Sparks and Malachuk (1968) have also used the technique successfully. Keith et al. (1959) and Flinders and Hansen (1972) further refined the method and applied it to analysis of stomach contents of gophers.

Stomach contents were dried in an oven at 70 C and then ground in a mill over a 1-mm screen. Two microscope slides were prepared from each stomach sample after it had been washed over a 0.1-mm screen (Sparks and Malachuk, 1968). Slides were prepared with Hertwig's solution (Baumgartner and Martin, 1939) and Hoyer's solution (Baker and Wharton, 1952) and were dried at 60 C for about 72 hr.

2.3.2.8.-6

Tissues of identified plants from the study area were mounted on microscopic slides as described by Brusven and Mulkern (1960). The histological characteristics of the epidermis of these identified plants were used as a basis for the identification of plant fragments that were found in the stomach contents of cottontails.

Relative percent of herbage in the monthly diets of cottontails was estimated by microscopic examination of the slides made from the stomach contents at 100X magnification. Forty fields were examined on the two slides made from each cottontail's stomach contents. Fields were selected in a restricted random manner so that each contained at least one fragment of epidermal tissue. Each recognized plant species within each field was recorded, and the percent frequency was then converted to particle density per field (Fracker and Brischle, 1944). Particle density of each food item was then expressed in relative terms, as the percentage of total number of particles of all plant species (Table 3).

A "preference index" was calculated for each item in the diet as:

$$PI = \frac{\text{average relative density per stomach}}{\text{relative ground cover}}$$

Relative density is as given in Table 4 and relative ground cover was calculated from the data of Tables 1 and 2. An index greater than 1.0 suggests that the item is being eaten in greater proportion than its availability in the habitat, i.e. it is selected for or "preferred". An index of less than 1.0 suggests that the item is being ignored. Of course, the coverage of trees and shrubs does not necessarily represent the leaves and young stems that are physically within reach of the cottontails. Coverage of trees and shrubs may overrepresent availability. The use of the PI index is confounded by the diet items that were not recorded in the plant transects or were present only in trace amounts. In these cases $PI = \infty$. For each sampling period the preferred dietary items were ranked (Table 4). Those items that had $PI = \infty$ were ranked according to their relative density, if it was 0.50 or greater. Other items were ranked according to their PI. Items with $PI = \infty$, but relative density of less than 0.50, and items with $PI < 1.0$, were not ranked.

Table 3. Seasonal occurrences of plants in diets of cottontails, plants listed in order of abundance in stomachs for the total period

Plant Species	March-April		May-June		July-August-September		Total for all periods	
	Frequency of occurrence (% of stomachs)	% Average relative density per stomach	Frequency of occurrence (% of stomachs)	% Average relative density per stomach	Frequency of occurrence (% of stomachs)	% Average relative density per stomach	Frequency of occurrence (% of stomachs)	% Average relative density per stomach
<i>Eragrostis superba</i> (G)	46.66	3.12	68.75	31.85	100.00	56.75	71.74	30.60
<i>Opuntia</i> spp. (S)	40.00	1.09	100.00	32.21	80.00	12.21	73.91	15.54
<i>Plantago purshii</i> (F)	40.00	22.13	37.50	.74	---	---	26.07	7.47
<i>Tridens pulchellus</i> (G)	80.00	15.38	43.75	6.48	13.33	.06	45.65	7.29
<i>Boerhaavia</i> sp. (F)	6.66	.02	18.75	6.16	60.00	14.11	28.26	6.75
<i>Acacia</i> spp. (S)	40.00	7.87	18.75	.76	53.33	7.88	36.96	5.40
<i>Eriogonum wrightii</i> (F)	66.66	15.75	6.00	.06	---	---	23.91	5.16
<i>Eriodum cicutarium</i> (F)	66.66	13.80	37.50	1.39	---	---	34.78	4.98
<i>Lupinus sparsiflorus</i> (F)	46.66	5.52	37.50	6.58	6.66	.20	30.43	4.15
<i>Bromus rubens</i> (G)	73.33	5.71	56.25	2.08	26.66	.23	52.17	2.66
<i>Erysimum capitatum</i> (F)	---	---	6.00	4.08	26.66	2.06	10.87	2.09
<i>Aristida</i> spp. (G)	40.00	1.33	50.00	2.22	53.33	2.06	47.83	1.88
<i>Cryptantha</i> spp. (F)	26.66	3.61	37.50	1.85	20.00	.06	28.26	1.84
<i>Sphaeroclea ambigua</i> (F)	13.33	.22	12.50	2.68	20.00	.27	15.21	1.09
<i>Solanum jamesii</i> (F)	---	---	---	---	26.66	2.68	8.70	.87
<i>Calliandra eriophylla</i> (S)	20.00	2.39	---	---	6.66	.06	8.70	.80
<i>Delphinium</i> sp. (F)	26.66	.75	---	---	---	---	8.70	.25
<i>Lepidium lasiocarpum</i> (F)	13.33	.43	---	---	---	---	4.35	.14
<i>Haplopappus larciifolius</i> (S)	13.33	.27	---	---	---	---	4.35	.09
<i>Yucca elata</i> (S)	6.66	.08	12.50	.09	---	---	6.52	.06
<i>Allium</i> sp. (F)	6.66	.08	---	---	---	---	2.18	.02
<i>Lycium velutina</i> (S)	6.66	.06	---	---	---	---	2.18	.02
<i>Berberis repens</i> (F)	6.66	.05	---	---	---	---	2.18	.02
<i>Franseria deltoidea</i> (S)	6.66	.05	---	---	---	---	2.18	.02

G = grass; F = forb; S = shrub or tree

Table 4. Preference indices (PI) of various taxa of plants in the three collecting periods

Category	Species	March-April		May-June		July-Sept.	
		PI	Rank	PI	Rank	PI	Rank
F	<i>Cryptantha</i> spp.	∞	(1)	∞	(6)	---	
G	<i>Eragrostis superba</i>	∞	(2)	∞	(1)	∞	(1)
F	<i>Delphinium</i> sp.	∞	(3)	---		---	
F	<i>Eriogonum</i> sp.	16.24	(4)	0.04	---	---	
G	<i>Tridens pulchellus</i>	13.25	(5)	3.81	(8)	0.06	---
F	<i>Lupinus sparsiflorus</i>	3.15	(6)	∞	(2)	a	---
F	<i>Erodium cicutarium</i>	2.73	(7)	1.36	(10)	---	
F	<i>Plantago purshii</i>	2.59	(8)	∞	(7)	---	
S	<i>Calliandra eriophylla</i>	2.46	(9)	---		0.04	---
S	<i>Acacia</i> spp.	1.13	(10)	0.06	---	0.65	---
F	<i>Boerhaavia</i> sp.	a*	---	∞	(3)	∞	(2)
F	<i>Erysimum capitatum</i>	-----		∞	(4)	∞	(4)
F	<i>Sphaeralcea ambigua</i>	a	---	∞	(5)	a	---
S	<i>Opuntia</i> spp.	0.13	---	2.20	(9)	0.83	---
F	<i>Solanum jamesii</i>	-----		-----		∞	(3)
G	<i>Bromus rubens</i>	0.72	---	0.61	---	a	---
G	<i>Aristida</i> spp.	0.08	---	0.39	---	0.41	---
F	<i>Lepidium lasiocarpa</i>	0.17	---	-----		-----	
F	<i>Allium</i> sp.	a	---	-----		-----	
F	<i>Berberis repens</i>	a	---	-----		-----	
S	<i>Haplopappus laevisifolium</i>	0.08	---	-----		-----	
S	<i>Yucca elata</i>	0.02	---	-----		-----	
S	<i>Lycium velutina</i>	0.32	---	-----		-----	
S	<i>Fraseria deltoidea</i>	0.02	---	-----		-----	
	All forbs	1.93		2.16		10.12	
	All grasses	1.08		3.58		2.77	
	All shrubs	0.27		0.43		0.26	

G = grass; F = forb; S = shrub or tree.

*a: PI = ∞, but relative density <0.50, therefore not ranked

RESULTS

Forty-six cottontails were collected in the three vegetative periods from March 1 to September 30, 1972. The sex ratio was 0.90 male to 1.0 female; the difference is not significant by a group-comparison *t*-test. Of the females, 50% were pregnant in the March-April period, 43% in May-June and 20% in July-September.

General food habits

The coverage of plant species in the study area is given in Tables 1 and 2. The mean number of species identified per stomach varied with sampling period (Table 5).

The most species were recorded for the March-April period and progressively fewer were found the next two periods. The greatest dietary difference between sexes was in March-April, when females ate an average of 9.8 species, which is 1.4 times the number eaten by males. The period of greatest plant diversity and cover coincided with that of greatest reproduction by cottontails. Fifty percent of the females were pregnant in the March-April period, 43% in May-June, and only 20% in July-September.

Table 5. Average number of plant species detected in seasonal diets of desert cottontails from March to September, 1972

	March-April	May-June	July, August, Sept.	Overall average
Males & Females	7.8	5.4	5.1	6.1
Males	7.2	5.2	6.0	5.7
Females	9.8	5.3	4.4	7.0

Twenty-four species or genera were identified in the stomach contents of the cottontails (Table 3): 4 grasses, 7 shrubs and trees, and 13 forbs. Only 16 of the 24 species individually made up at least 1% of the dry weight of the diet in at least one of the three sampling periods. Seven species accounted for 78% of the dry weight of the diet for the 7 months covered by Table 3.

The most abundant plant in the diet was a grass, *Eragrostis superba*, which accounted for 30.6% of the dry weight of the diet for the 7 months and occurred in 71% of the stomachs. A shrub-cactus, *Opuntia* spp., was second in abundance at 15.5% of total diet. *Opuntia* had the highest frequency of occurrence, 73.9%. It was not determined what portions of the cactus were consumed. However, the purple color that is characteristic of the fruits was observed in several stomachs. A forb, *Plantago purshii*, was the third most abundant dietary item (7.5% total weight), although it occurred in only 12 stomachs and was significant only in the first sampling period. One grass, 2 forbs and 1 shrub made up lesser amounts of the diet, but all were >5% of the total.

Seasonal food habits

Table 3 gives the composition of the diet for the three sampling periods, which were chosen to represent phases of plant reproduction. There was a successive decrease in the number of species in the diet and a greater concentration of dietary dominance in fewer species with each period.

2.3.2.8.-10

In the March-April period 22 items were identified in the diet. Five plant species made up 75% of the diet, in order: *Plantago purshii*, *Eriogonum* sp., *Tridens pulchellus*, *Erodium cicutarium* and *Acacia* spp. *P. purshii* was a minor item in the second period and was not recorded in the third period.

In May-June only 15 items were identified, and four of these made up 77% of the diet: *Opuntia* spp., *Eragrostis superba*, *Lupinus sparsiflorus* and *T. pulchellus*. *Opuntia* was always available as 8 to 15% of the total plant cover, but in this period the fruits were beginning to ripen. Bailey (1923) determined that *Opuntia* fruits are 80% water, and since May-June, 1972, was exceptionally dry, the cactus may have been eaten for its moisture content.

In the July-September period there were only 13 plant items in the diet and only three species made up 83% of the diet: *E. superba*, *Boerhaavia* sp., and *Opuntia* spp. *E. superba* increased in quantity and frequency of occurrence from the first to third period, when it was present in all stomachs and averaged 57% of the diet.

Food preferences

Preference indices are summarized in Table 4 for individual species and genera and for general categories (forbs, grasses, shrubs). In the March-April period forbs are 6 of the first 8 in the ranking. The grass category is barely preferred, but two grasses ranked second and fifth: *E. superba* and *T. pulchellus*. The shrub category was not preferred, but two species ranked ninth and tenth among the 10 preferred species.

In the May-June period grass is the most preferred category, due to the preeminence of *E. superba* in the diet, although only trace amounts were detected in the transects. Seven forbs and 1 shrub are also preferred. There was a shift in shrub preference from *Acacia* and *Calliandra* in the first period to *Opuntia* in the second period.

In July-September forbs are again predominantly preferred over grasses, and shrubs as a category are ignored. None of the ranked species was found in more than a trace amount in the plant transects. All the plants found in the transects in more than trace amounts are not preferred, according to the PI.

Only two grasses ever achieved "preferred" status. *Eragrostis superba* was consistently first or second in the rankings. *Tridens pulchellus* went from high preference to low preference to ignored, in successive periods, although there was no significant change in its relative cover. Forbs showed a changing pattern of preference. Six species were preferred in the first or the first and second periods, but not the third period. Four other species were preferred in the second and/or third period, but not the

first. Three species of shrubs were preferred in the first or second period. Among the 24 species in the diet, only 15 rated as preferred in one period or another.

Nutrient and energy content of food plants

The species included in the analyses comprised at least 85% of the 7-month diet. Unfortunately we did not anticipate that *E. superba* would be an important food plant, but this species will be collected and analyzed in 1973. Various analyses are given in Tables 6 to 10.

Table 6. Protein content (%) of cottontail food plants collected on the Sugarloaf Mountain study area, 1972

Species	March April	May June	July Aug. Sept.
<i>Opuntia</i> sp.	---	2.72	9.30
<i>Plantago purshii</i>	11.37	--	--
<i>Tridens pulchellus</i>	7.43	4.46	7.63
<i>Acacia</i> sp.	21.25	15.04	18.0
<i>Eriogonum</i> sp.	9.34	7.11	--
<i>Erodium cicutarium</i>	22.00	7.95	--
<i>Lupinus sparsiflorus</i>	7.79	14.00	--
<i>Bromus rubens</i>	7.40	8.69	--
<i>Aristida</i> sp.	6.81	4.59	6.42
<i>Cryptantha</i> sp.	10.72	--	--
<i>Sphaeralcea</i>	12.58	--	--
<i>Calliandra eriophylla</i>	---	10.79	14.67
<i>Lepidium lasiocarpum</i>	14.62	--	--
<i>Haplopappus larcifolius</i>	11.55	--	--

Table 7. Seasonal crude fiber content (%) of cottontail food plants collected on the Sugarloaf Mountain study area, 1972

Species	March April	May June	July Aug. Sept.
<i>Opuntia</i> sp.	---	19.84	19.50
<i>Tridens pulchellus</i>	26.80	25.72	18.15
<i>Acacia</i> sp.	22.04	19.11	26.32
<i>Eriogonum</i> sp.	23.39	16.34	--
<i>Erodium cicutarium</i>	24.20	14.44	--
<i>Lupinus sparsiflorus</i>	23.80	37.70	--
<i>Bromus rubens</i>	31.10	28.80	--
<i>Aristida</i> sp.	28.72	25.33	28.49
<i>Cryptantha</i> sp.	18.98	--	--
<i>Calliandra eriophylla</i>	---	36.19	15.11
<i>Lepidium lasiocarpum</i>	27.54	--	--
<i>Haplopappus larcifolius</i>	26.94	--	--

Table 8. Seasonal calcium content (%) of cottontail food plants collected on the Sugarloaf Mountain study area, 1972

Species	March April	May June	July Aug. Sept.
<i>Opuntia</i> sp.	---	4.130	2.530
<i>Tridens pulchellus</i>	.625	.438	.562
<i>Acacia</i> sp.	1.125	1.938	.212
<i>Eriogonum</i> sp.	1.406	1.438	--
<i>Erodium cicutarium</i>	.066	1.062	--
<i>Lupinus sparsiflorus</i>	1.180	1.170	--
<i>Bromus rubens</i>	.625	.750	--
<i>Aristida</i> sp.	---	.500	.500
<i>Cryptantha</i> sp.	2.812	--	--
<i>Calliandra eriophylla</i>	---	.750	1.688
<i>Lepidium lasiocarpum</i>	1.312	--	--
<i>Haplopappus larcifolius</i>	1.312	--	--

Table 9. Seasonal phosphorus content (%) of cottontail food plants collected on the Sugarloaf Mountain study area, 1972

Species	March April	May June	July Aug. Sept.
<i>Opuntia</i> sp.	---	.090	.110
<i>Tridens pulchellus</i>	.140	.090	.120
<i>Acacia</i> sp.	.310	.150	.110
<i>Eriogonum</i> sp.	.175	.120	--
<i>Erodium cicutarium</i>	.160	.210	--
<i>Lupinus sparsiflorus</i>	.540	.350	--
<i>Bromus rubens</i>	.215	.145	--
<i>Aristida</i> sp.	---	.100	.140
<i>Cryptantha</i> sp.	.405	--	--
<i>Calliandra eriophylla</i>	---	.110	.190
<i>Lepidium lasiocarpum</i>	.310	--	--
<i>Haplopappus larcifolius</i>	.180	--	--

Table 10. Seasonal net energy (therms. per 100 pounds) of cottontail food plants collected on the Sugarloaf Mountain study area, 1972

Species	March April	May June	July Aug. Sept.
<i>Tridens pulchellus</i>	38.66	40.42	52.76
<i>Acacia</i> sp.	46.41	51.19	--
<i>Eriogonum</i> sp.	44.21	55.71	--
<i>Erodium cicutarium</i>	---	58.80	--
<i>Bromus rubens</i>	31.65	35.40	--
<i>Aristida</i> sp.	35.53	41.05	36.23
<i>Cryptantha</i> sp.	51.40	--	--
<i>Calliandra eriophylla</i>	---	--	57.71
<i>Lepidium lasiocarpum</i>	37.45	--	--
<i>Haplopappus larcifolius</i>	38.43	--	--

DISCUSSION

Plant quality and diet composition

It would be enlightening to be able to see some relationships between plant quality and quantity consumed and preference ranking. This is difficult because the analyses incompletely covered the dietary spectrum. Even with a complete series of analyses such comparisons might be hopelessly confounded by unknown factors of palatability, such as odor, taste and physical nature of the food.

In five of the seven cases in which comparison is possible, protein content was lower in May-June than March-April; in all five cases protein content was higher in July-September than May-June (Table 6). This suggests that protein content was high during the spring growth period, decreased during the dry May-June period, and increased again after the late summer rains. It is reasonable to expect that protein content will affect food selection by rabbits. *Acacia* had the consistently highest protein content; it was exceeded only by *Erodium cicutarium* in March-April. *Erodium* did rank second in quantity eaten and *Acacia* fifth. The interpretation of ranking of *Acacia* is confounded by the fact that this species usually did not have low-growing branches, and cottontails would have to stand on their hind legs to feed upon it. *Acacia* and *Erodium* ranked tenth and seventh in preference in March-April (Table 4). *Tridens pulchellus* ranked third and fourth in quantity and fifth and eighth in preference in March-April and May-June, respectively, although its protein content was relatively low. This grass was ignored as a food in July-September although its protein content was higher than before and its relative coverage was the same. There is no clear evidence that cottontails were selecting food on the basis of protein content.

Opuntia was the most abundant item in the diet (32%) in May-June, and it was a preferred species (ninth ranking), although its protein content was the lowest of all the values. This suggests *Opuntia* was being chosen for water content during this exceptionally dry period.

Crude fiber content had the same seasonal changes as protein content (Table 7.) In general there was an inverse relationship between protein content and crude fiber. Energy content (Table 10) was in all cases higher in the dry May-June period than in March-April, which is opposite to the trend for protein and crude fiber. In March-April the species that ranked high in energy content (Table 10) also ranked high in preference (Table 5), as far as comparisons can be made between the two different lists of species. This is not true in May-June; comparisons are not possible for July-September.

2.3.2.8.-14

In general, phosphorus content was least in the dry May-June period (Table 9) and calcium was higher in May-June than March-April. It may be meaningful that *Cryptantha* ranked second in phosphorus and first in preference in March-April, and *Lupinus* ranked first in phosphorus and second in preference in May-June. Phosphorus is a limiting element for reproduction in some rodents. *Cryptantha* ranked first in calcium and preference in March-April. The very high calcium content of *Opuntia* may be related to its characteristic high oxalate content.

Other studies on different species of cottontails indicate that they usually preferred plants in the pre-seed growth stages, although some plants were important in all stages (Dusi, 1952; Bailey, 1969). Bailey reported that foods that are preferred and nutritious at one growth stage may be poor foods at other stages.

Diet composition, quantity and preference

Cottontails consumed about half the grasses and forb genera present in their habitat, indicating a moderate degree of dietary flexibility. Only one third of the shrub and tree genera that were present were detected in the diet.

Spring was clearly the time of greatest diversity of forbs (31 species were present in the transects); only 15 and 14 were present the other two periods. This diversity was repeated in the diet except that there were fewer dominants in the July-September diet. As is to be expected, the ranking of foods by their abundance in the diet is quite different from that of preference ranking. The difference between the quantity in the diet and preference in the diet and coverage in the plant transects suggests that the rabbits were very selective of some rare items or they were feeding part of the time in areas other than where the transects were taken.

There are several interesting changes in the status of a plant species from period to period, which are probably related to changes in its state of growth, or its condition relative to other plants. In successive sampling periods *Opuntia* goes from ignored, to low preference, to ignored; *Acacia* from very low preference in the first period to ignored in the last. Apparently *Opuntia* was preferred only in time of seasonal drought. *Tridens* goes from high preference, to low preference, to ignored in successive periods, although there was no significant change in its relative cover. Possibly the grass lost its succulence with time; judging from the protein contents, this grass did show new growth in August-September. Some forbs such as *Plantago* and *Lupinus* maintained a preferred status although their cover diminished. *Eriogonum* dropped from highly preferred to ignored, although its relative coverage increased.

EXPECTATIONS

Continuation of the proposed study during 1973 will yield at least the following: 1) A quantitative estimate of the kinds and relative amounts of plants consumed by the desert cottontail during five different seasons (the results of three seasons given in this report) in an environment such as the Silverbell Validation Site, 2) a quantitative estimate of the chemical levels of energy, nitrogen, calcium, and phosphorus on which desert cottontails are surviving on the validation site, 3) a quantitative estimate of the portion of the plant environment of importance to desert cottontails as food, 4) repeating analysis of the March-April and May-June periods will indicate how cottontails adjust to unusually dry periods, and 5) knowledge of all of the above-mentioned parameters will be available for a continuous 16-month period.

ACKNOWLEDGEMENTS

We are grateful to the Arizona State University Zoology Department for administrative assistance. D. Pinkava and Elinor Lehto assisted with plant identifications, and V. Scott and E. L. Boeker collected some cottontail specimens. P. Urness reviewed the manuscript.

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1972 PROGRESS REPORT

REPRODUCTION AND SURVIVORSHIP OF THE LIZARD, *Uta stansburiana*,
AND THE EFFECTS OF WINTER RAINFALL, DENSITY AND PREDATION
ON THESE PROCESSES

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MAY 1973

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Report Volume 3

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A B S T R A C T

Survival and reproduction by the iguanid lizard, *Uta stansburiana*, was investigated in 0.4 ha enclosures near Mercury, Nye County, Nevada. The study was formally commenced in the spring of 1972, but for some aspects, observations have been drawn from three preceding years. Mayhew's hypothesis relating egg production by certain insectivorous lizards to production of winter annuals was examined in detail. Artificial augmentation of normal winter rainfall by the addition of 5 cm of water during November was shown to increase dry matter production by winter annuals (ca. 8 g/m² vs. 0.5 g/m² in 1971-1972). Analysis of variance showed that lizards occupying irrigated areas registered greater body weight gains than those in non-irrigated areas in both years. This is interpreted as direct evidence of an increase of insect food for *Uta* as a result of additional winter rainfall.

The number of egg clutches produced was greater after irrigation during November -- approximately one additional clutch of eggs was produced by female *Uta* occupying irrigated areas during 1970 and 1972. Older females generally produced more clutches than yearling females. Clutch frequency (F) can be roughly predicted from November-December rainfall in cm (R):

$$F \text{ (yearlings)} = 0.34R + 0.47$$

$$F \text{ (older)} = 0.26R + 1.55$$

Analysis of variance involving the size of 46 first clutches laid in 1970 indicated pronounced effects due to both age and irrigation. A similar analysis based on 117 first and second clutches laid in 1972 indicated the age effect, but showed no influences owing to irrigation or density. Mean clutch size of yearling *Uta* was 3.19 in 1970, 3.65 in 1972. Mean clutch size of older *Uta* was 4.20 and 4.39, respectively, in these two years.

Annual survival of yearling and older *Uta* during three years was analyzed. There appeared to be differences between years. Survival of male and female *Uta* was very similar, but yearling lizards survived somewhat better than older individuals. When data from three years were combined there was an inverse relationship between percent annual survival (S) and density (d, per ha):

$$S = -0.0057d + 0.68$$

There is some suggestion that rates of survival observed in 0.4 ha enclosures may not be an adequate measure of mortality experienced in unrestrained populations.

INTRODUCTION

Uta stansburiana is a small insectivorous iguanid lizard, widely distributed in the western United States. Densities vary geographically, but values of around 40/ha have been observed in Texas (Tinkle, 1967) and southern Nevada (Turner et al., 1970). The functional importance of *Uta*, and of the more common lizards in desert environments, has not been adequately appreciated. It is true that the energy utilization of *Uta* is small when compared with total net primary production (Alexander and Whitford, 1968), but Chew and Chew (1970) showed that all of the small mammals in a southern Arizona desert utilize less than 2% of the net above-ground primary production. Hence, the energy utilization and production of *Uta* needs to be contrasted with that of some of the other vertebrates with which it coexists. The main point to be made from such comparisons is that secondary production by *Uta* in southern Nevada exceeds that of many coexisting mammals and probably most of the birds (Turner et al., unpubl.).

The size and composition of *Uta* in the Mohave Desert vary from year to year, owing primarily to annual differences in reproduction (Turner et al., 1970). Differences in egg production are related to winter rainfall, apparently in the manner suggested by Mayhew (1966a, 1966b) in connection with species of *Uma*. Mayhew's hypothesis is that sufficient winter rainfall promotes germination and growth of winter annuals, which in turn leads to increased food (arthropods) for some desert lizards, and hence greater egg production by these species. Among desert lizards of western North America, positive correlation between winter rainfall and egg production has been shown in *Uma notata* and *U. scoparia* (Mayhew 1966a, 1966b), *Xantusia vigilis* (Zweifel and Lowe, 1966) and *Uta stansburiana* (Hoddenbach and Turner, 1968). Similarly, Beatley (1969) has shown a positive relationship between winter rainfall and biomass of winter annuals. However, it has not been shown that increased biomass of winter annuals (or the conditions promoting this increase) actually leads to more food and available energy for lizards.

OBJECTIVES

The purpose of this study is to determine the functional relationships between reproduction and survival by *Uta* and whatever important independent variables may impinge on these two processes, e.g., population density, rainfall, and predation. These relationships can be utilized, then, to create a model capable of predicting time changes in the composition and size of populations of this desert lizard. The research during 1972 included analyses of reproduction and survival, as affected by rainfall and density. No work on predation was accomplished, but this will be done during 1973.

METHODS

Most of the work to be discussed in this report was done during 1972, and DSCODE A3UTJ72 refers to the 1972 Data Set. However, previous work during 1969, 1970 and 1971 has bearing on some of the findings to be reported here. Hence, the ensuing description of procedures will include not only what was done in 1972, but some of the earlier operations.

Study areas

During the winter of 1969 and during calendar 1970, work was conducted in five 0.4 ha enclosures 1.6 km west of Mercury, Nevada. These plots are about 45 x 90 m and enclosed by sheet metal fences 14 inches high buried 2-4 inches beneath the surface of the soil. Each plot was marked off in a rectilinear grid with numbered stakes. Further details are given by Medica et al. (1971). A sixth enclosure was constructed during 1971 and was used for the 1972 experiments.

Lizards

Field work usually began in mid-February and continued through mid-October. Lizards were captured by noosing, and conventional records of identity, sex, location, length, weight, and sexual condition maintained. Quick-drying paint patterns were applied to lizards to facilitate recognition in the field. Full details are given by Medica et al. (1971). During the breeding season we attempted to capture every female at least once a week. Detailed records were maintained on the reproductive state and body weights of these lizards. Clutch sizes were inferred from palpation and counts of follicles ≥ 5 mm in size. Hoddenbach and Turner (1968) showed that follicular atresia occurs only occasionally among yearling females and essentially not at all among older individuals. Clutch frequency was estimated on the basis of body-weight changes and palpation data (Turner et al., 1970; Medica et al., 1971).

Mortality was assessed 1) for hatchlings from shortly after birth until March of the following spring (i.e., over about the first eight months of life), 2) for yearlings between the age of 8-9 months in March to the age of about 20 months the following March, and 3) for older lizards from March to March. Hatchlings were not considered a member of the cohort to be analyzed unless they were ≥ 28 mm in size at time of marking (previous work has indicated that as hatchlings increase in age the likelihood of survival to the following spring increases). March rosters of yearling and older lizards included animals caught at least twice (in two different weeks) during March, and other obvious residents even though they were not registered until later in the spring.

Experimental treatments

Irrigation: Between October 28 and December 3, 1969, 5 cm of water were applied by rainbird sprinkler to one of the plots. Water was applied until it began to run off the surface. Time between applications averaged about 3 days. The maximum amount of water applied at one time was around 0.56 cm. The soil of this plot was kept permanently moist until 5 cm had been applied. Similarly, between November 8 and 21, 1971, 5 cm of water were applied with sprinklers to two of the plots (one of these was the same one irrigated in 1969). Natural winter rainfall was recorded in both years with a conventional rain gauge nearby.

Density manipulations: In February of 1972 densities of *Uta* were adjusted so that the 3 plots that formerly had high densities were lowered and those of low density were raised. These manipulations involved marked *Uta* of known age, and were completed by the end of February. The effect of these adjustments was to establish densities of around 74-86 lizards per ha in the dense plots and from about 30-50/ha in the low density plots. One leopard lizard was added to each of two plots (both unwatered) during March. Unfortunately these lizards did not stay in the plots and they were not seen after early May of 1972. Densities after manipulations were maintained through March. If individuals were no longer present in the plot at the end of March new known-age *Uta* were added to reestablish the desired densities. After March the populations within each of the plots were permitted to follow their natural courses.

Plants

During May of 1970 winter annuals were counted in the irrigated plot and one of the adjoining non-irrigated areas. In each plot 20 quadrats (20 x 20 cm) were randomly placed in bare areas and 20 quadrats beneath *Ambrosia dumosa*. All winter annuals were collected, dried and weighed. In late March of 1972 winter annuals were collected from both irrigated plots and from two non-irrigated ones. In each plot 20 quadrats were randomly distributed beneath *Krameria parvifolia*, 20 beneath *Ambrosia dumosa*, and 20 in open areas. Plants were dried and weighed as in 1970.

Statistical procedures

In considering relationships between survival and density and between egg production and winter rainfall, simple linear regressions were computed using one of the programs (BMD05R) in the library of the Health Sciences Computing Facility of the University of California at Los Angeles. Computations were carried out on a 360-91 computer at the UCLA Campus Computing Network via a Data 100 Remote Batch Terminal located in the Laboratory of Nuclear Medicine and Radiation Biology.

Mean clutch frequencies were regressed on 20 rainfall variables based on monthly precipitation recorded during the fall and winter preceding the breeding season. The variables tested were: single monthly totals between September and February (6), all two-month totals (5), all three-month totals (4), and all four-month totals (3) during this time; total rainfall between September and January, and total rainfall between September and February.

Factorial analyses of variance were done using one of the programs (BMDX64) in the library of the Health Sciences Computing Facility.

RESULTS

Rainfall and irrigation

Natural rainfall during the winters of 1969 and 1971 is shown in Table 1, together with amounts added artificially by irrigation.

Table 1. Natural rainfall and water added by irrigation to 0.4 ha enclosures in southern Nevada

	Natural rainfall (mm)		Water added by irrigation (mm)	
	1969-70	1971-72	1969	1971
September	2.03	0.51		
October	13.72	0.00		
November	10.67	1.02	50.80	50.80
December	0.00	39.88		
January	1.02	0.00		
February	18.80	0.00		

Winter annual biomass

In both 1969 and 1971 the additional water applied during November had obvious effects on germination and growth of winter annuals (Table 2). In 1970 about 75% of the material collected was the grass *Bromus rubens*. In 1972 *Bromus rubens* still dominated in plot 6 (ca. 37% of the total), but in the other watered plot the most important contributors were *Cryptantha recurvata*, *Festuca octoflora* and *Phacelia fremontii*. In the watered plots *Cryptantha nevadensis* was the major species by weight (20-34% of the totals). In both years the vast majority of annuals occurred beneath shrubs rather than in open areas.

2.3.2.9.-6

Weight changes in *Uta*

As mentioned previously, there has never been a direct connection established between increased biomass of winter annuals and improved food resources for insectivorous lizards in desert areas. Because the production of eggs by some desert lizards seems to be positively correlated with the abundance of winter annuals it has been inferred that this causal link exists. To actually show this directly by sampling arthropod abundance and observing the stomach contents of lizards would be a difficult task. However, some data have been acquired on body-weight changes in *Uta* which seem to be more directly related to the issue of food consumption than egg production per se.

The ensuing analyses pertain only to body-weight changes among yearling *Uta* between March and July (i.e., between the ages of about 8 and 12 months). The older lizards afforded small samples and, except for ovigerous females, usually did not exhibit pronounced changes in weight. Concentration has been on increments and decrements of individual lizards (rather than changes in group means). Table 3 summarizes data for yearling females in the spring of 1970. These data are restricted to females weighing between 1 and 2 g at the outset (i.e., unusually large or small females were not included in the analysis). A t test of the hypothesis that the mean weight changes for the watered (830 mg) and unwatered plots (506 mg) do not differ, yielded a t value of 2.29. With 20 d. f. the probability of a t value this large is about 0.03. Hence, the assumption is that the means do differ.

Table 2. Dry matter production by winter annuals in 0.4 ha enclosures in southern Nevada

Year	Plot	Combined dry weight of annuals (g/m ²)
1969-70	6 (watered)	7.98
	7	0.48
1971-2	6 (watered)	5.66
	13 (watered)	4.38
	7	0.11
	9	0.07

Table 3. Weight changes observed in 1970 among yearling *Uta stansburiana* in 0.4 ha enclosures in southern Nevada.

Plot	n	Mean initial weight (g)	Mean weight change (g)	Range (g)
6 (watered)	4	1.45	0.83	0.52 - 1.05
7	4	1.35	0.71	0.35 - 1.01
8	5	1.51	0.53	0.23 - 0.76
9	4	1.48	0.39	0.12 - 0.67
10	5	1.56	0.41	0.18 - 0.80
7-10	18	1.48	0.51	0.12 - 1.01

A similar approach was followed for 1972 but the analysis was expanded to include both sexes and to allow for a possible density effect. The basic data are given in Table 4. A 2 x 2 x 2 factorial analysis of variance gave the results set forth in Table 5 (with one d.f. in all cases). There were highly significant effects on weight changes owing to both irrigation and sex, but no effect on density. The difference between the sexes is thought to be associated with egg production, and the diversion of energy by females into eggs rather than into new somatic tissue. In both sexes there was apparently more energy available in the irrigated plots -- whether for reproduction or growth -- and this energy could only have come from more available food. These findings are interpreted as direct support for the previously assumed relationship between winter annual abundance and food available for ground-dwelling insectivorous lizards.

Table 4. Weight changes observed in 1972 among yearling *Uta stansburiana* in 0.4 ha enclosures in southern Nevada

Sex	Treatment	n	Mean change in wt. (g)	Mean initial weight (g)
Male	watered, low density	2	1.25	2.31
	watered, high density	4	0.60	2.91
	unwatered, low density	7	0.13	2.88
	unwatered, high density	9	0.30	2.92
Female	watered, low density	4	0.13	2.21
	watered, high density	4	0.16	2.24
	unwatered, low density	3	-0.50	2.76
	unwatered, high density	11	-0.28	2.48

Table 5. Results of a factorial analysis of weight changes among yearling *Uta stansburiana* in 1972

Factor	F	F _{.05}	F _{.01}
Water	23.57	4.11	7.39
Density	0.20		
Sex	28.88		
Water x density	3.87		
Water x sex	0.51		
Sex x density	2.06		
Water x density x sex	1.52		

2.3.2.9.-8

Egg production

In assessing the possible influences of density and rainfall on reproduction by *Uta stansburiana* two aspects of egg production were considered: clutch frequency and clutch size.

Clutch frequency: The frequency with which iteroparous lizards lay eggs has traditionally been difficult to estimate (Turner, 1968; Turner et al., 1970). The procedure in southern Nevada involved the repeated capture and observation of marked cohorts of females (Turner et al., 1970; Medica et al., 1971). Clutch frequency is defined as the number of clutches produced by a female surviving for the entire period of reproduction, recognizing of course that not every female will live out the season. For modelling purposes it seems best to estimate potential clutch frequency and then adjust for losses due to mortality as a separate operation. Table 6 gives clutch frequency data for 1970 and 1972 based only on those females which survived the entire breeding seasons. These figures show a definite effect owing to irrigation in 1972 and apparently the same tendency in 1970 -- though less clearly expressed among the yearling females that year.

Table 6. Mean numbers of clutches produced by female *Uta stansburiana* occupying experimental 0.4 ha enclosures in southern Nevada

Year	Age	Treatment	n	Mean number of clutches	Range
1970	old	watered	2	3.00	3
		unwatered	8	1.75	1 - 2
	young	watered	9	1.11	0 - 3
		unwatered	32	0.94	0 - 2
1972	old	watered	4	4.00	4
		unwatered	7	2.86	2 - 3
	young	watered	8	4.25	3 - 5
		unwatered	19	2.57	1 - 4

Can the observed clutch frequencies (F) be quantitatively related to rainfall in cm (R) during the preceding fall and winter? Mean clutch frequencies of both yearling and older *Uta* were regressed on 20 possible fall-winter rainfall variables. For yearling females the highest observed positive correlation (0.89) was with December rain and the next highest was with November-December rainfall (0.76). For older *Uta* the highest positive correlation was with November-December rain (0.98). The November-December relationships are illustrated in Figure 1. The equation for the least squares fitted regression lines are as follows:

Older females: $F = 0.26 (\pm 0.04) R + 1.55$ (1)

Yearling females: $F = 0.34 (\pm 0.21) R + 0.47$ (2)

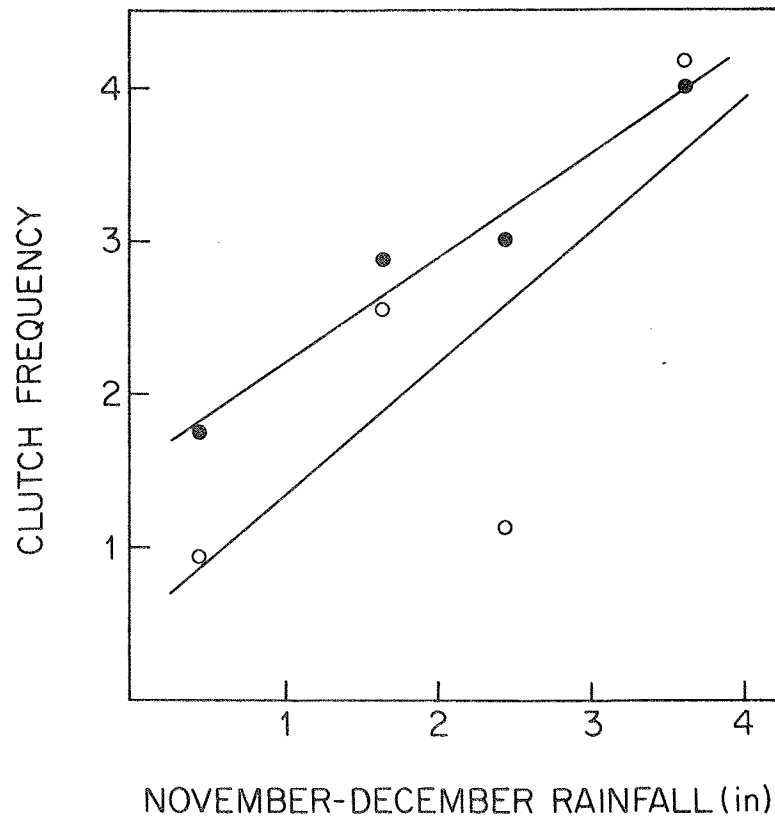


Figure 1. Relationship between the number of clutches of eggs laid by *Uta stansburiana* and rainfall during the preceding winter. Open circles (and lower line) pertain to yearling females; solid circles (and upper line) to older females.

2.3.2.9.-10

In 1970 50 females started the breeding season in five 0.4 ha plots. Total egg production of these females was examined by simply adding up all the clutches produced by each individual. When a female known to be carrying oviducal eggs disappeared before the laying of eggs could be confirmed, deposition of half the estimated clutch size was assumed. Egg production by females dying during the breeding season was included in the analysis, so the totals reflect an interaction between clutch size and frequency as well as the disappearance rate of females. Mean total egg production in 1970 is given in Table 7. A 2 x 2 factorial analysis of variance of these data indicated highly significant effects owing to both age ($F = 33.4$) and irrigation ($F = 13.2$). The value of $F_{.01}$ (with 46 d.f.) was 7.21.

Table 7. Mean total egg production in 1970 by female *Uta stansburiana* occupying five 0.4 ha enclosures in southern Nevada

Age of female	Treatment	n	Mean number of eggs produced per female
Yearling	watered	10	4.30
	unwatered	29	3.55
Older	watered	2	10.50
	unwatered	9	5.89

A similar approach was followed with the 1972 data, except that egg production was also examined in terms of spring densities (Table 8). The conspicuously greater productivity in 1972 was clearly associated with the greater number of clutches produced that year. A slightly different arrangement of these data is given in Table 9. A 2 x 2 factorial analysis of variance indicated no effect on egg production owing to density and no significant interactions. However, the effects of age ($F = 6.98$) and irrigation ($F = 9.57$) were highly significant ($F_{.05} = 3.99$; $F_{.01} = 7.04$).

Table 8. Mean total 1972 egg production by female *Uta stansburiana* occupying six 0.4 ha enclosures in southern Nevada

Age of female	Plot density	Treatment	n	Mean number of eggs produced per female
Yearling	high	watered	12	10.36
		unwatered	27	7.17
	low	watered	6	9.73
		unwatered	10	6.99
Older	high	watered	3	15.17
		unwatered	10	9.11
	low	watered	3	11.50
		unwatered	3	10.00

Table 9. Total egg production by female *Uta stansburiana* in 1972

Category	n	Mean number of eggs produced per female
Older females	19	10.58
Younger females	55	8.11
Watered plots	24	10.95
Unwatered plots	50	7.69
Low density	22	8.76
High density	52	8.74

Clutch size: In a given year, clutch size of *Uta* is markedly influenced by age and to a lesser degree by season. In general, the first two clutches of the season are larger than those produced later (Hoddenbach and Turner, 1968). Table 10 summarizes clutch-size data in 1970, based on the first clutches produced by 46 females. In four cases, a female produced a clutch of eggs but there was no estimate of its size. In estimating total egg production a value was assigned to this clutch -- the mean of the group -- but none was assigned in analyzing clutch size. Hence, the discrepancy between the number of females represented in Tables 7 and 10. Analysis of variance indicated highly significant effects due to age ($F = 26.2$) and irrigation ($F = 9.0$). The value of $F_{.01}$, with 42 d.f., was 7.27. The overall mean clutch size for ten older females was 4.20, for 36 yearling females 3.19.

Table 10. Mean sizes of first clutches produced by *Uta stansburiana* in 1970

Age of female	Treatment	n	Mean clutch size
Yearling	watered	10	3.50
	unwatered	26	3.08
Older	watered	2	5.00
	unwatered	8	4.00

A similar analysis of 117 clutches produced by female *Uta* was made during 1972 in six experimental plots. The clutches used in this analysis were the first and second produced by a given female. Table 11 summarizes these data. The analysis of variance indicated a highly significant age effect ($F = 21.5$; $F_{.01} = 6.90$), but no significant effects owing to density or irrigation. The overall mean clutch size for older females was 4.39, for yearling females 3.65.

2.3.2.9.-12

Table 11. Mean sizes of first and second clutches produced by *Uta stansburiana* in 1972

Age of female	Plot density	Treatment	n	Mean clutch size
Yearling	high	watered	17	3.59
		unwatered	46	3.57
	low	watered	8	3.63
		unwatered	18	3.94
Older	high	watered	5	4.80
		unwatered	15	4.20
	low	watered	3	4.33
		unwatered	5	4.60

From the foregoing analyses the following conclusions are drawn: 1) irrigation increased egg production by both yearling and older female *Uta*, 2) the increase in egg production was brought about more by an increase in the number of clutches laid (roughly one more clutch in the irrigated plots) than by an increase in clutch size, 3) over the range of densities examined in 1972, there was no detectable density effect on clutch size or frequency, and 4) age (and size) of females had a pronounced effect on clutch size and a lesser effect on frequency.

Survival

Data on survival will not become available until 1973, and so are not included in this report. However, it is instructive to consider previously-acquired data relating to survival of *Uta* in 0.4 ha enclosures.

Annual survival of yearling and older Uta: The basic data, involving the years 1969-1972, are given in Appendix A. The reader is reminded of the rules adopted in deciding which lizards composed the initial cohorts (Methods section). The data given in Appendix A have been condensed and the possible differences examined in annual survival (March-March) associated with years, age and sex (Tables 12, 13 and 14).

Table 12. Annual survival of *Uta stansburiana* occupying 0.4 ha enclosures in southern Nevada during three years

Year	Number of plots analyzed	Initial numbers	Annual survival
1969-1970	2	55	0.18
1970-1971	5	142	0.30
1971-1972	5	86	0.44

Table 13. Annual survival of male and female *Uta stansburiana* occupying 0.4 ha enclosures in southern Nevada

Year	Sex	Initial numbers	Annual survival
1969	males	20	0.15
	females	35	0.20
1970	males	52	0.29
	females	90	0.31
1971	males	40	0.48
	females	46	0.41
All years combined	males	112	0.33
	females	171	0.32

Table 14. Annual survival of yearling and older *Uta stansburiana* occupying 0.4 ha enclosures in southern Nevada

Year	Age (months)	Initial numbers	Annual survival
1969	20+	18	0.11
	8	37	0.22
1970	20+	22	0.23
	8	120	0.32
1971	20+	46	0.37
	8	40	0.53
All years combined	20+	86	0.28
	8	197	0.34

The following conclusions are drawn from these figures. First, there appear to be year-to-year differences in the survival of yearling and older *Uta*. For the present, comment will be withheld on possible causation. Second, there is no important difference in the survival of males and females. This is in keeping with earlier findings (Turner et al., 1969a), which indicated sex ratios of 1:1. Third, survival of yearling *Uta* is consistently better than that of older lizards.

Figure 2 illustrates annual survival (S) of *Uta* as a function of initial spring density (d). With S expressed as percentage and d as numbers per ha, the equation for the least squares fitted line is:

$$S = -0.0057 (\pm 0.0018)d + 0.68 \quad (3)$$

The correlation coefficient associated with these data is -0.712. The F value, with 11 d.f., is 10.28, indicating a slope differing significantly from zero ($F_{.01} = 9.65$). When data for 1970-1 (5 plots) and 1971-2 (5 plots) were examined separately

2.3.2.9.-14

the correlation coefficients were negative (-0.786 and -0.296, respectively), but the F values (4.86 and 0.29, respectively) did not indicate slopes differing significantly from zero ($F_{.05} = 7.71$).

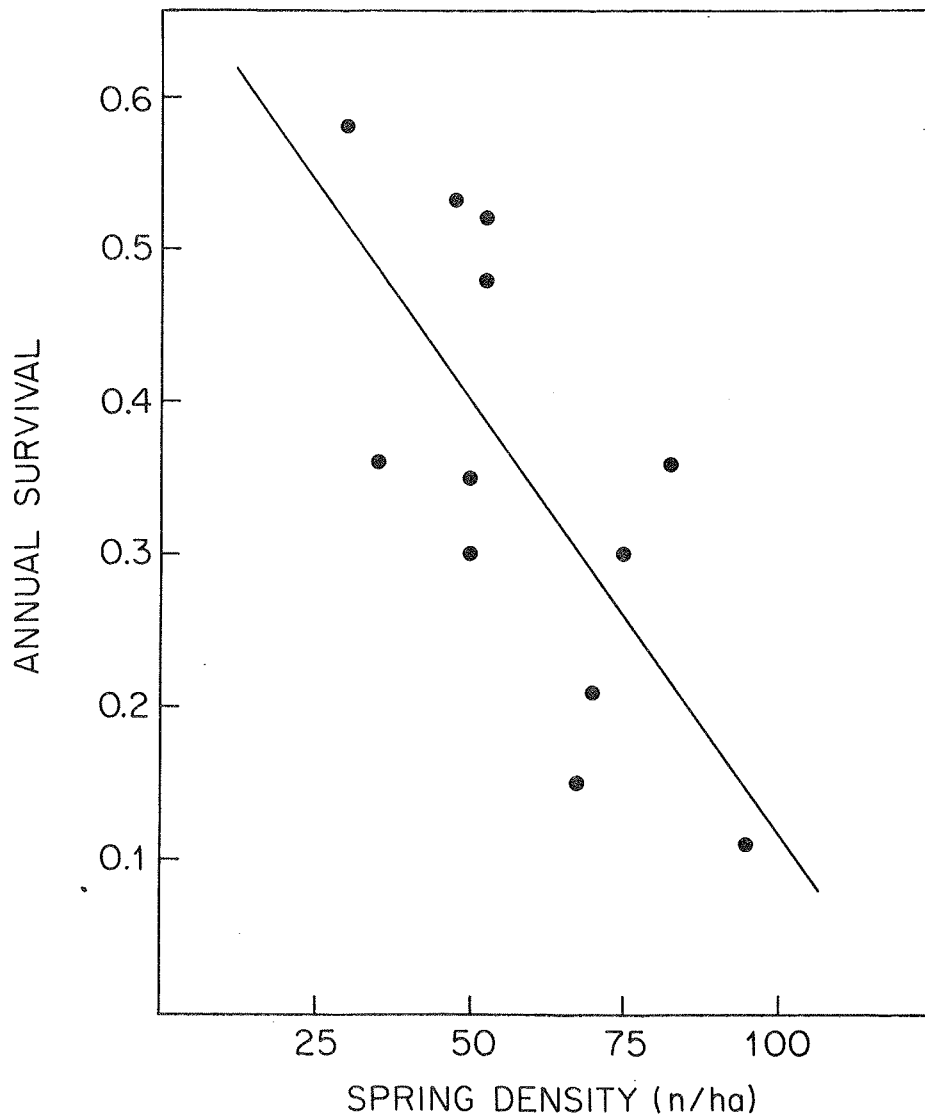


Figure 2. Relationship between annual survival and spring density of *Uta stansburiana* occupying one-acre enclosures in southern Nevada.

Eight-month survival of hatchling Uta: Prior to 1972 few hatchling *Uta* were marked in the experimental plots during the summer. Intensive registration was not begun until the spring. Summer registration of young *Uta* and recaptures the ensuing spring are indicated in Table 15. Except for the 1972 data, these figures pertain only to juveniles ≥ 28 mm in length at time of marking.

Table 15. Eight-month survival of hatchling *Uta stansburiana* occupying 0.4 ha enclosures in southern Nevada

Year	Sex	Hatchlings marked in July-August	Recaptured following February-March
1969	male	24	6
	female	24	10
1970	male	16	9
	female	16	11
1971	male	13	7
	female	21	16
1972	male	110	-
	female	116	-

DISCUSSION

The work with *Uta* in 0.4 ha enclosures during 1972 clearly confirmed the postulated correlation between winter rainfall and egg production. This relationship has been previously suggested for *Uta* (Hoddenbach and Turner, 1968), and a direct causal association between winter rainfall and germination and production of annuals has been demonstrated (Beatley, 1969). Better production of winter annuals also presumably leads to more insect food for *Uta*, but this step has not been demonstrated.

An investigation of body-weight changes during the spring among yearling *Uta* occupying irrigated and non-irrigated enclosures indicated significantly higher weight gains among those lizards in the irrigated areas. This is interpreted as direct evidence of more available food resources which were in some way promoted by winter irrigation.

The 1972 data, coupled with information acquired in 1969-70, indicated a high positive correlation (0.98) between the number of clutches laid by female *Uta* 20 months and older, and the amount of rain during November and December. The comparable correlation for yearling females (0.76) indicated a similar functional relationship but

2.3.2.9.-16

explained far less of the observed variation. Yearling females occupying an irrigated plot in 1969-70 produced about the same number of clutches (1.1) as females in non-irrigated enclosures (0.9), while in 1971-72 yearling females in irrigated areas produced conspicuously more clutches (4.3) than females in plots which did not receive water (2.6)

A preliminary analysis of growth by hatchling *Uta* has suggested that heavy fall and winter rains inhibit activity and growth. If this is so, yearling *Uta* in the spring (ca. 8 months of age) would be relatively small following winter seasons with heavy rainfall, and larger after dry winters assuming comparable regimens of temperature. Reproduction does not begin until a threshold body size is attained, so the same factors which promote more available food in the spring may also delay growth and the initiation of egg production. Such an effect would be less marked among older females (20+ months old) for they would have already attained essentially maximum body size by their second winter. However, if such an inhibitory effect operated on yearling females in 1969-70, it does not appear to have been expressed in 1971-72.

Within the range of spring densities examined in 1972 (ca. 30-100/ha) a density effect on clutch size was not detected, though the expected difference between yearling and older females was clearly manifest. In 1970 clutch size was apparently increased by irrigation, but the 1972 data did not reveal such an effect.

Earlier work with hatchling *Uta* was not adequate to make definitive comments regarding their survival. There is some indication that 8-month survival following the summer of 1969 (when reproduction was good) was not as good as that following the summer of 1970 (when few young were produced). Annual survival of yearling and older *Uta* indicated a density effect when data from 3 years were combined. The limited observations relating to survival of hatchlings indicate better survival in the 0.4 ha enclosures (ca. 33-60%) than observed in 1.4 ha plots in Rock Valley where *Uta* are essentially unrestrained. Turner et al. (1970) reported around 20-25% 8-month survival of juvenile *Uta* in 1966 and 1967. Similarly, the annual survival rates of older *Uta* (from around 10% to almost 60%) in the 0.4 ha plots were generally higher than that observed among older *Uta* in Rock Valley between 1966-7 and 1967-8. Turner et al. (1970) reported annual survival rates of 25 and 16%, respectively, for these 2 years. The point is that the enclosures themselves may have an influence on the demographic parameters under observation. Gentry (1969) reported that enclosed populations of *Microtus pinetorum* exhibited abnormally high densities which, in his opinion, would not have been sustained in the absence of fencing. What appear to be unusually high densities of horned lizards in the 0.4 ha enclosures used for the *Uta* studies have also been observed (Medica et al., 1973).

EXPECTATIONS

Further irrigation experiments are not planned for 1973 because the effect of additional winter rainfall on annual production and reproduction by *Uta stansburiana* seems well established. Natural rainfall during the winter of 1972-73 will be recorded, and measurements of egg production and winter annual biomass during the spring of 1973 will be determined as in 1972.

Densities in four 0.4 ha enclosures will be experimentally altered during the early spring of 1973 in a manner comparable to that used in 1972. The main change in operations during 1973 will be another attempt to assess the impact of leopard lizards on survival of *Uta*. In 1972 it was found that these large predatory lizards could neither be restrained nor excluded by the low fencing surrounding the 0.4 ha experimental plots. Hence, predation pressure could not be controlled. In 1973 portions of two of the 8-ha enclosures in Rock Valley (Medica et al., 1971) will be used in a predation experiment. It is known from earlier work in these enclosures that adult leopard lizards are restrained by the fencing (Turner et al., 1969b). During 1972 Plot C was subdivided into two 4-ha semicircular plots (Chew, 1973). During the spring of 1973 all of the leopard lizards will be removed from one half of Plot C. A normal, or slightly augmented, density of leopard lizards will be maintained in adjoining Plot A. Studies of *Uta* reproduction and survival will be carried out in one 1.4 ha subplot in that portion of Plot C lacking *Crotaphytus*, as well as in a similar plot in Plot A (with a normal population of leopard lizards).

The work in 1973 will provide information on survival of lizards marked in 1972. Hatchling *Uta* will be marked in the summer of 1973 as in 1972. Survival of lizards marked in 1973 will be assessed by a final sampling in all plots during the spring of 1974. Attempts to derive quantitative expressions predicting egg production and mortality as a function of rainfall, density, predation and temperature will continue.

ACKNOWLEDGEMENTS

We acknowledge the assistance in the field of William Cobb, Michael Johnson, Sherburn Sanborn, and Michael Skivington. We are particularly grateful to Thomas Ackerman for his aid in the identification of annual plants. Donald W. Tinkle and Robert M. Chew both offered valuable advice and encouragement in planning the experiments. Finally, we acknowledge the indispensable support of the Civil Effects Test Organization at the Nevada Test Site. Some of this work was supported by Contract AT(04-1)GEN-12 between the U.S. Atomic Energy Commission and the University of California, Los Angeles.

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APPENDIX A. Survival of *Uta stansburiana* in 0.4 ha experimental enclosures in southern Nevada

Time period	Age (months)	Sex	Plot										All plots
			6	7	8	9	10						
March 1969- March 1970	20+	m	6	1	3	1							
		f	4	0	5	0							
	8	m	5	1	6	0							
		f	12	2	14	5							
Totals			27	4	28	6						55	10
March 1970- March 1971	20+	m	3	0	1	0	3	1	2	1	-		
		f	3	0	5	2	2	0	1	1	2	0	
	8	m	11	1	10	5	9	3	9	4	4	0	
		f	21	3	17	5	16	5	9	5	14	7	
Totals			38	4	33	12	30	9	21	11	20	7	142
March 1971- March 1972	20+	m	3	1	2	1	6	3	5	1	2	0	
		f	3	1	5	4	6	3	7	1	7	2	
	8	m	6	4	2	1	7	4	5	2	2	2	
		f	9	4	3	1	-	-	3	2	3	1	
Totals			21	10	12	7	19	10	20	6	14	5	86

1972 PROGRESS REPORT

POPULATION STRUCTURE, FORAGING BEHAVIOR AND DAILY
MOVEMENTS OF CERTAIN SONORAN DESERT BIRDS

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Research Memorandum, RM 73-27

MAY 1973

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Report Volume 3

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A B S T R A C T

This study investigated the role of birds in the desert ecosystem at Tucson IBP sites.

Birds nested from February to September; on the Silverbell site about 70% of all nests constructed were begun before the onset of summer rains, but some species did not nest before the rains began. An adult breeding population of 7.5 kg (22 species) on a 20 ha plot of the Silverbell site produced a fledgling biomass of 4.6 kg; 41% of all nests that contained at least one egg fledged young and 32% of all eggs laid produced fledglings. Nesting failures were due primarily to predation (37%) and cowbird parasitism (22%). On the Santa Rita 20 ha plot, 15 species nested after June 15, 39% of all eggs laid produced fledglings, and a total fledgling biomass of 3.3 kg resulted. Fledging success was highest in late July and August and coincided with the peak in insect abundance. It does not appear that the drought in the first five months of 1972 had an adverse effect on nesting success. Wintering sparrows consumed mostly seeds of *Aristida*, *Panicum* and *Paspalum*.

INTRODUCTION

Unlike most other vertebrates, birds are highly mobile. The species diversity and abundance may change abruptly from one season to another, and from one breeding season to the next. The breeding population may be suddenly augmented by additional bird species and numerous individuals when habitat conditions are exceptionally favorable. Or species may leave an area when drought reduces the food resources. Some birds forage far from their nesting sites. Wintering flocks of migrant sparrows may be of major importance as primary consumers in some years, but be virtually absent in other years. This project investigated demographic patterns, growth rates, dispersion, movements, and foraging behavior in an effort to establish the relationship between the annual cycle of birds and the variables in the desert environment.

In this second year of the project, the Cactus Wren and Curve-billed Thrasher have continued to receive special emphasis. These are abundant permanent residents, and study of them provides insight into the importance of birds in energy transfer in the desert. The most intensively studied community in 1972 was the palo verde (*Cercidium*)-saguaro (*Cereus*) dominated Silverbell site. Study on the Santa Rita site was restricted to the summer nesting season. Mesquite-grassland dominates the Santa Rita site.

OBJECTIVES

The basic objective has been a general ecological study of the bird community in the Sonoran Desert. This report contains data on the following two objectives.

1. To determine growth and reproductive rates of birds on the Silverbell and Santa Rita sites.
2. To evaluate the importance of wintering flocks of sparrows as primary consumers and determine the foods consumed. Energy requirements will be estimated later.

The following two objectives were studied in 1972, but the data are being analyzed and will be reported in a subsequent Research Memorandum.

1. To determine the extent of movements of birds on the Silverbell site and define their foraging niches.
2. To study the foraging behavior of Curve-billed Thrashers and Cactus Wrens to determine food habits, and to determine time-energy budgets in order to estimate energy requirements.

METHODS

Data on reproductive activity (DSCODES A3URJ14, A3URJ15 and earlier A3URJ02) were collected throughout 1972 on the Silverbell site and from June 15 to the end of the breeding season on the Santa Rita site. A 20 ha plot at each site was covered as often as necessary (daily during the height of activity) in order to find nests as they were constructed and follow them until their fate was established. When nests were first found, data on nest placement were obtained, and the location of the nest plotted on a map. Individual pairs of birds were identified and their movements plotted on study area maps (not submitted through data processing). Nestlings of some species were weighed and measured to obtain growth rates (A3URJ04).

Individuals of the most abundant insectivorous species have been followed by an observer who recorded their foraging behavior (A3URJ03). Curve-billed Thrashers and Cactus Wrens have been subjected to a more comprehensive time-budget analysis (A3URJ06 and A3URJ07) at various seasons of the year. The time budget study results in relatively few minutes of data for each hour in the field because the birds are easily disturbed, even by a cautious observer. These studies also yield information on food items consumed.

In 1971, the effect of widely dispersed rains in summer upon the distribution of nesting bird species was studied. This was done by conducting a 3-minute bird census (A3URJ08 and A3URJ09) at each of 25 stations one mile apart in the Santa Rita and the Avra Valley sites. Also at each station, an 8-minute survey (A3URJ10 and A3URJ11) of bird activity was conducted, features of insect density noted, precipitation measured, and plant phenology recorded. No data from this part of the project are presented in this report; computer analysis is in progress.

In the winter of 1971-72, eighty sparrows were collected and their crops and gizzards examined to determine seeds consumed. The seeds from each bird were sorted and identified (to genus) and weighed. Efforts to determine relative abundance of foods available were unsuccessful.

On the Santa Rita site, insects were sampled at about one week intervals from July 18 to September 18. One hundred passes of a 38 cm diameter sweep net were made in grass and another 100 sweeps in mesquite boughs. Each 100 sweeps constituted a sample. The insects in each sample were weighed (both fresh and after drying in an oven), sorted by species and counted. Samples were taken at 1000 hrs (MST) on still or relatively calm days.

RESULTS

Data for the Silverbell and Santa Rita Experimental Range Sites are presented in separate sections.

Silverbell site

Table 1 (DSCODES A3URJ12 and A3URJ14) distinguishes between residents, breeding visitors, non-breeding visitors, and irregular visitors (Table prepared for Validation report). Residents are present year-around and nest on the plot. Breeding visitors are present during the nesting season, but go elsewhere during the remainder of the year. Doves that nest on the plot forage in agricultural areas to the east and find little of their food on the plot (Russell et al., 1972). Non-breeding visitors are birds that occur in numbers on the plot but nest elsewhere. Irregular visitors occur as transients. The occurrence of bird species on the 20 ha plot based on frequency of observation is tabulated in the Validation report (DSCODE A3URJ13). Although this report does not include a description of the extent of movements within the plot, Table 3 (DSCODE A3URJ14) indicates the number of pairs of each species that had territories or nested on the 20 ha intensive study plot.

Reproductive activity began in February and young in some nests were not fledged until September (Table 2, DSCODE A3URJ14). A table presenting the date and the fate of each nest is available upon request from the authors. The number of pairs of each bird species on the 20 ha plot and the results of their nesting efforts appear in Table 3. The results of reproductive efforts in terms of biomass produced are found in Table 4 (DSCODE A3URJ14). Table 5 (DSCODE A3URJ14) indicates the plants in which nests were placed, the plant height, the nest height, type of nest constructed and the fate of the nest (a more detailed table is available from the authors). The overall nesting success is presented in Table 6 (DSCODE A3URJ14) and Table 7 itemizes the causes of nesting failures.

Other data collected but not reported here are discussed under Expectations.

Table 1. Number of individuals regularly occurring each month on the Silverbell plot A3URJ12, A3URJ14, (in part)

[illegible]

Table 2. Breeding phenology of birds on the Silberbell plot A3URJ14

Species	No. Nests	Ave. No. Eggs Per Nest	Date of First Egg	Ave. No. Fledglings Per Nest	Date of last Fledging	Percent nests Successful
Harris Hawk	1	0	-	0	-	00.0
Gambel Quail	2	?	17 Jun.	3.5	10 Jul.	100.0
White-winged Dove	4	1.5	16 May	0.5	14 Jul.	25.0
Mourning Dove	10	1.5	29 Feb.	0	-	00.0
Elf Owl	2	?	06 May	2.0	20 Jul.	100.0
Gilded Flicker	2	?	08 Apr.	2.5	07 Jun.	100.0
Gila Woodpecker	5	?	27 Mar.	2.0	04 Aug.	80.0
Wied Crested Flycatcher	2	?	06 Jun.	2.0	11 Jul.	50.0
Ash-throated Flycatcher	1	3.0	05 Jun.	0	-	00.0
Verdin	8	3.3	09 Mar.	1.9	20 Jul.	62.5
Cactus Wren	8	3.4	01 Mar.	0.6	13 Apr.	25.0
Curve-billed Thrasher	13	2.3	25 Feb.	0.8	26 Jul.	38.5
Black-tailed Gnatcatcher	14	1.0	13 Mar.	0.3	12 Apr.	07.1
Scott Oriole	1	0	-	0	-	00.0
Brown-headed Cowbird	9	1.3	09 May	0	-	00.0
Pyrrhuloxia	4	3.0	25 Mar.	1.3	04 Sep.	75.0
House Finch	2	2.5	04 Mar.	0	-	00.0
Brown Towhee	4	1.3	04 Mar.	0.2	16 Aug.	20.0
Rufous-winged Sparrow	2	1.0	26 Jun.	1.0	15 Aug.	50.0
Black-throated Sparrow	7	1.7	27 Apr.	1.3	26 Aug.	42.9
Overall		2.1	25 Feb.	0.9	04 Sep.	33.3

Table 3. Breeding species diversity on the Silverbell plot A3URJ14 (in part)

Species	Number of Pairs on 50 Acre Plot With:				Fledglings
	Territories	Nests	Eggs	Nestlings	
Harris Hawk	1	1	0	0	1
Gambel Quail	5	2	2	2	3
White-winged Dove	4	3	3	2	1
Mourning Dove	4	4	4	2	0
Elf Owl	2	2	2	2	2
Gilded Flicker	3	2	2	2	2
Gila Woodpecker	2	2	2	2	2
Ladder-backed Woodpecker	2	2	2	2	1
Wied Crested Flycatcher	2	2	2	1	1
Ash-throated Flycatcher	3	1	1	0	1
Purple Martin	1	0	0	0	1
Verdin	5	4	4	3	3
Cactus Wren	8	7	7	6	2
Curve-billed Thrasher	6	5	5	5	4
Black-tailed Gnatcatcher	6	5	4	1	5
Scott Oriole	2	1	0	0	1
Brown-headed Cowbird	4F - 3M	-	+	0	0
Pyrrhuloxia	2	2	2	2	2
House Finch	2	2	2	1	0
Brown Towhee	3	2	2	2	1
Rufous-winged Sparrow	2	1	1	1	2
Black-throated Sparrow	12	5	3	2	4

Table 4. Productivity of birds on the Silverbell plot A3URJ14

Species	Biomass (in grams) of:				Gross Biomass Produced	Net Biomass Produced
	Breeding Adults	Eggs*	Nestlings*	Fledglings		
Harris Hawk ¹	1563	0	0	0	0	0
Gambel Quail	678	?	0	1187	1187	1187
White-winged Dove	875	27	0	292	319	292
Mourning Dove	1050	76	45	0	121	0
Elf Owl	80	?	?	80	80	80
Gilded Flicker	416	?	?	520	520	520
Gila Woodpecker	280	?	?	700	700	700
Wied Crested Flycatcher	184	?	?	184	184	184
Ash-throated Flycatcher	56	10	0	0	10	0
Verdin	59	8	22	111	141	111
Cactus Wren	536	40	188	192	420	192
Curve-billed Thrasher	820	47	545	902	1494	902
Black-tailed Gnatcatcher ²	55	8	0	22	30	22
Scott Oriole ³	77	0	0	0	0	0
Brown-headed Cowbird	233	23	0	0	23	0
Pyrrhuloxia	142	19	31	178	228	178
House Finch	76	4	50	0	54	0
Brown Towhee	180	9	64	45	118	45
Rufous-winged Sparrow	31	0	0	31	31	31
Black-throated Sparrow	131	6	0	118	124	118
Total	7522	277	945	4562	5784	4562
Off plot nesting of pairs labeled 1, 2, 3.	-	2	?	1617	1619	1617

*Only eggs not hatched, and nestlings not fledged are included in these columns.

Table 5. Nest placement and success of birds on the Silverbell plot A3URJ14

Species	Nests	Plant Species	Ave. Plant Height (cm)	Ave. Nest Height (cm)	No. Nests Fledging Young
Harris Hawk	1	<i>Carnegiea gigantea</i>	762	610	0
Gambel Quail	2	Ground	0	0	2
White-winged Dove	1	<i>Cercidium microphyllum</i>	762	236	0
White-winged Dove	2	<i>Carnegiea gigantea</i>	808	447	0
White-winged Dove	1	<i>Opuntia fulgida</i>	290	203	1
Mourning Dove	3	<i>Cercidium microphyllum</i>	396	158	0
Mourning Dove	1	<i>Cercidium floridum</i>	762	305	0
Mourning Dove	1	<i>Olneya tesota</i>	1067	427	0
Mourning Dove	3	<i>Carnegiea gigantea</i>	864	323	0
Mourning Dove	2	<i>Opuntia fulgida</i>	236	102	0
Elf Owl	2	<i>Carnegiea gigantea</i>	1067	762	2
Gilded Flicker	2	<i>Carnegiea gigantea</i>	899	853	2
Gila Woodpecker	5	<i>Carnegiea gigantea</i>	1201	871	4
Wied Creseted Flycatcher	2	<i>Carnegiea gigantea</i>	1219	1067	1
Ash-throated Flycatcher	1	Dead tree	457	91	0
Verdin	5	<i>Cercidium microphyllum</i>	493	193	3
Verdin	1	<i>Cercidium floridum</i>	244	114	0
Verdin	1	<i>Opuntia fulgida</i>	168	94	1
Verdin	1	<i>Opuntia versicolor</i>	147	114	1
Cactus Wren	2	<i>Carnegiea gigantea</i>	762	300	1
Cactus Wren	6	<i>Opuntia fulgida</i>	201	165	1
Curve-billed Thrasher	13	<i>Opuntia fulgida</i>	244	188	5
Black-tailed Gnatcatcher	4	<i>Cercidium microphyllum</i>	495	175	0
Black-tailed Gnatcatcher	1	<i>Cercidium floridum</i>	305	155	1
Black-tailed Gnatcatcher	9	<i>Phoradendron californicum</i>	546*	411	0
Scott Oriole	1	<i>Phoradendron californicum</i>	1067*	488	0
Pyrrhuloxia	1	<i>Cercidium microphyllum</i>	701	216	0
Pyrrhuloxia	2	<i>Cercidium floridum</i>	503	262	2
Pyrrhuloxia	1	<i>Phoradendron californicum</i>	610*	241	1
House Finch	1	Dead saguaro	366	236	0
House Finch	1	<i>Opuntia fulgida</i>	274	208	0
Brown Towhee	3	<i>Cercidium microphyllum</i>	538	155	1
Brown Towhee	1	<i>Olneya tesota</i>	686	191	0
Rufous-winged Sparrow	1	<i>Cercidium microphyllum</i>	406	150	1
Rufous-winged Sparrow	1	<i>Acacia gregii</i>	183	94	0
Black-throated Sparrow	1	<i>Cercidium microphyllum</i>	274	112	0
Black-throated Sparrow	1	<i>Olneya tesota</i>	762	251	0
Black-throated Sparrow	2	<i>Acacia gregii</i>	249	119	2
Black-throated Sparrow	1	<i>Opuntia versicolor</i>	142	48	1
Black-throated Sparrow	1	<i>Phoradendron californicum</i>	396*	251	0

*Height of host tree

Table 6. Nesting success of birds on the Silverbell plot A3URJ14

	Number	%Producing Eggs	%Producing Nestlings	%Producing Fledglings
Nests Built	93	79.6	51.6	33.3
Nests with Eggs	74	----	64.9	41.9
Nests with Nestlings	48	----	----	64.6
Eggs Laid	161	----	49.7	31.7
Eggs Hatched	80	----	----	63.8
Fledglings	51	----	----	----

Table 7. Causes of nesting failure of birds on the Silverbell plot

	Predation	Weather	Cowbird Parasitism	Interference by Other Species	Human Interference	Infertile Eggs	Unknown
Number	22	6	13	2	7	1	9
Percent	36.7	10.0	21.7	3.3	11.7	1.7	15.0

Santa Rita Experimental Range Site

Intensive studies began on the Santa Rita site in mid-June. All nests found on the 20 ha intensive study site are summarized in Table 8 (DSCODE A3URJ15; a more detailed table may be obtained from the authors). Although the plot was not systematically searched for nests before mid-June, nine nests containing eggs were located on April 10 (Table 9). Breeding success is summarized in Tables 10 and 11 (DSCODE A3URJ15). Both the Gilded Flicker and Gila Woodpecker successfully fledged young from their nests in the single large Saguaro on the plot, but the number of eggs laid, nestlings and fledglings are estimated. Four pairs of Rufous-winged Sparrows were found, each with two fledglings. The number of eggs and fledglings in these cases are guesses. Scaled Quail young were found on the plot; it is possible that their nest was not located on the 20 ha plot. In Table 11, the 198 eggs accounted for in the upper part of the Table is matched by only 189 in the lower portion. Nine eggs in 3 nests, plus the Woodpecker and Flicker nests were started in May. In these tables nest success is based upon the number of nests that contained at least one egg. Some nests were started and abandoned before an egg was laid. Table 12 (DSCODE A3URJ15) summarizes the location of nest sites. Insects sampled with a sweep net are noted in TABLE 13 (no DSCODE). Tables submitted as a part of the Validation report on birds on Santa Rita indicate the seasonal distribution of all species recorded on the plot, their density, and biomass.

An analysis of crop and gizzard contents of 80 sparrows is presented in Tables 14, 15 and 16 (no DSCODE).

Table 8. Distribution of nesting dates in 1972 on the 20 ha Santa Rita plot from 15 June to end of breeding season

Species	No. of Nests	Total No. Eggs	Date of First Egg	Date of First Egg in Last Nest	Total No. Nestlings	Total No. Fledglings	No. of Cowbird Eggs *
Scaled Quail	1	10	1 June	---	1	---	
Mourning Dove	7	13	7 June	15 August	6	6	
Lesser Nighthawk	1	2	4 June	---	2	2	
Gilded Flicker	1	?	15 May+	---	?	2+	
Gila Woodpecker	1	?	10 May†	---	?	2†	
Verdin	2	6	8 June	13 June	6	3	
Cactus Wren	5	15	31 May	12 June	9	6	
Curve-billed Thrasher	5	15	23 May	22 June	10	8	
Black-tailed Gnatc.	1	?	20 July	---	?	0	1
Blue Grosbeak	1	1	26 August	---	0	0	
Brown Towhee	4	12	10 June	27 July	3	3	
Rufous-wg. Sparrow	44	116	11 June	20 August	54	42	6
Black-thr. Sparrow	1	1	26 July	---	0	0	

*The only cowbird egg to hatch was in a gnatcatcher nest (and it was swallowed as a nestling by a *Masticophis*).

Table 9. Bird nests found April 10, 1972, on the Santa Rita Experimental Range (20 ha) plot

Species	No. of Eggs
Roadrunner	4
Cactus Wren	3
Cactus Wren	3
Cactus Wren	4
Cactus Wren	3
Cactus Wren	3
Curve-billed Thrasher	2
Curve-billed Thrasher	2
Curve-billed Thrasher	2

Note: all nests contained eggs but the fate of these nests is unknown.

Table 10. Reproductive success and biomass produced by birds found nesting on the 20 ha study plot in the Santa Rita Experimental Range after June 15, 1972

Species	No. Pairs	No. Eggs†	No. of Nestlings†	No. of Fledglings†	Biomass (in grams) of:		
					Eggs*	Nestlings*	Fledglings
Quail, Scaled	1	(10)	(10)	7	0	100	1200
Dove, Mourning	7	13	6	6	28	0	450
Nighthawk, Lesser	1	2	2	2	0	0	60
Flicker, Gilded	1	(2)	(2)	(2)	-	-	200
Woodpecker, Gila	1	(2)	(2)	(2)	-	-	130
Verdin	2.5	6	6	3	0	16	21
Wren, Cactus	8.5	15	9	6	22	75	180
Thrasher, C.-bld.	7.5	15	10	8	30	104	448
Cowbird, B.-hd.	-	7	1	0	21	20	0
Grosbeak, Blue	1	1	0	0	3	0	0
Towhee, Brown	4	12	3	3	39	0	96
Sparrow, Ruf.-wg.	20	116	55	42	110	117	504
Sparrow, Blk.-thr.	3.7	1	0	0	2	0	0
Total	58.2	202	106	81	255	432	3289

*Only eggs not hatching and nestlings not fledging are included in these columns.

†Figures in parentheses are estimates.

Table 11. Breeding success of birds on the 20 ha study plot in the Santa Rita Experimental Range after June 15, 1972 (in percent)

Species	Eggs Hatch	Eggs Fledge	Hatched Fledged	Nests Successful	No. Eggs	No. Nests
Quail, Scaled	100	70	100	100	(10)	1
Dove, Mourning	46	46	100	43	13	7
Nighthawk, Lesser	100	100	100	100	2	1
Flicker, Gilded	-	-	-	100	--	1
Woodpecker, Gila	-	-	-	100	--	1
Verdin	100	50	50	50	6	2
Wren, Cactus	60	40	67	40	15	5
Thrasher, Curve-billed	67	54	80	60	15	5
Cowbird, Br.-hd.	14	0	0	0	7	-
Gnatcatcher, Blk.-tl.	0	0	0	0	0	1
Grosbeak, Blue	0	0	0	0	1	1
Towhee, Brown	25	25	100	25	12	4
Sparrow, Ruf.-wg.	48	36	76	36	116	44
Sparrow, Blk.-thr.	0	0	0	0	1	1
Total	52	39	76	41	198	74
June	55	30	54	26	64	23
July	41	30	73	30	73	27
August	54	52	97	58	52	19

Table 12. Nest site selection in birds breeding on the Santa Rita Experimental Range

Species	No. of Nests	Plant Species	\bar{x} Plant Height (cm)	\bar{x} Nest Height (cm)	% Nests Successful
White-winged Dove	1	<i>Opuntia fulgida</i>	167	121	0
Mourning Dove	7	<i>Prosopis</i>	348	216	29
Roadrunner	1	<i>Celtis</i>	305	124	?
Gilded Flicker	1	<i>Cereus giganteus</i>	610	535	100
Gila Woodpecker	1	<i>Cereus giganteus</i>	610	458	100
Verdin	3	<i>Cercidium</i>	438	167	100
Verdin	1	<i>Celtis</i>	229	159	0
Cactus Wren	9	<i>Opuntia fulgida</i>	206	172	?
Curve-billed Thrasher	8	<i>Opuntia fulgida</i>	180	129	?
Curve-billed Thrasher	1	<i>Opuntia spinosior</i>	213	151	0
Blue Grosbeak	1	<i>Prosopis</i>	432	335	0
Brown Towhee	1	<i>Cercidium</i>	380	264	0
Brown Towhee	2	<i>Prosopis</i>	420	262	0
Brown Towhee	3	<i>Celtis</i>	243	142	67
Rufous-winged Sparrow	25	<i>Celtis</i>	265	116	20
Rufous-winged Sparrow	15	<i>Cercidium</i>	343	173	13
Rufous-winged Sparrow	11	<i>Opuntia spinosior</i>	140	82	54
Rufous-winged Sparrow	3	<i>Opuntia fulgida</i>	180	147	67
Rufous-winged Sparrow	2	<i>Acacia greggi</i>	283	162	50
Rufous-winged Sparrow	1	<i>Lycium (?)</i>	167	114	100
Black-throated Sparrow	1	<i>Acacia greggi</i>	183	112	0

Table 13. Number, weight, and species diversity of insects captured in a 38cm diameter sweep net passed 100 times through grass (A) and mesquite (B) Santa Rita Experimental Range, 1972

	Sample Date†							
	18 July	25 July	1 Aug.	8 Aug.	17 Aug.	26 Aug.	6 Sept.	18 Sept.
A. Grass								
No. of species	15	46+	62	79+	125/2*	64	79	73
No. of individuals	22	121	188	484	319	331	294	257
Fresh weight (g)	0.39	1.81	3.24	3.80	3.83	2.82	4.68	2.07
Dry weight (g)	0.17	0.59	1.07	1.39	1.33	1.13	1.61	0.66
B. Mesquite								
No. of species	22	27	52	46	59	84	51	56
No. of individuals	50	64	103	103	247	526	233	136
Fresh weight (g)	1.09	1.32	1.00	3.99	1.34	2.11	1.10	0.80
Dry weight (g)	0.37	0.46	0.31	2.09	0.61	0.93	0.40	0.28

* The 125 represents insect species in 200 sweeps of the net.

† Samples were taken at 1000 hrs. (MST).

Table 14. Seed contents of sparrow crops from Santa Rita Experimental Range, winter 1971-72

Month	Number of Birds	Average Number of Seeds per Crop					
		<i>Aristida</i>	<i>Paspalum</i>	<i>Amaranthus</i>	<i>Panicum</i> sp.1	<i>Panicum</i> sp.2	<i>Setaria</i>
A. Brewer's Sparrow							
October	2	65.0	1.0	5.0	29.0	6.5	0.0
November	10	25.9	0.2	1.7	6.3	1.3	0.0
December	10	45.8	0.1	1.4	4.7	0.5	0.0
January	9	37.2	0.0	1.9	3.1	0.3	0.3
February	10	27.9	0.1	0.0	7.3	2.5	0.3
March	8	14.3	0.0	0.3	8.0	0.8	0.0
B. Rufous-winged Sparrow							
October	1	0.0	15.0	0.0	0.0	10.0	0.0
November	5	2.4	4.6	3.8	5.0	1.4	0.0
December	5	3.0	1.6	18.6	5.4	6.4	0.0
January	5	1.0	0.4	0.6	12.0	7.4	2.2
February	5	3.6	0.2	5.0	15.6	5.4	0.0
March	2	4.5	0.0	3.5	10.0	0.0	0.0
C. Black-throated Sparrow							
October	--	---	---	---	---	---	---
November	2	0.0	0.0	0.0	2.5	0.5	0.0
December	2	6.0	0.5	10.0	0.0	3.0	0.0
January	1	2.0	0.0	1.0	0.0	2.0	0.0
February	0	---	---	---	---	---	---
March	0	---	---	---	---	---	---

Table 15. Seed contents of sparrow crops from the Santa Rita Experimental Range, winter 1971-72

Month	Number of Birds	Average weight (g) of seeds per crop, as percent total weight seed per crop					Total seeds wt. (gm)
		<i>Aristida</i>	<i>Paspalum</i>	<i>Amaranthus</i>	<i>Panicum</i> sp.1	<i>Panicum</i> sp.2	
A. Brewer's Sparrow							
October	2	53.2	1.2	11.2	23.9	10.6	.0489
November	10	65.2	.62	11.9	15.7	6.2	.0159
December	10	82.4	.45	6.7	8.5	1.8	.0222
January	9	80.9	0.0	11.4	6.5	1.1	.0184
February	10	69.1	.6	0.0	17.9	12.3	.0162
March	8	58.1	0.0	3.1	32.6	6.1	.0098
B. Rufous-winged Sparrow							
October	1	0.0	52.9	0.0	0.0	47.0	.0170
November	5	10.7	30.1	45.1	2.1	11.7	.0093
December	5	4.1	3.4	70.9	7.6	17.6	.0290
January	5	3.3	1.6	5.8	40.0	49.1	.0120
February	5	7.4	.5	31.2	35.3	24.4	.0176
March	2	18.5	0.0	40.2	41.2	0.0	.0097
C. Black-throated Sparrow							
October	0	---	---	---	---	---	---
November	2	0.0	0.0	0.0	71.4	28.6	.0014
December	2	14.8	1.8	68.2	0.0	14.8	.0161
January	1	22.8	0.0	31.4	0.0	45.8	.0035
February	0	---	---	---	---	---	---
March	0	---	---	---	---	---	---

Table 16. Crop contents of sparrows* from Santa Rita Experimental Range, winter 1971-72, expressed as percent of specimens containing each food type

Bird Species	October-December						January-March						Total		
	SPI- BRE	AIM- CAR	AMP- BIL	PIP- FUS	AMM- SAV		SPI- BRE	AIM- CAR	AMP- BIL	MEL- MEL			SPI- BRE	AIM- CAR	AMP- BIL
No. of Specimens	22	11	4	1	1		27	12	1	1			49	23	5
<i>Aristida</i>	95	45	25	100	100		96	58	100	100			96	52	40
<i>Paspalum</i>	18	36	25	00	00		04	17	00	00			10	26	20
<i>Amaranthus</i>	18	45	25	00	00		15	50	100	100			16	48	40
<i>Panicum</i> sp.1	82	45	50	00	00		78	75	00	00			80	61	40
<i>Panicum</i> sp.2	45	73	50	100	100		26	58	100	100			35	65	60
<i>Setaria</i>	00	00	00	00	100		11	17	00	00			06	09	00
Insects	09	18	00	100	00		04	00	00	00			06	09	00

*Species Code

SPIBRE	=	Brewers Sparrow	PIPFUS	=	Brown Towhee
AIMCAR	=	Rufous-winged Sparrow	AMMSAV	=	Grasshopper Sparrow
AMPBIL	=	Black-throated Sparrow	MELMEL	=	Song Sparrow

DISCUSSION

One of the basic objectives involves relating events in the birds' annual cycle to variables in the environment. Critical information on temperature and precipitation is not yet available. Studies emphasize the Silverbell site.

The period of mid-December, 1971, to late May, 1972, was characterized by drought. Birds on both the Silverbell and Santa Rita sites appear to have not been adversely affected by the dryness. Perhaps the heavier-than-usual rains in the fall of 1971 moderated the drought effects.

Silverbell site

Species composition and occurrence: To date, 87 species have been recorded on or immediately adjacent to the 20 ha study plot. Twelve of these species are permanent residents within the area (Table 1), 10 are regular breeding visitors, 11 are regular non-breeding visitors, and the remainder are either transitory migrants or only occasional visitors.

Timing and sequence of breeding events: The 1972 breeding season began in early February and the last young fledged in early September (Table 2). There were three peak periods of activity. The first occurred in early March and involved the major resident species plus one breeding visitor. The second, and largest, peak was in early June and resulted from the arrival of breeding visitors and second nestings by resident species. A small third peak in late July and early August was primarily due to late activity of Black-throated Sparrows and Rufous-winged Sparrows.

Breeding diversity: Twenty-two species nested, or attempted to nest, within the 20 ha plot in 1972. Seventy-eight pairs (plus four female Brown-headed Cowbirds) held territories, 53 pairs built nests, and 48 pairs laid eggs within this plot (Table 3).

Breeding biomass and productivity: A breeding biomass of 7.5 kg/20 ha produced a gross biomass of 5.8 kg/20 ha and a net biomass of 4.6 kg/20 ha within the 20 ha study plot in 1972. A few pairs had second nestings off the plot and these produced an additional net biomass of 1.6 kg/20 ha (Table 4).

Nest placement: Sixty-five percent of all nests built were distributed rather evenly between *Opuntia fulgida* (23%), *Cercidium microphyllum* (21%), and *Carnegiea gigantea* (20%). Nests placed in *C. gigantea* were the most successful (55% fledging young). The vegetation in which nests were placed averaged 205 inches in height while nest sites averaged 119 inches above the ground (Table 5).

2.3.2.10.-18

Nesting success: Thirty-three percent of all nests built produced fledged young, while 42% of all nests in which eggs were laid produced fledged young. The major cause of nest failure was predation, mainly by snakes (Tables 6 and 7).

Santa Rita site

Timing and sequence of breeding events: Light rains in late May and early June stimulated nesting attempts by Rufous-winged Sparrow (the most abundant resident species). Not one of ten nests started in June fledged any young (Table 8). Another flurry of nesting activity began about 10 July (after more substantial rains had fallen and some were successful. All passerine birds nesting on the plot feed insects to their young. In August nests, 97% of all eggs hatching resulted in fledged young (Table 11). Our insect sampling indicated a peak about August 8 and an abundance of insects persisting to September 6 -- during the period of maximum nestling and fledgling demand (Table 13). However, Cactus Wrens and Curve-billed Thrashers are not active nesting birds at this time; they normally nest before the summer rains start.

Breeding diversity: Thirteen species nested on the plot in the summer of 1972 (Table 10); this includes all species usually nesting in the area but includes only one of the five "nomadic" species that nested in the plot after the heavy rains of 1970. A Lesser Nighthawk successfully nested on the plot in 1972 -- the first time this insectivorous species has nested there. A pair of Scaled Quail with seven half-grown young appeared on the plot in July. The nest had not been found and it may have nested off the plot but its presence emphasizes the difficulty involved in studying such secretive but common birds. In all, 58 pairs of birds held territories or nests on the 20 ha plot in summer.

Nest placement: Breeding birds generally selected rather spinescent shrubs of the most common species for their nests (Table 12). The preference of *Opuntia fulgida* for nest sites by Curve-billed Thrashers and Cactus Wrens is well known. *Celtis* is so favored by Rufous-winged Sparrows that they rarely occur where this plant is absent. Thus it is of interest that more nests placed in *Opuntia spinosior* were successful than in *Celtis*. The lack of sites for hole-nesting species undoubtedly prevents a number of species from occurring there (the Silverbell site is rich in hole-nesting species and has greater species diversity and biomass).

Nesting success: Forty-one percent of the nests containing eggs were successful (i.e., fledged at least one young bird). This figure is very close to the 42% on the Silverbell site and to success in previous years on the Santa Rita site.

Wintering sparrow flocks: In the period of late October, 1971, to March, 1972, individuals of several species of Fringillidae were collected on the Santa Rita Experimental Range in order to determine the foods they were consuming. A total of 80 birds was dissected and the contents of each crop, proventriculus and gizzard were removed (Tables 14-16). The genera *Aristida* (1-4 mm diameter), *Paspalum* (3 x 2 x 2 mm), *Amaranthus* (0.5 x 0.5 mm), *Setaria*, *Panicum* sp. 1 (1 x 1 x 1 mm), and *Panicum* sp. 2 (2 x 1 x 1 mm), were the samples identified.

Most of the birds examined were Brewer's Sparrows (49), Rufous-winged Sparrows (23), and Black-throated Sparrows (5). These were the most frequently encountered species in the winter of 1971-72. Brewer's Sparrows consumed almost solely seeds of *Aristida* and *Panicum*. Rufous-winged Sparrows appear to be less selective and regularly take seeds of all species except *Setaria*; the intake of *Paspalum* decreases as the winter progresses and the number of *Panicum* sp. 1 seeds increases later in the winter. Black-throated Sparrows consume seeds of several species; there may be some preference for *Panicum* sp. 2.

EXPECTATIONS

Project funding terminated 31 December, 1972. However, a considerable portion of the data collected must still be analyzed. Much of this data is presently on coding forms or in the data bank; assurances of continued support through IBP Central Office facilities and Data Processing will permit continued work on several phases of the project.

The following studies are expected to be reported on in supplementary Research Memoranda.

1. An evaluation of the reproductive characteristics of the 1971 and 1972 breeding seasons in terms of environmental variables.
2. Growth rates, weights of study site birds (DSCODE A3URJ04).
3. Foraging niches of insectivorous study site birds (DSCODE A3URJ03).
4. Bird populations and reproductive success on a creosote-bush association.
5. The effect of widely dispersed rains in summer on the distribution of breeding bird species (DSCODES A3URJ08, 09, 10, 11).
6. Time-energy budgets of Cactus Wrens and Curve-billed Thrashers (DSCODES A3URJ06, 07).
7. An analysis of habitat characteristics involved in territory selection.

2.3.2.10.-20

ACKNOWLEDGEMENTS

Special thanks is extended to George T. Austin who contributed immensely to the project in its earlier phases and who has continued to provide thought provoking-input.

LITERATURE CITED

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1972 PROGRESS REPORT

POPULATION STUDIES OF THE DESERT COTTONTAIL (*Sylvilagus auduboni*)
AND BLACK-TAILED JACKRABBIT (*Lepus californicus*) IN THE SONORAN DESERT

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Research Memorandum, RM 73-20

MAY 1973

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Report Volume 3

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A B S T R A C T

Monthly censuses of *Lepus alleni*, *L. californicus* and *Sylvilagus auduboni* were conducted on the Silverbell bajada. Collections were made on the Silverbell bajada and the adjacent portions of the Avra Valley with a monthly goal of ten females of each species from January through April to complete our first collection year. From June through December this rate was reduced to five females of each species each month. A total of 329 rabbits was collected and fertility rate, sex ratio and adult weights were found to be similar to the 1971 collection. Breeding was found to occur at any month of the year, extending by three and four months the known breeding season for these Sonoran Desert species as reported by earlier investigators. Two peaks of breeding occur, one in February and a second in July and August. Reproductive success was related to the frequency of occurrence of grass and forb plants, which were measured on the study area monthly (except in February and May) on both disturbed and natural sites. Plant abundance was directly related to seasonal rainfall, and the number of species preferred by cotton tails and jackrabbits was found to be greater on the disturbed sites.

Radio-location transmitters were attached to two *Sylvilagus auduboni* and to two *Lepus californicus*. Triangulation and observations showed a tentative home range of 0.96 and 0.58 ha for the two cottontails. Only limited data on the black-tailed jackrabbits were gathered but movements of 329 m were noted. Telemetry yielded but a minor amount of information considering the time, equipment, vehicles and manpower involved.

INTRODUCTION

The lagomorphs are among the larger Sonoran Desert consumers, especially *Lepus alleni* and *Lepus californicus*, and their relative mobility in comparison with desert rodents can increase their influence on habitats. The two native jackrabbits and the cottontail, *Sylvilagus auduboni*, all have variable breeding and survival rates in response to climatic and other factors. Determination of the processes involved in terms of computable functions started with reproductive, mortality and dispersal rates in 1971 and continued into 1972.

The research in 1972 continued the collection of data on breeding, sex and age structure of the populations and population trends in numbers, but a smaller sample of animals was collected each month. Additional research effort yielded data on plant food abundance in response to seasonal rainfall. Reproduction and survival was therefore relative to precipitation time and amount. The daily movement and habitat selection of individual animals was investigated by tagging and by radio-location telemetry.

OBJECTIVES

1. To determine the age and sex structure, and the increment and loss rates for certain populations which control their density in the Sonoran Desert.
2. To determine the rate of reproduction, and the effects upon it of side variables such as weather, plant phenology, quantity of vegetation, and modifications to vegetation.
3. To measure the rate of dispersal and mobility.
4. To determine the overall rate of mortality, and its seasonal variations.
5. To construct a life table from the sum of information.

The bulk of our efforts in 1972 have been directed toward fulfilling objectives number two, three, and portions of number one. The mortality rate and life table work has been postponed until definitive age classes can be established.

METHODS

A monthly census was conducted along a 7.8 km route with the observer recording species and flushing distance at each encounter. The King strip method was used to compute estimated population size as the modified method reported by Hayne (1949) proved unreliable with the low densities found in this area. DSCODE A3UHP01.

Collections of the three lagomorphs on the Silverbell bajada (*Lepus alleni*, *Lepus californicus* and *Sylvilagus auduboni*) were made twice a month. From January through April an effort was made to collect ten females of each species. In June this rate was reduced to five females of each species each month.

The rabbits were refrigerated and within 24 hrs after collection the eyes, one half of the mandible, one humerus and the reproductive organs were removed, tagged and stored. Standard weight and measurements were recorded along with incidence of parasites, testes position, nipple pigmentation, lactation and number of visible implanted fetuses. DSCODE A3UHP02.

The eyes were stored in 10% formalin for at least 30 days, after which the lenses were removed and dried in a vacuum oven at 80 C for four days. After drying, the lenses were weighed to the nearest 0.1 mg. DSCODE A3UHP02.

The reproductive organs were stored in 10% formalin and analyzed within two weeks of collection. The testes were stripped of associated structures and weighed to the nearest 0.1 g. The female reproductive organs were macroscopically analyzed for the following: number and size of visible implantation sites, number and size of corpora lutea and corpora albicantia in each ovary, striations of the uterine horns, position, length, weight and age of each embryo. Embryos over 40mm in length were sexed. DSCODE A3UHP02.

The humeri were checked for the condition of the epiphyseal cartilage. The mandibles were stored in 10% formalin for future analysis by thin sectioning. DSCODE A3UHP02.

References for the above analyses are: eye lens weights, Lord (1959); epiphyseal cartilage, Hale (1949); reproductive organs, Bookhout (1964) and Rongstad (1969).

Live specimens of all three species were captured using a modification of the technique reported by Griffith and Evans (1970). High intensity quartz-iodine automotive driving lights were used for illumination. One light was manipulated by a man in the back of each of two pick-up trucks. The trucks also carried one or two other men in the back to act as netters. The netters rode in the bed of the truck and not on outrider structures (Griffith and Evans, 1970) because the vehicles were not permanently assigned to the project and could not be modified. The minimum crew was six men: two drivers, two light men and two netters. The maximum crew was eight, the additional men acting as netters. The two vehicles traveled the roads of the capture area side by side and upon encountering a rabbit attempted to surround the animal. The resulting noise, light and confusion unsettled the rabbits sufficiently to allow capture in about fifty % of the attempts. The success ratio was held down by the

2.3.2.3.-4

roughness of the terrain and the denseness of the vegetation in the area. It was found that a higher percentage of capture was afforded by using two vehicles instead of one.

Radio transmitters in the 148 MHz range were affixed to the cottontail rabbits by means of a buckskin harness and to the jackrabbits with a collar of flat braided nylon. Radio locations of the rabbits were obtained by triangulating from semi-permanent sites 160-320 meters apart. A short three meter mast on a tripod base was used to support a three element yagi antenna. Holes in the tripod feet were placed over steel rods at each triangulation site to assure the proper orientation of the tripod and mast. Two fixes per location of the rabbit were used as only one receiver was available and the time lag in moving from one triangulation site to the next negated the usefulness of a third or fourth fix.

Two 1.6 km plant transects were established on the study area, one on a disturbed and one on an undisturbed site. These transects were run at least monthly, except February and May when no records were made. A flexible, circular drop frame covering one m² was used to take a sample every twenty meters along each transect. The resulting data were used to calculate frequency of occurrence values.

RESULTS

Aging

The lack of known age animals has prevented the construction of a lens weight curve for the rabbits of this study. The closure of the epiphyseal cartilage is an accurate indicator of age as can be seen by comparison with other indicators such as the reproductive status and the eye lens weight of the individual. Figure 1 shows the correlation between epiphyseal closure and eye lens weight.

Lagomorph teeth do not show annual layering as in higher animals. However, the mandibles often have an interruption in the layers of the periosteum around the tooth root (Klevezal and Kleinenberg, 1967). Thin sectioning of the mandible to show these layers was tested on four jaws from the collection. While adhesion layers were identified, we found no correlation with the lens weights or closure of the epiphysis of those individuals. Sectioning of a larger sample of mandibles will be carried out to determine conclusively the worth of the technique to this study.

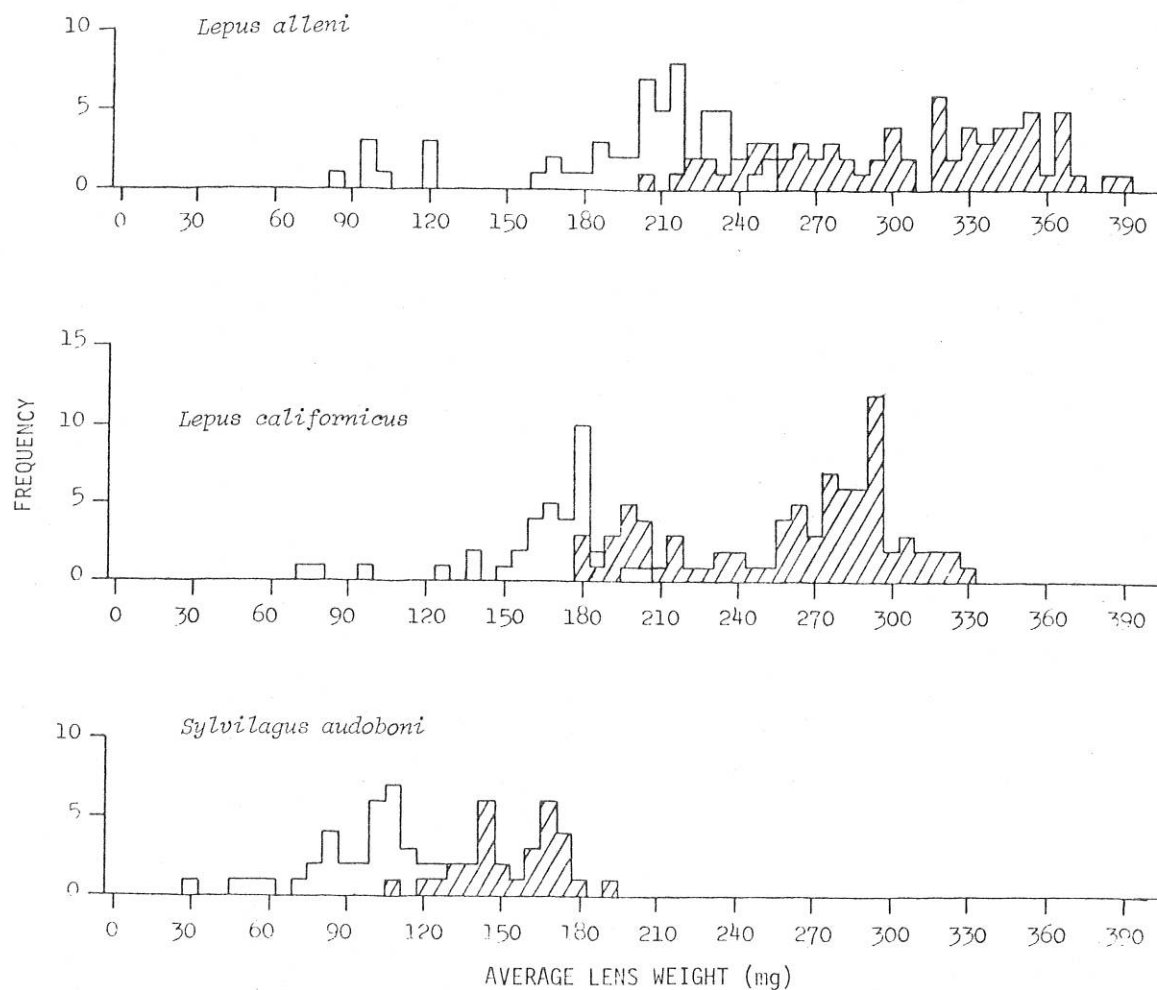


Figure 1. Distribution of average eye lens weights in the 1972 Silverbell collection. Crosshatching indicates lens weights from adult rabbits as determined by closure of the epiphyseal cartilage (Hale, 1949). DSCODE A3UHP02

Site variables

Rainfall data were gathered from six locations in and around the census area. Although a fair amount of variation existed in the quantity of rain gathered in each gauge, the average yearly precipitation for the study site was close to that for the two nearest recording stations in the valley (Table 1).

2.3.2.3.-6

Table 1. 1972 monthly precipitation (inches, ave six gauges) at the census plot for this study compared to the records from the towns of Silverbell, 5.0 mi. west; Cortaro, 20.0 mi. east; and the IBP Avra Valley study plot, 4.5 mi. northwest (DSCODE A3UHP02)

Month	Silverbell	Cortaro	IBP	Census
J	0.00	0.00	0.00	0.00
F	0.00	0.00	0.00	0.00
M	0.00	0.00	0.00	0.00
A	0.00	0.00	0.00	0.00
M	0.36	0.17	0.13	0.08
J	2.14	0.83	1.49	3.00
J	1.09	1.00	2.22	1.75
A	1.75	2.17	2.44	2.50
S	1.35	0.50	1.53	1.28
O	5.60	4.50	4.48	4.58
N	2.96	2.39	1.97	2.22

The spring of 1972, January to May, was the driest on record for the past fifteen years. However, the heavier than normal winter rains have put the total for this year about three inches above the long-term average for the valley, with the month of December yet to be included.

The two plant transects were run thirteen times each during 1972. Below are the number of species encountered on each and their general classification.

	Natural	Disturbed
Cactus	6	4
Grass	10	12
Forbs	15	26
Shrubs	9	11
Trees	3	4

As can be seen, the disturbed area supports a larger and more diverse plant community than the natural area. Some of the plants found on the perturbed area are strictly disturbed-site species and not found elsewhere on the study plot. Other plants found on the disturbed site are also encountered in the natural areas but at such low frequencies as to not show up in the transect results.

Table 2 shows the monthly frequencies of occurrence for the grasses, forbs and shrubs. The values for the cacti and trees remain virtually constant. The values for bare ground are included to give an indication of the amount of ground cover.

Table 2. Monthly frequencies of occurrence of the major plant groups found on the natural and disturbed areas of the Avra Valley study plot

	J*	M	A*	J	J	A	S	O	N
NATURAL									
GRASSES	13.7	2.2	2.0	8.5	11.2	13.6	11.8	14.5	9.4
FORBS	20.4	1.3	1.2	1.6	2.8	1.6	1.6	15.2	27.0
SHRUBS	15.9	23.7	13.4	20.2	16.3	16.4	18.0	20.8	23.8
BARE GROUND	--	20.5	33.0	26.0	22.5	20.6	21.9	3.8	0.0
DISTURBED									
GRASSES	65.6	7.0	9.8	5.4	7.9	14.4	15.6	19.8	15.6
FORBS	16.9	4.0	2.0	3.4	3.8	4.6	5.2	18.9	25.9
SHRUBS	15.1	13.1	12.4	9.2	6.6	11.8	11.8	8.9	11.8
BARE GROUND	--	--	37.6	33.0	31.3	25.2	18.2	10.0	3.8

* No data were gathered in February or May

Census

Figure 2 shows the results of the monthly censuses for 1971 and 1972. The large variation month to month arises in part from the technique used to census the populations. The results can be significantly affected by the alertness and experience of the observer at spotting the rabbits. However, even when the observer is attentive and accustomed to the procedure, a great deal of variation can result.

We have some reservations as to the accuracy of this method for estimating the monthly population sizes. However, the estimated population for October, 1971, was within one rabbit of the total actually seen during a drive census through the same area. Unfortunately, a similar drive could not be arranged for 1972 but one is planned in the spring of 1973.

Despite large monthly variations, the annual mean population estimates for the two years are very close. The average estimated population size for 1972 was 2.2 rabbits/40 ha and for 1971 was 2.6/40 ha. The student's t test shows no significant difference between these estimates ($t = 0.46$, $P > .60$).

2.3.2.3.-8

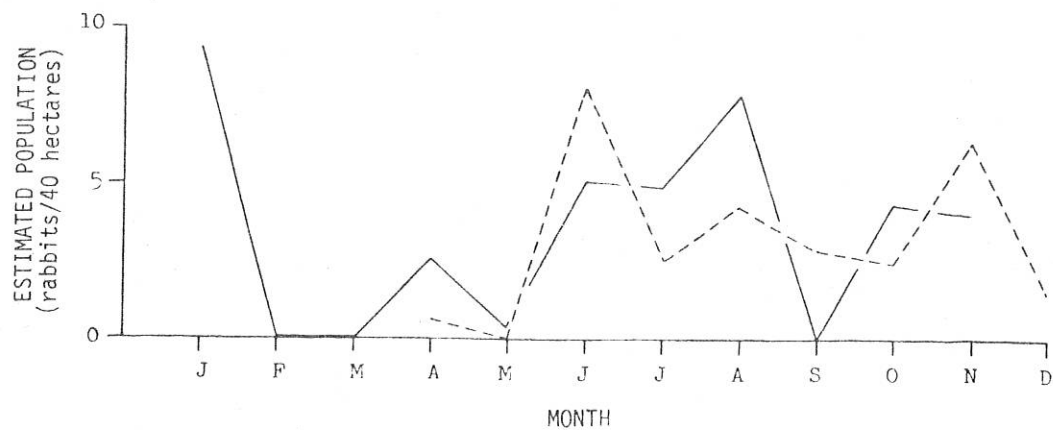


Figure 2. Estimated rabbit population (*L. californicus* and *S. auduboni*) on the Silverbell bajada for 1971 (broken lines) and 1972 (solid lines).
DSCODE A3UHP01

Reproduction

Table 3 shows the monthly breakdown by species of the 329 rabbits collected in the Avra Valley in 1972. The sex ratios of the samples taken did not differ significantly from the expected of 50:50 ($P < .005$).

Table 3. Monthly collections of rabbits from the Avra Valley (DSCODE A3UHP01)

	<i>S. auduboni</i>			<i>L. californicus</i>			<i>L. alleni</i>		
	Total	Male	Female	Total	Male	Female	Total	Male	Female
Jan	5	5	0	21	12	9	15	5	10
Feb	3	1	2	24	14	10	22	12	10
Mar	10	8	2	23	11	12	17	7	10
Apr	11	5	6	14	4	10	21	12	9
May									
Jun	9	4	5	6	1	5	11	6	5
Jul	11	6	5	6	1	5	6	1	5
Aug	9	4	5	9	4	5	7	2	5
Sep	6	1	5	5	0	5	13	8	5
Oct	9	3	5	7	2	5	6	1	5
Nov	6	1	5	9	4	5	9	4	5
	78	38	40	124	53	71	127	58	69

The general fertility rates (Lord, 1961) for 1971 and 1972 are shown in Figure 3. The general fertility rate is the product of the mean litter size (number of viable fetuses) and the percentage of pregnancy.

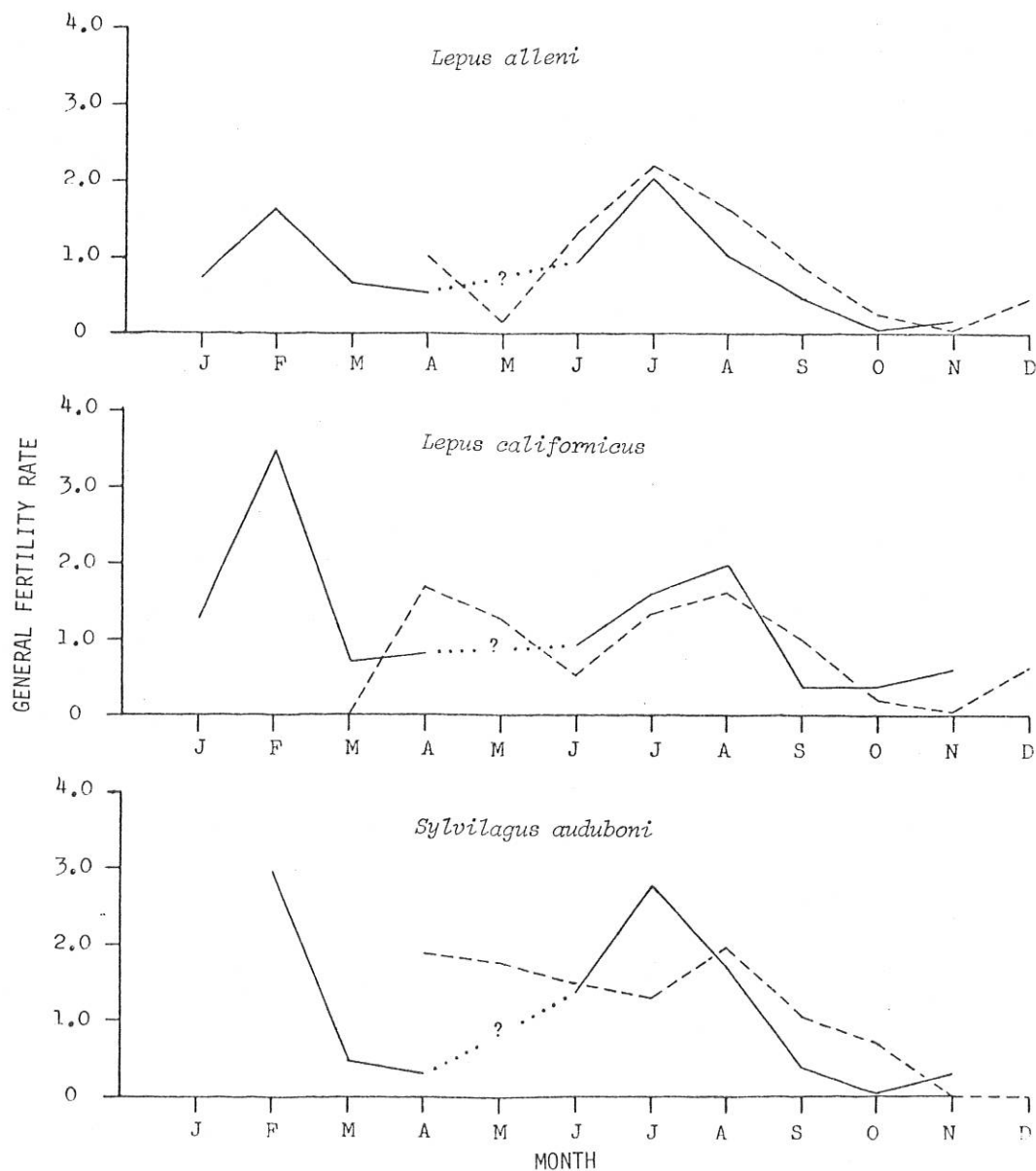


Figure 3. General fertility rates (Lord, 1961) for the Silverbell bajada collections of 1971 (broken lines) and 1972 (solid lines). No collections made in May 1972.

2.3.2.3.-10

The female cottontail was captured and instrumented at the same wash crossing but on the east side of the gas-line road. This rabbit was instrumented on September 9, 1972. However, no triangulation was attempted as the transmitter pulse rate began to increase almost immediately, indicating a battery failure. The week of September 9 to 16 was spent in an effort to recover the transmitter package. Unfortunately, the radio ceased to function before we could recapture the rabbit and, without the aid of the radio-tracking, we were unable to locate her.

The two female black-tailed jackrabbits were instrumented on October 9 and 13. By October 13, the transmitter fitted to the rabbit on October 9 had ceased to operate. The radio put on the second rabbit on October 13 was no longer working by October 20. Since the radio stopped functioning, this second rabbit has been observed twice within 320 m of the original capture site. Neither time were we able to get close enough to attempt to shoot her without risking damage to the radio package.

Forty-five man hours were spent in trying to recover the faulty radio on the *L. californicus*. Nine of these man hours were donated by volunteer helpers.

Figure 4 gives the percentage of juveniles in the monthly collections for both 1971 and 1972. No rabbits were collected in May of 1972.

Dispersal and mobility

In 1972, fifteen *L. californicus*, one *L. alleni* and five *S. auduboni* were captured, ear-tagged and released. Of these twenty-one rabbits, four were equipped with transmitter-battery packages, a male and female cottontail and two female black-tailed jackrabbits. The male cottontail was tracked from August 15 to 29, 1972. On August 29 it chewed out of the harness used to fasten the radio. During this period the rabbit's activities were centered mainly on the south edge of the dry wash shown in Figure 5. This area was in an ecotone between the predominant creosote bush community and the mesquite, palo verde and catclaw along the wash. The site was covered with grasses and forbs and offered a great deal of protection in the form of catclaw thickets and brushpiles washed up during heavy run-offs. The rabbit spent a large amount of time in and around the rock-pile indicated by the dotted line in Figure 5. There were numerous burrows among and under these rocks.

One advantage to the observer of the use of the rock-pile by the rabbit was that the radio transmission was cut out whenever the animal was in a burrow under the rocks. We were thus able to ascertain accurately the beginning and ending of activity periods. While there was no discernable pattern to the rabbit's activities, it was generally out of its burrow between 7 and 8 p.m., active intermittently during the night, and back into the burrows by 9 a.m.

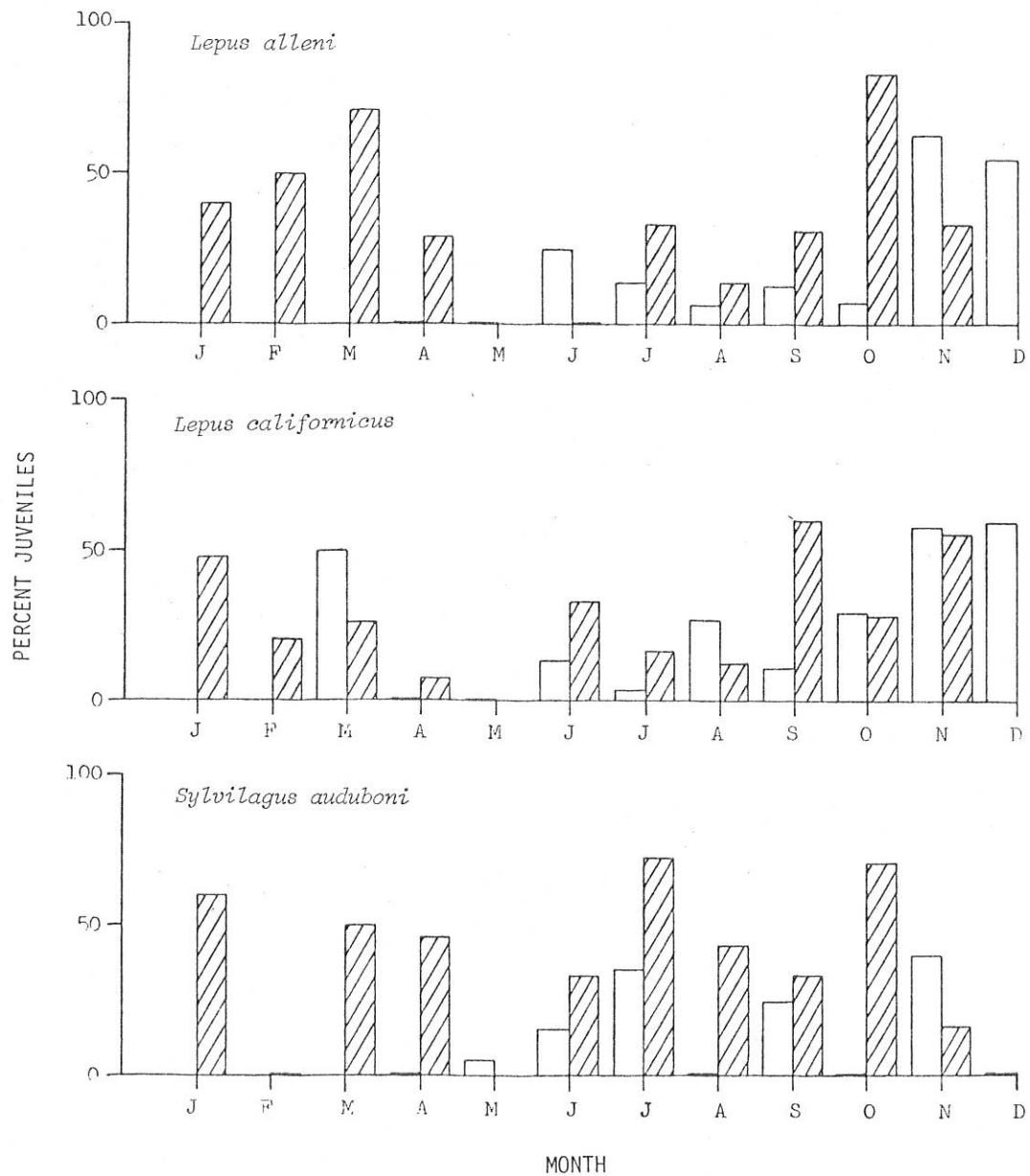


Figure 4. Percentage of juveniles in the monthly Silverbell bajada collections of 1971 and 1972 (crosshatched). No collections made in May 1972.

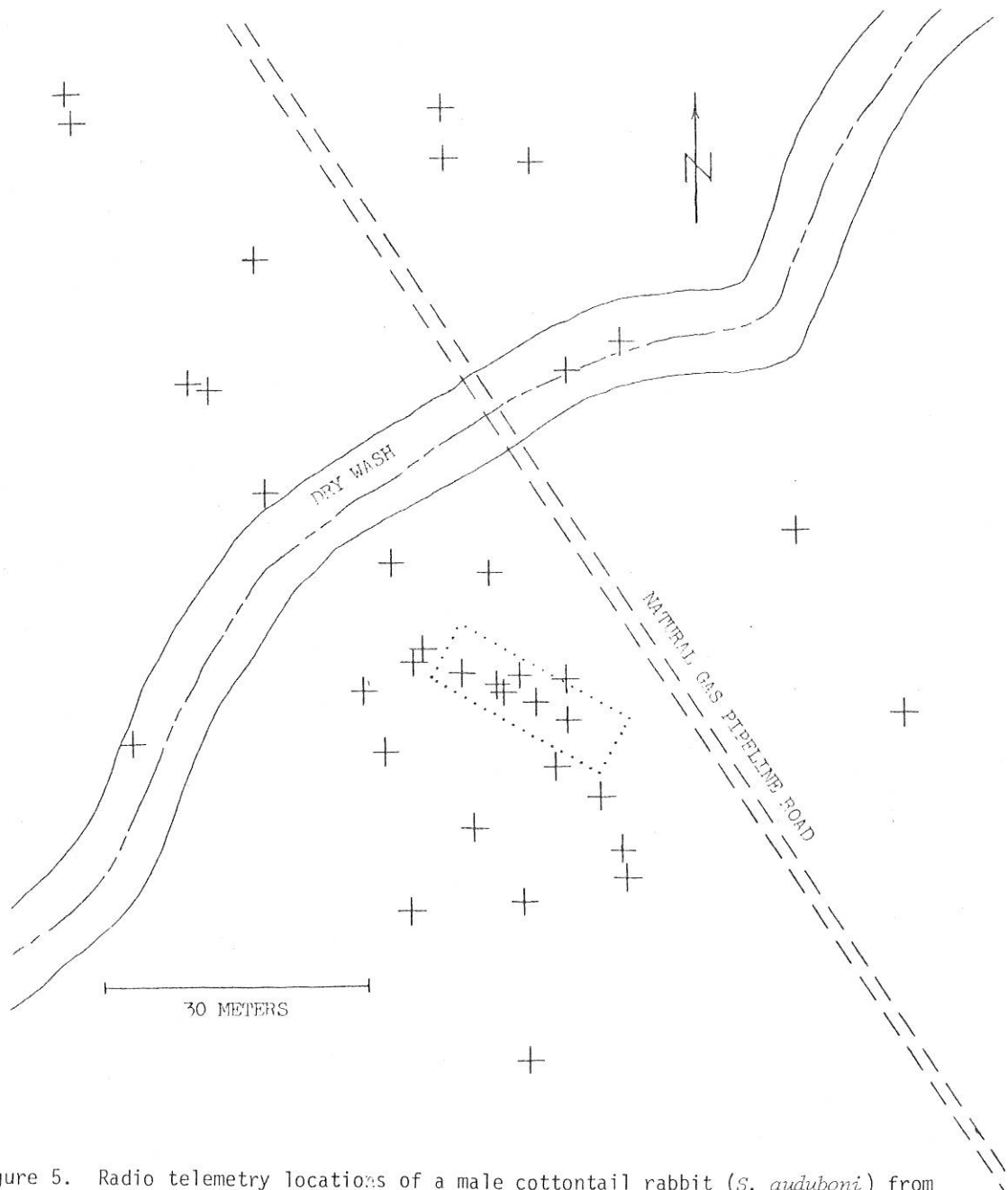


Figure 5. Radio telemetry locations of a male cottontail rabbit (*S. auduboni*) from 15 to 29 August 1972 on the Silverbell bajada. Dotted lines indicate the rock-pile (see Results, dispersal and mobility).

DISCUSSION

Breeding season and influencing factors

The specimens collected during the two years of this study indicate that breeding occurs in all three species of rabbits in the Sonoran Desert on a year-round basis. We have collected pregnant females of each species every month in 1972. These data extend the breeding season for cottontails reported by SOWLS (1957) as January to August and for jackrabbits reported by VORHIES and TAYLOR (1933) as December to September.

Although the breeding season for the rabbits in this area is year-round, there are two major peaks, the first in February and the second in July-August. The highest values for the frequency of occurrence of grass and forbs, reported by VORHIES and TAYLOR (1933) and DeCALESTA (1971) as comprising the bulk of the rabbit diet, occurred in September and October. These values began to increase in June and July following the start of the summer rains. Thus, the late summer breeding activity seems to be closely correlated with the onset of the summer rains and the resultant plant growth. The early breeding activity during this study has been in the middle of the driest part of the year. Our plant data show the highest amount of forage is available in the winter months and it is possible that the winter green-up lasts long enough to stimulate breeding in the spring.

Dispersal and mobility

The radio-telemetry data have not given us the information we need to define and quantify the dispersal of the rabbits in this study. Part of the problem has been the difficulty in capturing young of the year to instrument, and part has been the short duration of the tracking operations due to untimely radio failures.

The known locations of the male cottontail shown in Figure 5 indicate a home range during this study of 0.96 ha. An approximate home range value for the female cottontail, based on nine visual sightings while trying to recapture her, is 0.58 ha. This figure is, of course, highly suspicious in that it is based on only a few locations which were obtained while the rabbit was under the stress of being chased by a group of desperate researchers.

As was mentioned in the Results section of this report, the second female jackrabbit instrumented has been observed on two different occasions within 320 m of the location of original capture. However, these sightings were seven days apart, on October 21 and 28. As the rabbit was not seen again on five other days, between October 28 and November 5, we have no indication of the size of the range covered. The jackrabbit could have been in the same area on each subsequent search but was not spotted, or she could have been in an entirely different part of a much larger range.

This project has had more than its share of the usual telemetry problems. So much so in fact that the returns on our time and effort have been very meager. It was extremely discouraging to spend forty-three man hours (twenty-one of which were volunteered) in capturing and instrumenting the two female jackrabbits and in putting in the triangulation sites in exchange for the sketchy data received. Nevertheless, we have on hand the parts for ten more radios and the suggestions of the local men experienced in the field of telemetry as to improvements we can make on the battery package and antenna design that should increase the input for the dispersal and mobility phase of the project.

EXPECTATIONS

A bi-monthly sample of the three lagomorph species will be continued to gather data on their reproductive condition as well as the sex and age structure of the populations on the Silverbell bajada. The collection of these animals is important as it is related to the seasonal rainfall and plant growth.

Capture and monitoring of the movement and dispersal of individuals with radio-location transmitters will continue as long as present equipment is available. An attempt will be made to capture and equip with a radio package as many young animals as possible. Visible color markers on other individuals will be used as a secondary procedure to establish movement and dispersal rate and distance.

Rainfall will be measured in six rain gauges on the study area and rainfall measurements made by other investigators and in surrounding communities will be compared with our records. Seasonal plant growth, especially of fast-growing annuals, will be measured by frequency plots. Our objective will be to quantify the relative abundance and duration of availability of such plants to the rabbits. The timing of the reading of the plant frequency plots will vary with rainfall during the year.

Population demography, including increment and loss in the populations of these species, will be calculated from collection, observation and census data gathered this year and previous years. A life table will be constructed to show the dynamic state within the populations of these three species.

Age categories will either be estimated by eye lens weight change or by annulations in the periosteum of the mandible for those individuals not ageable by other procedures.

Further unknowns relating to our original objectives may be quantified through computer analysis of data from this and associated studies.

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1972 PROGRESS REPORT

THE CONSUMPTION, UTILIZATION AND MODIFICATION OF NUTRITIONAL
RESOURCES BY THE JACKRABBIT (*Lepus californicus*)
IN THE MOHAVE DESERT

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Research Memorandum, RM 73-22

MAY 1973

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It is subject to revision and reinterpretation. The authors
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Report Volume 3

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ABSTRACT

Summer diet, behavior and water and energy fluxes were determined for jackrabbits living in enclosures containing natural desert vegetation that had been watered the previous spring. The diet of these nocturnal animals consisted primarily of annual plants, particularly *Abronia villosa* and *Schismus barbatus*. Caged animals maintaining weight on this diet assimilated 34.5% of the energy in the food ingested. Jackrabbits in the enclosures turned over 154 ml $\text{H}_2\text{O kg}^{-1} \text{ day}^{-1}$. We calculated that these animals ate food at a rate of about 40 g dry matter $\text{kg}^{-1} \text{ day}^{-1}$. Of this, 26 g $\text{kg}^{-1} \text{ day}^{-1}$ was returned to the environment as feces. Jackrabbits did not prune much vegetation during summer, but in the fall about 10 g of dry plant material was cut and left uneaten each day.

These measurements will be continued in 1973 in order to obtain the data necessary to construct an annual material and energy budget for jackrabbits.

INTRODUCTION

Jackrabbits are conspicuous and important components of Southwestern desert ecosystems. They are relatively large (ca 2.5 kg) herbivores which differ from their better-studied rodent counterparts in a number of important respects. Whereas herbivorous rodents are primarily seedeaters, rabbits and hares largely utilize grasses and shrub browse. They are the primary mammalian consumers of these resources and, despite relatively sparse populations, may contribute a major component to the biomass and energy turnover of mammals in deserts (Chew and Chew, 1970).

Achievement of the objectives outlined below will help to define in quantitative terms the effects of jackrabbits on the movement of matter and energy through the ecosystem. A certain amount of the primary productivity will be dissipated through the metabolism of the hares, and this will be measured. Additionally, these animals probably convert a significant amount of living vegetation into fecal material and also prune material from shrubs which becomes detritus. While not significantly altering the amount of chemical potential energy in the ecosystem, these latter processes do alter the availability of this energy to other consumers and to decomposers. Moreover, effects of pruning have significant implications on rates of primary productivity. Thus, information obtained in this study should, when combined with other process studies, elucidate the impact of jackrabbits at all levels of the ecosystem.

OBJECTIVES

The primary objectives of this study are as originally proposed:

1. To make seasonal measurements of the amount and kinds of food consumed by jackrabbits in the Mohave Desert.
2. To make a quantitative assessment of the plant material cut, but not eaten.
3. To estimate the amount of organic material returned to the environment via elimination and excretion.

In 1972 observations were made primarily in summer and early fall. During 1973 we plan to obtain information throughout the year.

METHODS

We approached measurement of matter and energy exchanges by measuring water turnover in hares. This is theoretically feasible if all water input is associated with the food, either as preformed water or metabolic water, and the water content and digestibility of the food is known. To this end we measured water turnover in jackrabbits in fenced compounds containing natural vegetation in the Mohave Desert. We also determined the major dietary components, and assessed the relative amounts of water, energy and dry mass in the diet. We measured assimilative efficiency using caged animals fed a natural diet.

Enclosures

Two 0.40 ha pens were constructed on the Mohave Desert near Hinkley, California, at the Barstow Unified School District Desert Research Station. One enclosure was watered during the spring of 1972 and contained relatively lush vegetation, including some annual plants, throughout the summer. The vegetation in the other enclosure resembled that in the surrounding desert, which was suffering from a 3-year drought. Enclosures were square and constructed of chicken wire buried 0.3 m deep and extending 1.5 m above ground. This proved adequate for containing jackrabbits and excluding coyotes.

Animals

Six very young jackrabbits were obtained in the Barstow area and hand reared. These were kept out-of-doors in conventional rabbit cages. Five of these were used in the feeding trials described below. Some were also used for measurements of water turnover in the enclosures. Five additional animals were captured as adults and introduced directly into the compounds. Their water turnover was measured and they were eventually sacrificed for analysis of stomach contents.

Water turnover

Hares were injected with 0.1 to 0.2 mc of tritiated water (0.1 mc/ml in physiological saline) via an ear vein. Equilibration of isotope with body water was complete within 4 hr. After equilibration, a blood sample was taken and the animals were released into the compounds. Animals were recaptured periodically for blood sampling and, as required, reinjection with tritiated water. Usually only one animal was kept in each enclosure, but occasionally two were placed together in a compound.

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Tritium activity in the plasma was measured by placing 0.025 ml of plasma in 10 ml of dioxane scintillation fluid containing 100 g of naphthalene and 5 g of PP0 per liter. Samples were counted to 1% error, checked for differential quenching and corrected for background (DSCODE A3USD25).

Diet analysis

Following measurement of their rates of water turnover in the enclosures, wild-caught adults were killed and their stomach contents analyzed (DSCODE A3USD27). Stomach contents were sorted under a dissecting microscope. Items were identified by comparison with ground samples of plants from the enclosures. Dry weight proportions of the various components of the stomach contents were determined and taken to represent these proportions in the diet. Identification of dietary items was confirmed by direct observation of animals feeding in the compounds. Attempts were made to obtain stomach contents without sacrificing the animals by stomach pumping and administering emetic drugs. These efforts were unsuccessful.

Plant composition

Samples of plants from the compounds were collected periodically. After their fresh weights were measured they were dried to constant weight at 70 C to obtain water content (DSCODE A3USD20). Dried samples were combusted in a bomb calorimeter to determine energy contents.

Feeding trials

The average diet of the animals in the enclosures was determined and fed to three caged jackrabbits deprived of drinking water (DSCODE A3USD30). For comparative purposes, additional animals were fed a diet of ryegrass (*Lolium* sp.). Measured amounts of food were given each night, and unconsumed food was collected and weighed at about 0800 hr. The dry weight of the food consumed was obtained from these data. A control feeder containing the same amount of food was placed next to the cages to determine the amount of water evaporated during the feeding period. Thus, the amount of water taken in with the food could be estimated. This value was compared with rates of water turnover determined isotopically in the same animals.

During feeding trials, the cages were fitted with devices for collecting feces and urine. Feces were collected on a 6.3 mm mesh hardware cloth beneath the cage. A funnel for urine collection was fashioned from a large plastic bag fitted to the cage and a rigid plastic funnel leading through a vented stopper into a collecting bottle. The bottle contained 1.0 ml of formaldehyde (to prevent bacterial degradation of

organic excretory products) covered with a layer of mineral oil. Quantitative collections of urine and feces were made daily. A sample of fresh feces from each animal was collected for determination of water content.

The animals were weighed daily and the amount of food given was adjusted to that required for maintenance of body weight. Markers consisting of plastic surveyor's tape were force-fed at the beginning and end of the feeding trials so that the feces derived from this food could be identified. However, we found that the change of diet caused easily recognizable changes in the appearance of the feces. This provided a better means of identifying the feces associated with a particular diet. The energy contents of food and feces were determined by bomb calorimetry.

Behavioral observations

A tower was constructed next to the enclosures so that the animals could be observed. A light amplification telescope, obtained from the U.S. Marine Corps., permitted visual surveillance of the enclosures at night when there was some moonlight. To permit location and visual tracking of the animals, hares were fitted with collars bearing a miniature lightbulb that emitted weak flashes of light. The units were equipped with a photocell which prevented unnecessary battery drain by opening the circuit during the day. Thus the nocturnal behavior of the jackrabbits in the enclosures was easily observed. Daytime observations were made with a conventional telescope and binoculars.

Cuttings

Compounds containing jackrabbits were inspected at intervals ranging from a week to a month, and all plant cuttings were collected. Primary attention was given to shrub material, as we could more readily determine whether this litter was actually cut or had broken off. All of these cuttings were removed from the enclosure, sorted by species and their dry weights determined (DSCODE A3USD28). We made some observations on disturbance of small annual plants by jackrabbits, but these were of necessity more subjective.

RESULTS

Enclosure studies

Plants: The enclosure that was watered during the spring of 1972 contained a variety of plants, both annuals and perennials, throughout the summer. They were apparently

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in good condition, although they became somewhat drier as the summer progressed (Table 1). In the unwatered compound, *Larrea* was the only green plant, and it was much drier than *Larrea* in the wet enclosure. Consequently, the watered enclosure was used for most of the water turnover studies.

Animals: Eight jackrabbits were introduced into the watered enclosure (which was partitioned in half to form two 0.2ha compounds) for periods ranging from 2 to 8 days between July 10 and September 7. A total of 26 measurements of water turnover were made on these animals. During the first few days in the enclosure, the hares tended to lose weight and had somewhat low rates of water turnover (90 to 143 ml H₂O kg⁻¹ day⁻¹). However, their weights soon stabilized and rates of water turnover increased. Rates of water turnover for jackrabbits maintaining weight are shown in Table 2. Smaller animals turned water over somewhat more rapidly than did larger ones.

One animal (1543 g) was introduced into the unwatered enclosure for two successive periods of 3 days each. It lost weight continually and turned over relatively little water (52 ml kg⁻¹ day⁻¹). After it had lost 23% of its original weight it was sacrificed and the stomach contents examined.

Diet: Jackrabbits in the watered compound ate primarily two species of plants: *Abronia villosa* (Sand Verbena) and *Schismus barbatus* (Frost Grass). Insignificant amounts of several other species were also eaten (Table 3). This trend was substantiated by direct observations of feeding.

The stomach of the animal from the unwatered compound contained mainly wood fibers. Flakes of bark mixed with these appeared to be from *Larrea divaricata* stems. Examination of the enclosure revealed extensive fresh cutting of *Larrea* stems. There was no evidence that leaves were eaten.

Cuttings: Relatively little shrub material was cut and left uneaten in the watered compound during the summer, when annual plants were available. Cutting activity increased in the fall as annual plants disappeared, and marked shifts in the species cut were apparent (Table 4). Cutting of *Salsola* began as annual plants disappeared, and continued until the *Salsola* dried up. *Larrea*, on the other hand, was cut at a fairly uniform rate.

Behavioral observations: During the summer, jackrabbits were entirely nocturnal and crepuscular. Daylight hours were spent crouching in the shade in forms under shrubs. Jackrabbits moved from these forms only when alarmed or when exposed to sunlight by the changing position of the sun. Shortly after sunset, animals left their forms, and began to browse and graze. They remained abroad for the entire night, and entered

forms again shortly after sunrise. The time abroad was primarily spent feeding, punctuated by periods of up to 20 minutes during which the animals sat or stood apparently motionless in the open.

Table 1. Plants in the watered compound and their water contents at various times of the summer of 1972 DSCODE—A3USD20

Plant species	Part	Water content (ml H ₂ O/g dry weight)			
		July 13	Aug. 2	Aug. 21	Sept. 7
<i>Ambrosia dumosa</i>	lvs, stems	2.96	2.49	2.00	2.17
<i>Atriplex polycarpa</i>	lvs	1.32	1.25	1.20	dry*
<i>Atriplex canescens</i>	lvs	-	1.02	-	1.59
<i>Lycium pallidum</i>	lvs	5.67	5.96	4.66	4.98
<i>Lycium andersonii</i>	lvs	-	6.18	4.41	-
<i>Eurotia lanata</i>	lvs, stem	-	0.87	1.65	1.08
<i>Stanleya pinnata</i>	lvs, stem	-	3.83	2.58	3.42
<i>Salsola iberica</i>	stems	5.67	4.33	4.28	4.36
<i>Abronia villosa</i>	lvs, fls.	7.08	6.13	3.74	6.70
<i>Euphorbia polycarpa</i>	whole	-	1.99	1.45	1.34
<i>Schismus barbatus</i>	whole	1.81	1.18	0.33	0.42
<i>Larrea divaricata</i>	lvs, stems	1.71	1.18	0.89	0.98
<i>Phacellia</i> sp.	whole	-	1.68	-	-
<i>Coldenia plicata</i>	whole	-	1.33	1.12	0.72
<i>Hilaria rigida</i>	lvs, stems	-	1.16	1.03	-
<i>Condalia lycoides</i>	lvs	-	1.39	1.16	dry*
<i>Lepidium fremontii</i>	lvs	-	1.57	1.37	dry*
<i>Oryzopsis hymenoides</i>	lvs, stems	-	0.74	0.27	dry*

* dead when collected

Table 2. Rates of water turnover for jackrabbits maintaining weight in the watered enclosure during the summer of 1972 DSCODE—A3USD25

Animal	Approximate weight (g)	Water turnover (ml kg ⁻¹ day ⁻¹)		
		July	August	September
1	1120	212, 189		
3	1550		154	
5	2050		88, 110, 110	
7	1020		170, 151, 156	
8	1250		197	
9	1650		102, 169	193
Mean = 154 ml H ₂ O kg ⁻¹ day ⁻¹ (S.D. = 38.6)				

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Table 3. Results of stomach content analysis for jackrabbits maintaining weight in the watered enclosure during summer of 1972 DSCODE—A3USD27

Plant species	Part	% of total dry stomach contents			
		Animal no. 5	7	8	Mean
<i>Schismus barbatus</i>	lvs, roots	41.3	6.4	30.0	25.9
<i>Abronia villosa</i>	lvs, stems	50.8	90.8	70.0	70.5
<i>Atriplex polycarpa</i>	lvs	0.6	0	0	0.2
<i>Ambrosia dumosa</i>	lvs	6.6	0	0	2.2
<i>Stanleya pinnata</i>	lvs	0.7	0	0	0.2
<i>Euphorbia polycarpa</i>	lvs, fruit	trace	0	trace	trace
<i>Salsola iberica</i>	lvs, stems	0	2.8	0	0.9

Table 4. Dry weights of plant material cut but not eaten by jackrabbits during the summer and fall of 1972 DSCODE—A3USD28

Plant species	g dry weight cut animal ⁻¹ day ⁻¹			
	Dates 8/29-9/21	9/21-10/20	10/21-11/4	11/4-11/30
<i>Larrea divaricata</i>	3.07	1.99	2.21	3.40
<i>Salsola iberica</i>	6.74	1.32	1.40	0
<i>Atriplex polycarpa</i>	3.99	2.30	2.82	0.31
<i>Atriplex canescens</i>		0.89	6.82	6.69
<i>Lycium pallidum</i>		1.15	2.44	6.63
<i>Ambrosia dumosa</i>		0.66	2.87	2.41
<i>Stanleya pinnata</i>				0.53
Total	13.80	8.31	18.56	19.97

Meteorological data: Air temperatures (mean maximum and minimum) and precipitation at the study site are summarized by month for 1970-1972 in Tables 5 and 6.

Table 5. Mean maximum and minimum air temperatures (C) at the Desert Research Station, Hinkley, California DSCODE—A3USD10

Year		Month											
		Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
1970	max	17.2	20.5	21.6	23.8	33.3	39.4	43.8	43.8	36.1	36.0	24.4	15.5
	min	-3.8	1.6	2.2	2.2	10.0	13.8	21.1	18.8	8.3	5.0	1.1	-2.7
1971	max	18.0	20.7	23.9	26.4	30.0	37.5	42.8	43.4	33.5	28.8	22.2	11.2
	min	-5.0	-2.2	1.4	3.7	8.3	11.9	19.0	19.2	8.8	2.7	-1.7	-4.4
1972	max	16.6	22.7	28.8	28.3	33.8	41.1	43.3	38.3	36.1	25.5	18.8	13.8
	min	-6.1	-1.6	2.7	3.8	8.8	15.5	18.8	16.1	11.1	6.6	1.1	-5.5

Table 6. Precipitation (mm) at the Desert Research Station, Hinkley, California DSCODE—A3USD11

Year		Month												Total
		Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	
1970		6.9	28.4	12.2	1.8	0.0	0.0	1.5	1.3	0.0	0.0	8.1	8.6	68.8
1971		0.0	0.5	3.6	1.8	12.2	0.0	0.0	1.0	0.0	0.8	0.0	24.3	44.2
1972		0.0	0.3	0.0	0.0	0.0	3.6	0.0	3.6	0.5	8.1	17.3	13.2	46.6

Studies on caged animals

Five caged animals previously maintained on commercial rabbit pellets and water *ad libitum* were initially shifted to a diet of *Lolium* (ryegrass). After their weights had stabilized (4 days) three of the animals were given a diet consisting of 73% *Abronia* leaves and petioles and 27% whole *Schismus*, by dry weight, for 6 days. This diet contained 3.94 ml of water and 2.99 kcal per gram dry weight. Two animals were continued on *Lolium* containing 1.98 ml of water and 3.60 kcal per gram dry weight. At the end of the feeding trial the diets were reversed so that the feces associated with the test diet could be collected quantitatively. We were surprised to find complete passage of food and markers in a single night.

Feces of jackrabbits fed the *Abronia-Schismus* diet contained 2.98 kcal g^{-1} . The dry weight of the feces was 65.7% of the dry weight consumed. Their assimilative efficiency was thus 34.5%. Jackrabbits fed *Lolium* produced feces which contained 3.88 kcal g^{-1} and represented 61.7% of the dry weight consumed. Their assimilative efficiency was 33.5%. Urine samples have not yet been analyzed for energy content, so no metabolic efficiencies are reported here. However, these should be only slightly lower than the assimilative efficiencies.

Total water turnover in the caged animals, as measured isotopically, was 116 and $97 \text{ ml kg}^{-1} \text{ day}^{-1}$ in animals fed *Abronia-Schismus* and *Lolium*, respectively. Corresponding values for preformed water taken in as part of the food were 98 and $90 \text{ ml kg}^{-1} \text{ day}^{-1}$. The difference between the two values is presumably due in part to metabolic water production.

DISCUSSION

We are now in a position to estimate the food consumption of jackrabbits in the field during summer by using the data reported above. The rationale for this calculation is as follows. Total water turnover (W_t) in a non-drinking animal is the sum of the preformed water in the food (W_f) and the metabolic water production (W_m).

$$W_t = W_f + W_m$$

W_f is related to the dry mass of the food (M_f) by the food's water content (W_f/M_f).

$$W_f = M_f \times (W_f/M_f)$$

W_m is related to the dry mass of the food through the weight-specific energy content of the food (E_f/M_f), the metabolic efficiency (E_m/E_f) and the yield of metabolic water

per unit of energy metabolized (W_m/E_m).

$$W_m = M_f \times \frac{E_f}{M_f} \times \frac{E_m}{E_f} \times \frac{W_m}{E_m}$$

For W_m/E_m we used the value of 0.12 ml H_2O kcal⁻¹ (Brody, 1945). For W_f/M_f we used the values for the *Abronia-Schismus* diet fed to the caged animals: 3.94 ml H_2O /g dry wt and 2.99 kcal/g dry wt. [The laboratory diet has the same proportion of *Abronia* and *Schismus* found in the stomachs of field animals. Since these species made up more than 96% of the field diet, we believe the other constituents of the field diet can be ignored in this calculation. This water content is representative of the values for the plants during the bulk of the water turnover measurements in the field.]

Substitution of the second and third equations into the first, and solving for M_f yields

$$M_f = \frac{W_t}{\frac{W_f}{M_f} + \left(\frac{E_f}{M_f} \times \frac{E_m}{E_f} \times \frac{W_m}{E_m} \right)}$$

Using this equation we calculated that jackrabbits ingested 37.9 g dry food kg⁻¹ day⁻¹ during the summer of 1972.

The amount of feces produced each day can also be assessed. The rate of dry feces output can be calculated by multiplying the rate of dry food input by the fraction of dry food egested in the caged animals (0.687). The result of this calculation is 26.0 dry feces kg⁻¹ day⁻¹. When food intake and feces production rates are converted to kilocalories, the difference is the rate of energy assimilation, which should be very close to the rate of energy metabolism in animals maintaining weight. This value for the wild jackrabbits is 39.1 kcal kg⁻¹ day⁻¹, or 0.34 ml O_2 g⁻¹ hr⁻¹. The resting metabolic rate of an animal the size of a jackrabbit, as predicted by Kleiber's (1961) equation, is about 0.47 ml O_2 g⁻¹ hr⁻¹. Thus, our metabolic rate estimate for animals active in the field is lower than previously-reported values for resting jackrabbits. This is probably due to our method of calculating energy metabolism from water flux data and the water content of dietary items. The large differences in water content among the plant species growing in the enclosures (Table 1) account for much variation in this calculation. This effect will be reduced considerably for winter data, as plant water contents are more uniform. Nevertheless, we hope to measure metabolic rates directly, using O^{18} labelled water.

The amount of vegetation cut but not eaten during August was small. However, in late September and October, jackrabbits left about 14 g dry weight animal⁻¹ day⁻¹,

2.3.2.5.-12

or about $10 \text{ g hg}^{-1}\text{day}^{-1}$, of cuttings on the ground. This is only about one-fourth of the amount of dry material eaten each day in August.

It is difficult to interpret these results on a strictly seasonal basis, because the jackrabbits in the enclosures were experiencing a summer climate, but spring vegetation conditions. This is unfortunate, but considering the unusually dry vegetation existing outside the enclosure, we had no alternative. Hopefully, there will be sufficient rainfall this winter to permit us to conduct studies under more natural conditions in 1973 for determination of material and energy budgets during spring, summer and fall. Winter measurements are currently in progress.

EXPECTATIONS

During 1973 we plan to make essentially the same kinds of measurements described above. Our major thrust will be to broaden the study by making our observations under a wider variety of conditions associated with season and plant availability. Time spent in developing techniques during 1972 should pay off with increased efficiency of data collection in 1973.

We also plan some expansion of the scope of the measurements to include analysis of samples for electrolytes and nitrogen. This will permit us to estimate turnover rates of these materials. Finally, it is hoped that energy utilization estimates can be checked using doubly labeled water.

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1972 PROGRESS REPORT

DEMOGRAPHIC AND INDIVIDUAL GROWTH STUDIES FOR

Dipodomys ordii and *Peromyscus maniculatus*

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Research Memorandum, RM 73-23

MAY 1973

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Report Volume 3

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A B S T R A C T

This study provides detailed laboratory information on the growth rates of *Dipodomys ordii* and *Peromyscus maniculatus* and preliminary field data on their birth and death rates in North American deserts.

Growth rates for control and experimental animals, using the standard small mammal body measurements, several skull measurements, and eye lens weights, were determined in the small mammal research laboratory at Brigham Young University. Instantaneous relative growth rates (k) for the different parameters were determined and the distributions plotted on an arithmetic scale. All of the distributions have significant (.95) R^2 values, but dried eye lens weights seem to have the strongest correlations with age. Manipulation of light caused k to shift enough to suggest that independent environmental variables can possibly affect growth, but this required additional study.

Two 8.35 mm mesh hardware cloth enclosures were built during 1971-72 to facilitate field studies of birth and death rates. The *Dipodomys* enclosure (6.07 ha) is located at the Desert Range Experiment Station in Pine Valley, Millard Co., Utah; whereas, the *P. maniculatus* enclosure (2.02 ha) is located at the Benmore Experimental Range, Tooele Co., Utah.

Natality and mortality data were recorded from the enclosures, but these life table data require more time to complete. In the interim, litter sizes are being determined for *P. maniculatus* and *D. ordii* in the laboratory, and birth rates from field-caught animals. Litter sizes were measured directly in the laboratory, but the number of placental scars or embryos is being used for litter estimations on field-caught animals. Age structure and birth rates determined for the field-caught animals will be used to predict birth inside the enclosures until the specific age of the enclosed animals can be determined.

INTRODUCTION

Ecosystem analyses are basic to an understanding and modelling of a biome, since only when the ecosystem is understood can the contribution of its component parts (biotic and abiotic) be clearly managed to benefit man. Too often the additive principle (a whole equals the sum of its parts) is used in ecological analyses, but the abiotic and biotic components are non-additive and their many dynamic interactions must be understood if meaningful systems analyses are to become a reality.

Although the most important primary consumers in North American desert ecosystems have not yet been determined, they are likely to be small mammals, particularly several species of *Peromyscus* and *Dipodomys*, but their respective roles in the energetics of desert ecosystems have not yet been demonstrated. These interactions require comprehensive systems analyses of the respective species that include their dynamic relationships among the ecosystem components.

There are several species of *Peromyscus* and *Dipodomys* throughout the deserts in North America, but four (*Dipodomys merriami*, *Dipodomys microps*, *Dipodomys ordii*, *Peromyscus maniculatus*) occupy the largest total space and likely have the greatest impact on the ecosystem energetics. Due to this probable impact, the original proposal called for a detailed study on these four species; however, a decrease in the original funding level caused *D. merriami* to be dropped from consideration and the currently extremely low numbers of *D. microps* have made them difficult to study.

This study provides for intensive examinations of birth, death and growth rates of *D. ordii* and *P. maniculatus* in the North American deserts. When these parameters are determined along with the interactions of some of their primary independent variables, the biomass production of *P. maniculatus* and *D. ordii* can be determined, modelled, and possibly predicted.

A considerable amount of data on growth rates of the two species has been accumulated and partially analyzed over the past two years. The brief growth study data reported in RM 72-26 (Smith and Jorgensen, 1972) will be elaborated in this report. All of the standard growth data have been gathered, and their analyses are in the process of being completed at this time, along with experiments on the reactions of growth to changing independent variables. The animals for the natality studies have all been collected from the field and are being analyzed, and the field mortality studies are in their third sampling period. The remainder of the data will be gathered, analyzed and reported on in the final year of this study.

Demographic data, due to their nature, require considerable time and effort, but are necessary if a complete analysis is desired.

OBJECTIVES

Although the number of species studied has been reduced from four to two, the objectives have remained:

1. To determine individual growth rates for *D. ordii* and *P. maniculatus*, and determine how these rates respond to independent variables.
2. To determine the birth rates for *D. ordii* and *P. maniculatus*, and how they respond to independent variables in both laboratory and under field conditions.
3. To determine death rates for *D. ordii* and *P. maniculatus*, and how they respond to independent variables in natural conditions.
4. To develop a submodel that will use the data of the first three objectives to describe the demography of the two species and provide predictive capabilities.

Objective one is essentially complete. Growth rates have been characterized for both species under normal laboratory conditions and the effects on growth of food, photoperiod and temperature have been or are being studied. Representative specimens for both species have been collected for two years, and their age will be determined by using the growth curves established under objective one.

Objective two, natality, has been determined for both species in the laboratory, and the field animals have been collected for this determination under field conditions. These animals will be examined for reproductive activity along with the data that will be gathered from them for growth analyses and age determinations. This work is presently underway and will be complete by June, 1973.

Objective three, due to its nature, takes the longest to accomplish. Animals have been marked, released and monitored for two successive sampling periods in the *P. maniculatus* field enclosure and three in the *D. ordii* enclosure. Animals in these enclosures will be monitored on a pre-and post-reproductive schedule for the duration of the study in 1973. Objective four can be satisfied after the data in objectives 1-3 have been analyzed in August.

METHODS

Growth rates

Dipodomys ordii: Specimens used in this portion of the work came from several sources. The initial colony, 45 females and 15 males, were live-trapped at the Desert Range Experiment Station (Pine Valley), 81 km west of Milford, Utah, in Millard County. Ten additional pregnant, lab-reared females were purchased from Ecodynamics Inc. of Salt Lake City, Utah. These animals had been previously bred and housed at Dugway Proving Grounds in Tooele County, Utah. An additional 350 females and 50 males were trapped at various times throughout the year near Pahvant Butte, Millard County, Utah, and Ecodynamics collected an additional 400 females from Dugway Proving Grounds. About 100 females were used as replacements in the controlled and experimental laboratory studies, and the remainder were observed for field pregnancy. The laboratory colony was maintained at 85 females and 15-20 males.

The main breeding colony, which provided the normal growth data, was housed in the small mammal research laboratory at Brigham Young University, whereas the experimental animals were kept in controlled chambers. One half of the animals were caged in individual Metaframe aquaria (51.5 cm long, 26.5 cm wide, and 31.0 cm tall) with perforated aluminum reptile covers. The other half were caged in galvanized metal boxes (45.5 cm long, 38.0 cm wide, and 25 cm tall) with covers of 8.35 mm wire mesh. Sand (6-8 cm deep) was used as the substrate in each cage and nest cans with cotton were provided. There was a continuous water supply and a standard food mixture of sunflower seeds, rolled oats and pigeon mix (Ecodynamics). Purina mouse breeder chow was also provided. Nine rats were also fed fresh green feed for a period of five months to possibly aid reproductive success. The temperature was held constant at 22 C and the photoperiod artificially maintained at 12 hr light and 12 hr dark with varying intensities simulating dawn and dusk.

The sexes were kept separate except when mating was attempted and the females were checked daily for estrus. External changes in the morphology of the vulva as described by Pfeiffer (1960) were used as indicators of estrus. When the full-flowered vulvar condition was achieved, it was presumed to indicate estrus and a male was introduced into the female's cage. Usually vigorous fighting ensued, but if the male survived, he was left with the female for 3-4 days, then returned to his cage. The females were checked for vaginal plugs as an indication of successful coitus.

When a litter was born it was not disturbed until the following day, at which time the young were toe clipped and measured. The following measurements were taken daily from days 2 to 22 and then weekly up to 10 weeks: 1) body weight, 2) total length, 3) tail length, 4) ear length, and 5) hind foot length. Body weight was determined to the nearest 0.05 g on an Ohaus triple beam balance; total and tail lengths were measured to the nearest 0.5 mm with a clear plastic metric rule, and ear and hind foot lengths were measured to the nearest 0.01 mm with a Mitutoyo dial caliper. After the eyes had opened and the individuals became more active, they were anesthetized with Penthrane to facilitate handling and obtaining accurate measurements. Daily observations were recorded for each litter to determine behavioral changes during development.

A separate mixed group of eight females and four males was housed in a large metal arena 2.5 m square and 1.5 m tall with 10 cm of sand on the floor. This arena was divided into three interconnected compartments. The compartments on each side contained water dishes, nesting cans, and nesting material, while the center compartment was used primarily for feeding. Reproduction was limited to a single litter (which was abandoned) under these conditions.

Peromyscus maniculatus: All of the animals used in this portion of the study were the progeny of 50 pairs of *Peromyscus maniculatus sonoriensis* collected approximately 19.32 km SE of Benmore Guard Station (Benmore Experimental Range), Tooele, Co., Utah, on July 16, 1971.

The colony was housed in the same laboratory and physical conditions as the *Dipodomys*, with the exception that wood shavings were used for the substrate and Purina mouse breeder chow provided as the food. Only Metaframe aquaria were used for caging.

When the animals were brought into the laboratory, they were sexed and paired, one pair to a cage. Each cage was checked daily for food and water and inspected for the presence of a litter. When a litter was found, each member was marked by toe clipping. The same daily and weekly measurements and observations were made for *Peromyscus* as for *Dipodomys*, but over 100 animals were included in each daily age interval to reduce the variance and refine the confidence in relating age with the growth parameters.

Linear, quadratic, cubic, combined linear-quadratic, and linear-quadratic-cubic distributions were used to characterize the growth of *Peromyscus* (Smith and Jorgensen, 1972). The instantaneous relative growth rate (IGR) of Brody (1945) is used in

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this report to express growth as a function of the rate between times of measurements and percentage of maximum size. This rate is expressed as $(dW/dt)/W$, where W is the parameter measured at the instant the rate of change dW/dt is measured. Since it is not entirely possible to develop the "instantaneous" rate of growth, it was necessary to integrate the infinite number of growth rates to derive:

$$W = Ae^{kt}$$

This is conveniently rewritten as:

$$\ln W = \ln A + kt$$

where $\ln W$ is the natural logarithm of the variable (W) at time $t-1$, $\ln A$ is the natural logarithm of the variable (W) at $t = 0$, and k represents the instantaneous relative growth rate (when multiplied by 100, k = percentage growth rate). For comparative purposes, the instantaneous relative growth rate (k) is determined with:

$$k_n = \frac{\ln W_n - \ln W_{n-1}}{t_n - t_{n-1}}$$

thus, k is definite and can be used to compare differences in rates of growth.

Additional studies on skull measurements and eye lens weights were also made to correlate age with the previously mentioned growth measurements. Ten individuals were sacrificed each day from 1-22 days for these data. On the day that an animal was to be sacrificed, it was removed from the nest and killed with an overdose of Penthrane. The standard daily measurements were taken and then the whole animal was placed into a 10% formalin solution to fix the lenses. After a minimum of four days the animal was removed from the formalin solution; the head was removed, skinned, and the lenses extracted by making a slit in the cornea with a hooked insect pin applying pressure to the sides of the eyeball with curved forceps. The lenses were then stored in a vial of 10% formalin, placed on spotting plates, and dried at 100 C for one week. After drying, they were removed from the oven and weighed individually to the nearest 0.0001 g on a Mettler laboratory balance.

After the lenses had been extracted, the skull was placed into a labeled paper cup, frozen and later stained and measured. The staining followed basically the methods described by Humason (1967), except that the amount of Alizarine stock solution used was increased 10 times. The skulls were thawed, placed into a compartmentalized tray, and covered with a 0.2% KOH solution. After two days this

solution was replaced for two days with a 0.2% solution containing 3 liters of the 0.2% KOH and 30 ml of Alizarine stock solution. The skulls were then rinsed with water and again covered with 0.2% KOH for two days, after which the skulls were rinsed with water and allowed to dry for measuring. The 1) total length, 2) zygomatic breadth, 3) foramen magnum height, 4) mastoidal breadth, 5) nasal length, and 6) cranium width were taken with dial calipers to the nearest 0.01 mm on each skull.

Controlled laboratory experiments were conducted to test the effect of different environmental parameters on the growth of *P. maniculatus*. Five pairs of previously unbred mice were placed in each of two environmental chambers where temperature was held constant at 22 C and photoperiod was set at 9 hr of artificial light and 15 hr of darkness in one chamber and 15 hr of light and 9 hr of dark in the other. Caging was the same in both chambers. In another experiment, five pairs of previously unbred mice were placed into two environmental chambers where the photoperiod was held constant at 12 hr light and 12 hr dark. All other variables were held constant except temperature, which was 10 C in the cold chamber and 30 C in the hot chamber. When litters were born they were marked, weighed, measured, and observed using the standard procedure described earlier.

Experiments are now being initiated to test the effects of different foods on growth and development. Throughout the growth study, all data taken were key-punched on IBM cards for subsequent analyses.

Birth rates and death rates

Two hardware cloth enclosures were built during 1971-72 to facilitate studies of birth and death rates of both *D. ordii* and *P. maniculatus* in the field. The *Dipodomys* enclosure (6.07 ha) is located 11.27 km NE of the headquarters at the Desert Range Experiment Station in Pine Valley, Millard Co., Utah. The construction site was selected after 10 days of trapping revealed a localized population of *D. ordii*.

The enclosure was constructed of 8.35 mm mesh hardware cloth, 120 cm wide, buried about 20 cm deep, so it projected about 90 cm above the ground. The hardware cloth was secured on the inside of steel posts placed every 3 m. Two Young live traps were placed at each stake in a 12 x 12 grid, 20 m apart, within the enclosure. The grid was first trapped for ten consecutive days in August, 1971. The animals caught were sexed, aged, marked by toe clipping, and released after the grid location where caught was recorded. Trapping was repeated in May, 1972, and August, 1972.

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Simultaneously with the trapping inside the enclosure, animals were collected with Museum Special snap traps from similar habitats outside of the enclosure. These specimens were returned to the laboratory for studies on age structure, birth rates (by counting placental scars) and growth correlation with the laboratory-reared animals. Skull measurements and dried lens weights are being taken for this correlation.

The *P. maniculatus* enclosure was constructed in April, 1972, and is located 0.4 km N of Benmore Guard Station (Benmore Experimental Range), Tooele Co., Utah. Its construction and trap design were similar to the *D. ordii* enclosure, except: 1) the fence is topped with a galvanized metal flashing which projects away from the fence on the inside to prevent animals from climbing out, 2) it encompasses only 2.02 ha which seems sufficient for the smaller home range requirements of *P. maniculatus*, 3) Sherman traps were used instead of Young traps, and 4) the traps included on the 12 x 12 grid were spaced 12 m apart.

Although the area was selected as typical for *P. maniculatus* habitat and because of the presence of *P. maniculatus* in the fall, 1971, in the initial May, 1972, sampling period only *Perognathus parvus* were caught. Consequently, 15 pairs of *P. maniculatus* were introduced into the enclosure at that time, and the area was trapped again in September, 1972.

Concurrent with the trapping periods inside the grid, about 100 female *P. maniculatus* were collected each time in comparable habitat outside of the grid. These are being examined for placental scars and skull measurements to compare with the laboratory data. The natality and mortality collection studies are being closely coordinated with the growth studies since both often use the same specimens and rely on a reasonable assessment of the age structures.

Mortality rates will be determined from life tables which are being generated from the enclosure data, and will include mortality rate (q^x), life expectancy (e_x) and probability of death (Q_x). An effort is being made in this study to coordinate laboratory and field studies for *D. ordii* and *P. maniculatus*; since field mortality is being studied by recording the ages at death of animals marked at the time they first become trappable, but whose births are not necessarily at the same time, and mortality rates of postnatal, but non-foraging, animals are being determined from young born and retained in the laboratory. A field estimate of this will also be obtained by determining the number of young introduced into the natural population and subtracting this from the estimate of those reproduced. Data for these analyses are being obtained by repeated trapping of marked animals within the established enclosures, and, of course, this necessitates other population estimates for the data to be particularly meaningful.

RESULTS

Growth rates

Dipodomys ordii: Growth curves along with tables of the instantaneous relative growth rates (k) and R^2 for *D. ordii* are presented for body weight, total length, tail length, ear length, and hind foot length in Figures 1-5. The R^2 values provide an indication of how much variation is accounted for in the analyses, and after they were converted to r ($= \sqrt{R^2}$) all were found to be significant at the 0.95 level; thus, there was a significant correlation between the appropriate $\ln W$ (log of the variable) and the age of the growing animals when time is partitioned into intervals of 1-3, 4-12, 13-22, and 23-70 days. These intervals were established on the basis of analyses reported in Desert Biome RM 72-26 (Smith and Jorgensen, 1972). These curves were plotted on arithmetic scales to better illustrate the correlation (r) between time (age in days) and the dependent variables. The k values provide the rate of growth for the above-mentioned intervals as a function of maximum size attained. It may also be referred to as the percentage of maximum size attained each day. The curves reflect the correlation rather than the k values which can be illustrated by plotting $\ln W$ on a semilogarithmic scale. Examples of how a k plot would appear are found on Figure 14 for body weight. Instantaneous relative growth rates (k), as defined by Brody (1945), are used as a convenient way to compare different growth rates. Figures 1-5 present k values for the above-mentioned time intervals.

Peromyscus maniculatus: Growth curves along with the instantaneous relative growth rates (k) for *P. maniculatus* are presented for body weight, total length, tail length, ear length, and hind foot in Figures 6-10. Analyses of the dried eye lens weight data are provided in Figure 11. Although one-half of the r values for the skull measurements were not significantly correlated with age at the 0.95 level (Table 1), the skull and nasal lengths were for most of the growing period, and also provided relatively high percentage (R^2) of the variation (Fig. 12,13).

There was a question of how closely the antilogs of $\ln W$ followed the actual data means, since this understanding is important in evaluating k . Means for dried eye lens weight are given in Figure 15 and the estimates of k are given in Figure 11 and 16. The $\ln W$ antilog and mean curves are almost identical. The wide standard error on the tenth day was due to the inclusion of one specimen with extremely atrophied eyes.

Data for animals retained in different photoperiods are reported in Figures 17-21 for body weight, total length, tail length, ear length and hind foot length. The r values are also significant at the 0.95 level, but the k values are more interesting since they can be used to compare the rates of growth under experimental conditions.

Since the correlations of growth parameters with age are significant (except for some skull measurements), one might consider using these parameters to predict age and, conse-

2.3.2.6.-10

quently, evaluate the population age structure. Although the procedure seems evident at first, since it would simply involve reading the predicted age from a graph, the results are questionable because of the lack of variation among days. That is, one cannot estimate age of animals with confidence by simply reading this type of curve backwards. The analyses of these data to provide age determinations awaits non-parametric procedures, which should provide much better results.

Table 1. Analyses for skull growth of *Peromyscus maniculatus* using dependent variables

Days	Statistics			
	R^2	Mean ²	lnA	k
<i>Skull Total Length</i>				
1- 3	.04144	.04043	2.57337	-.04973
4-12	*.56910	.00643	2.53206	.03613
13-22	*.29546	.00106	2.92890	.00728
<i>Zygomatic Breadth</i>				
1- 3	.06776	.04252	1.87072	-.06665
4-12	*.30443	.00926	1.90635	.02457
13-22	*.12450	.00616	2.09949	.01026
<i>Foramen Magnum Height</i>				
1- 3	.01227	.03721	.87440	.02547
4-12	*.37512	.01068	.94833	.03230
13-22	.00505	.02371	1.24585	.00381
<i>Mastoidal Breadth</i>				
1- 3	.00239	.04572	1.78600	.01240
4-12	*.25868	.01406	1.87614	.02825
13-22	.00400	.00303	2.20901	.00121
<i>Nasal Length</i>				
1- 3	.019427	.08928	1.50519	-.05042
4-12	*.57022	.01119	1.31158	.04639
13-22	*.35931	.33040	1.81674	.01473
<i>Cranium Width</i>				
1- 3	.04096	.02569	2.03463	-.03940
4-12	*.62524	.00362	2.02471	.02910
13-22	.01624	.11260	2.58174	-.01490

*Significant at the .95 level.

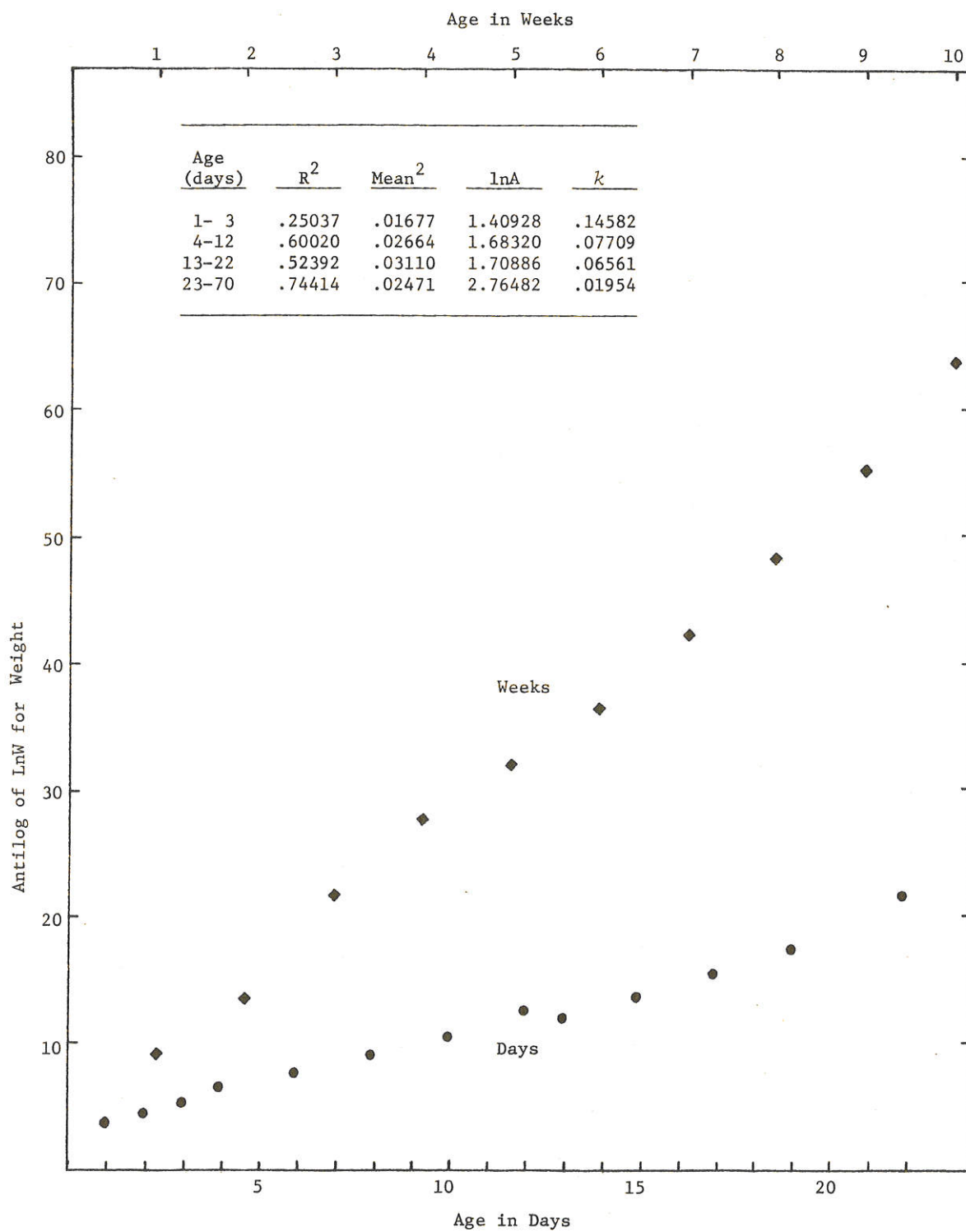
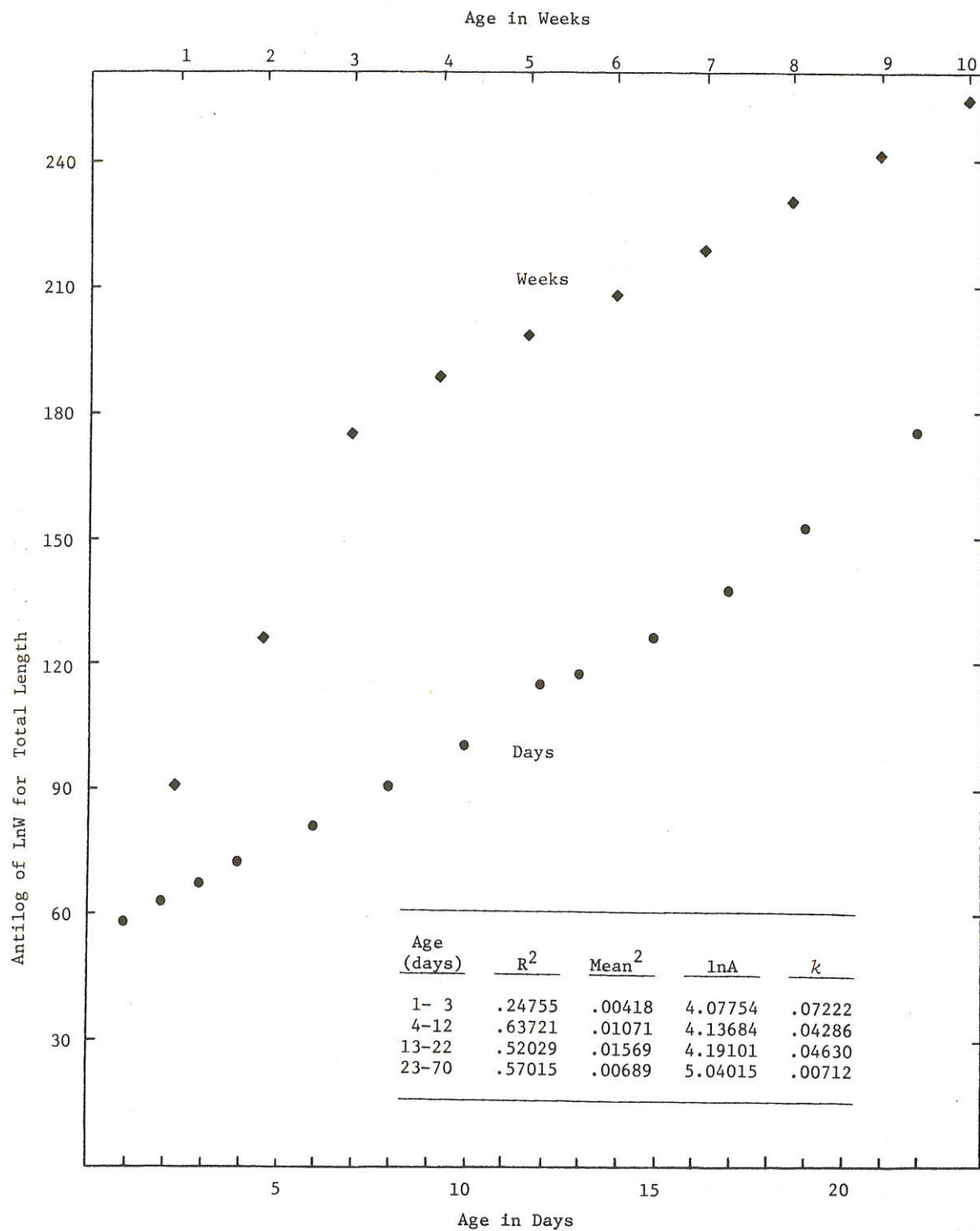
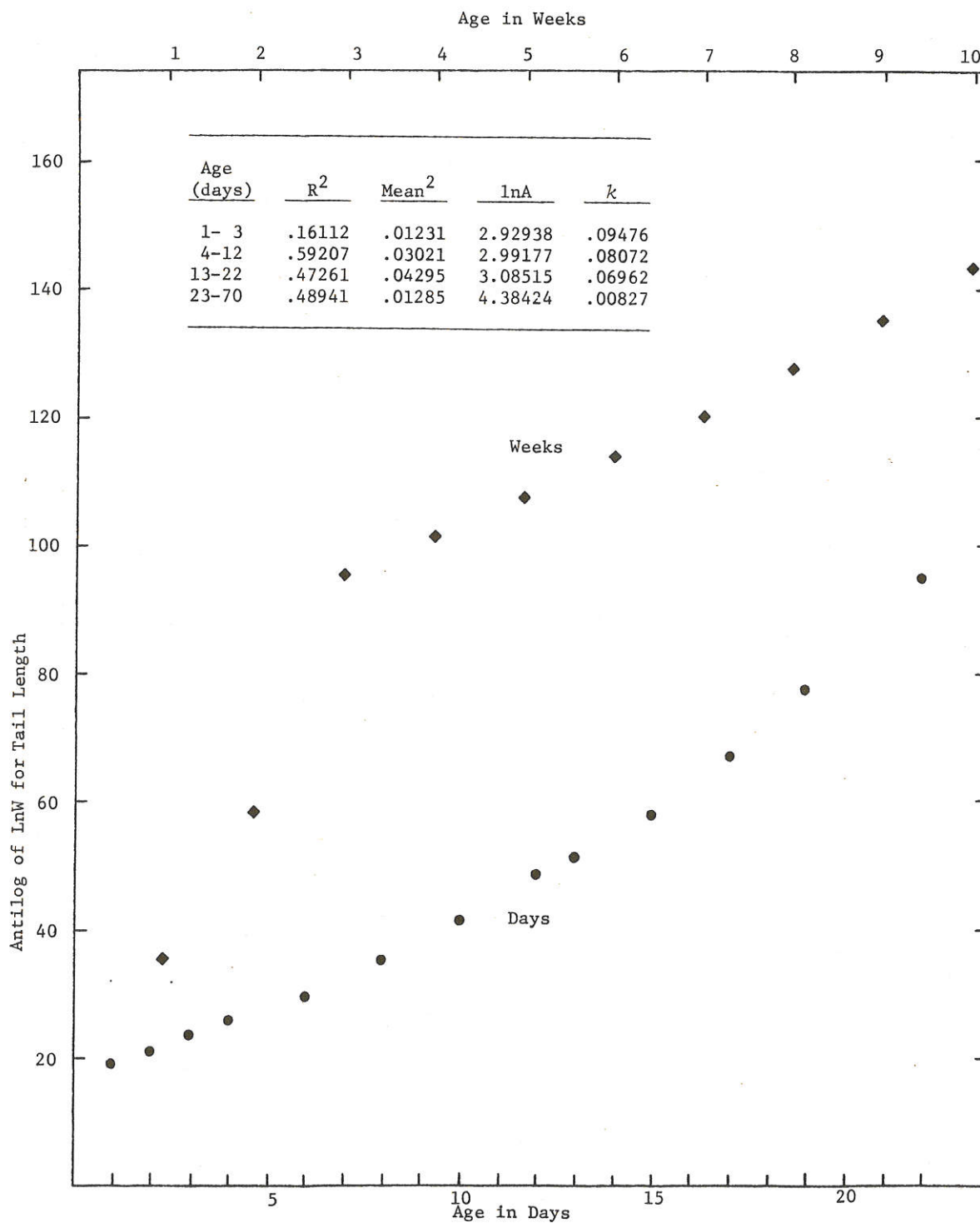
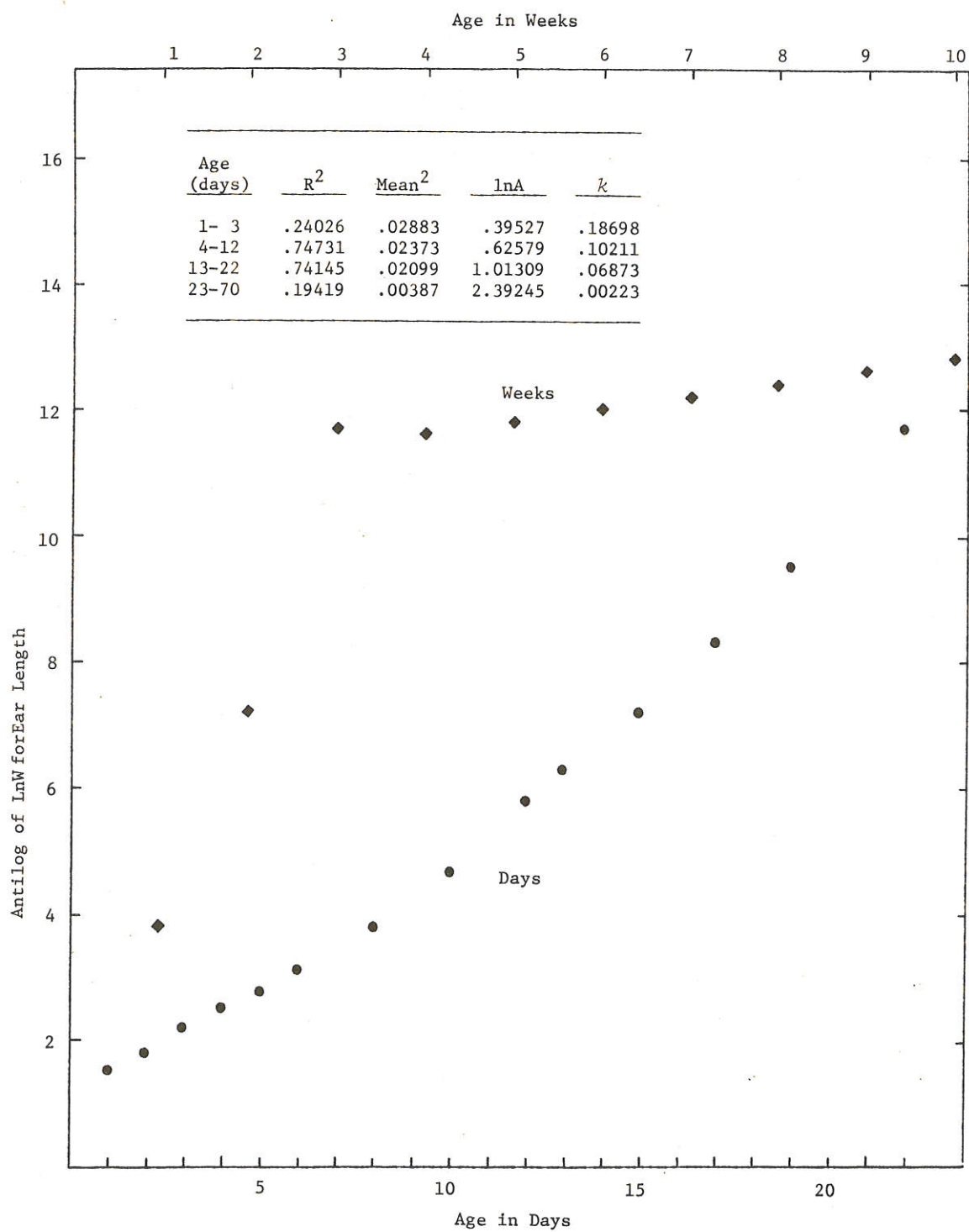


Figure 1. Growth curve for weight of *Dipodomys ordii*.

Figure 2. Growth curve for total length of *Dipodomys ordii*.

Figure 3. Growth curve for tail length of *Dipodomys ordii*.

Figure 4. Growth curve for ear length of *Dipodomys ordii*.

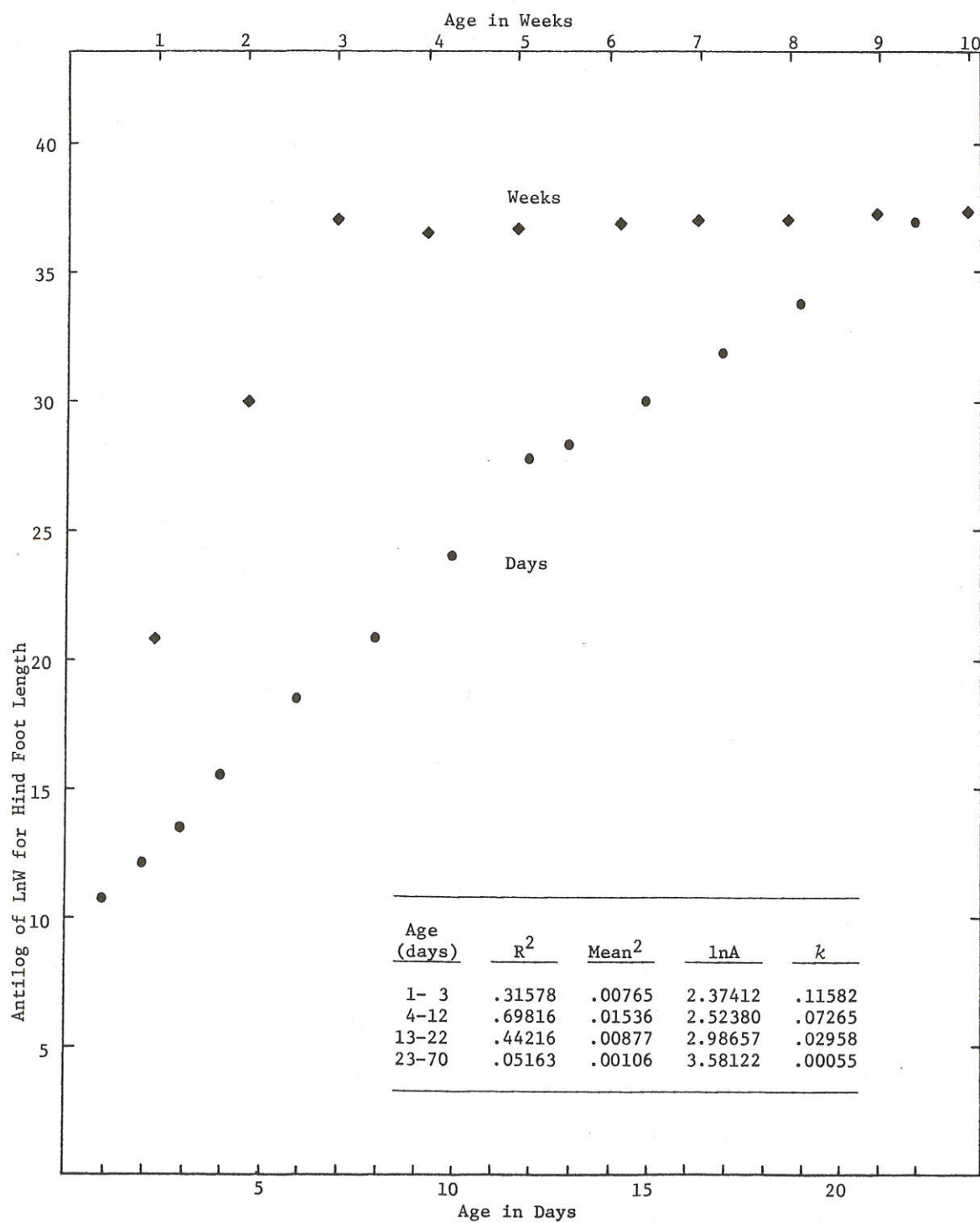
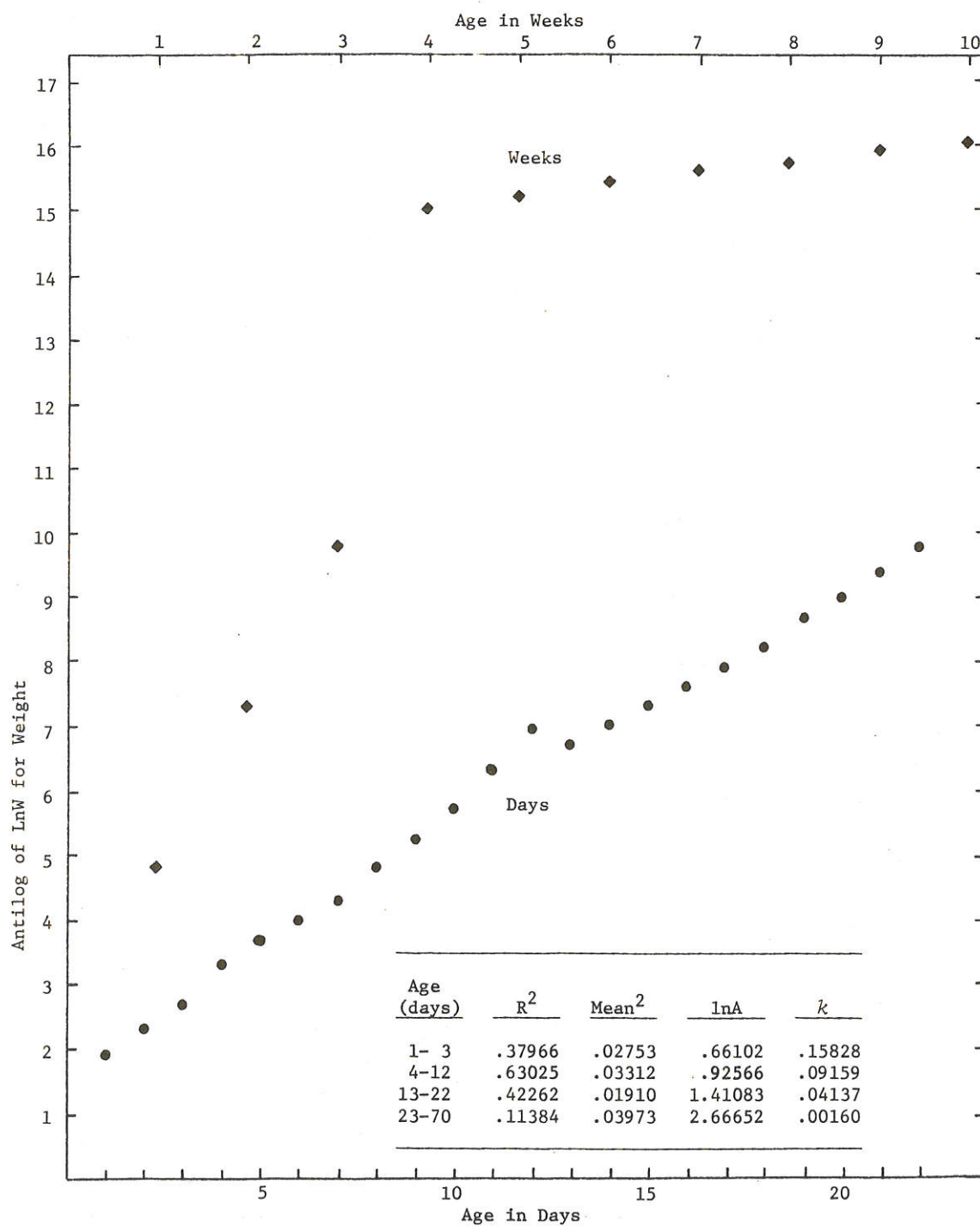


Figure 5. Growth curve for hind foot length of *Dipodomys ordii*.

Figure 6. Growth curve for weight of *Peromyscus maniculatus*.

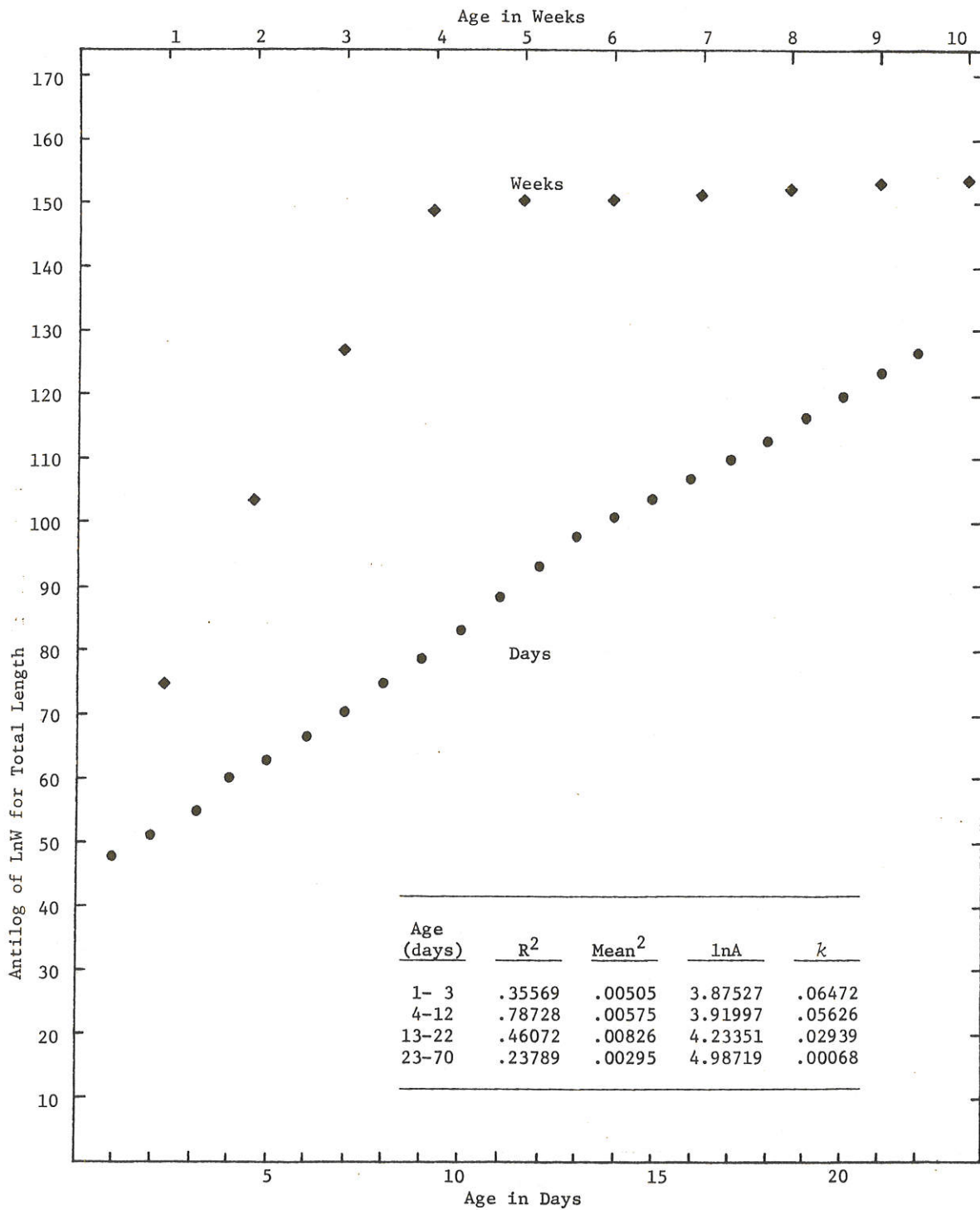


Figure 7. Growth curve for total length of *Peromyscus maniculatus*.

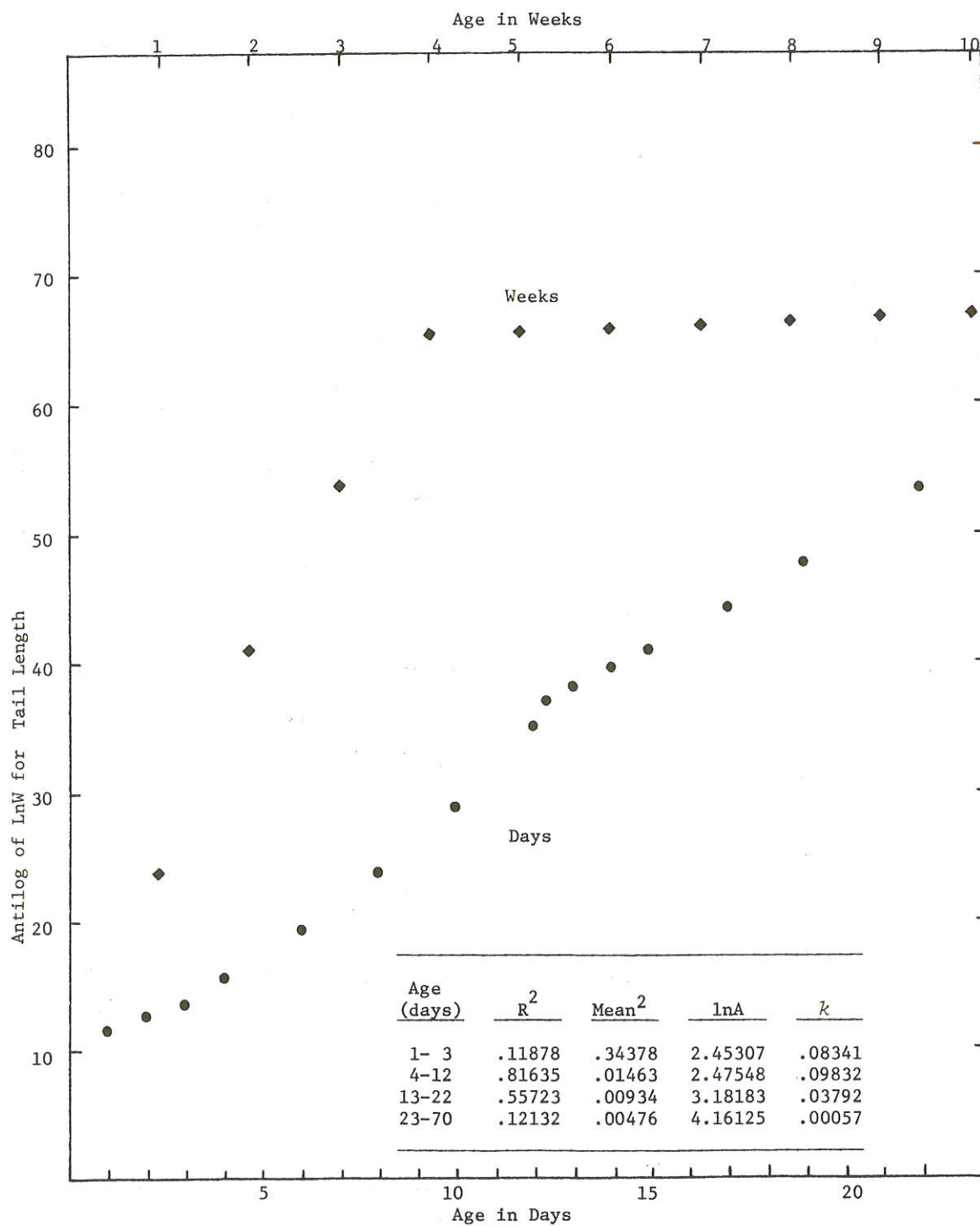


Figure 8. Growth curve for tail length of *Peromyscus maniculatus*.

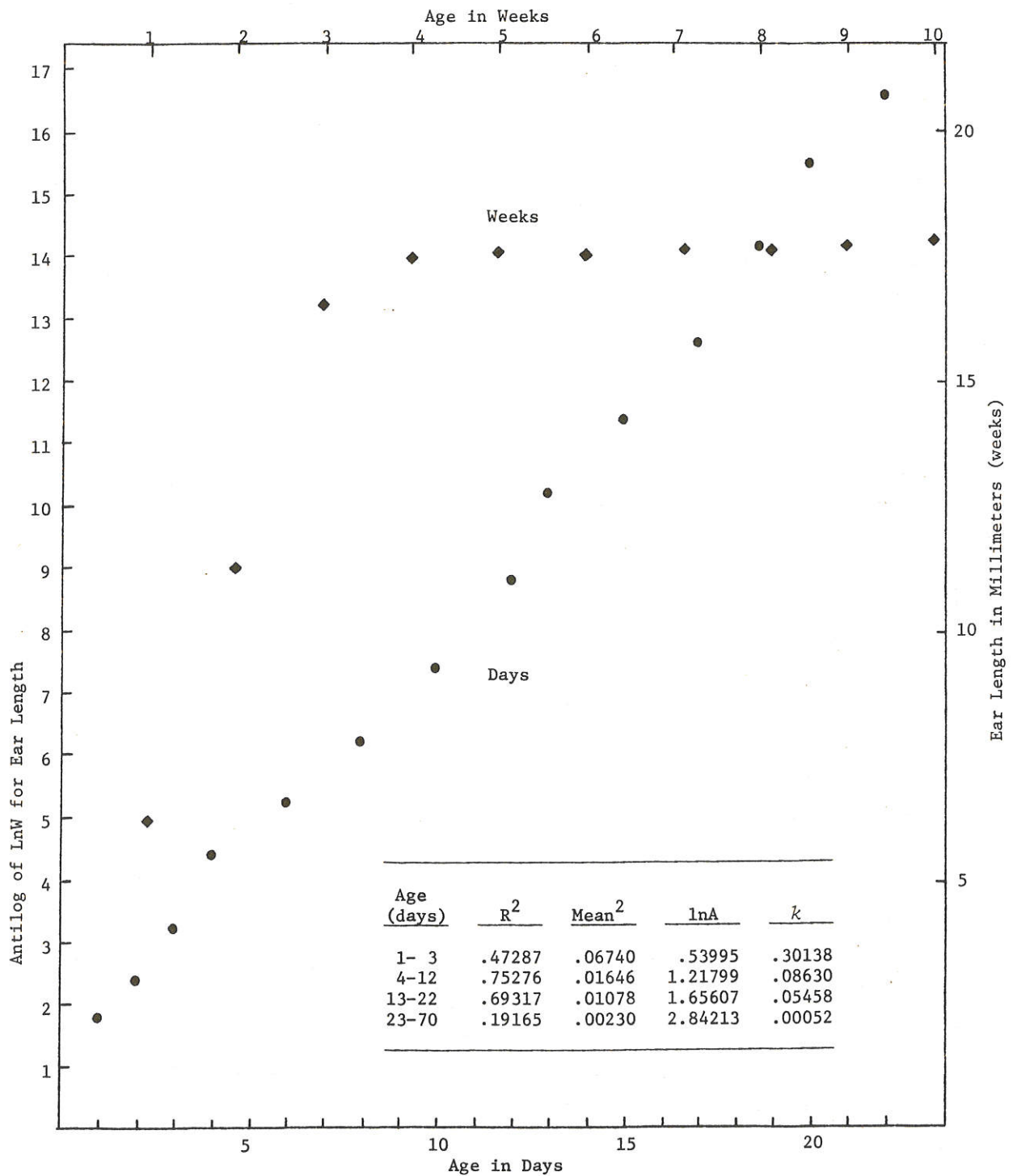


Figure 9. Growth curve for ear length of *Peromyscus maniculatus*.

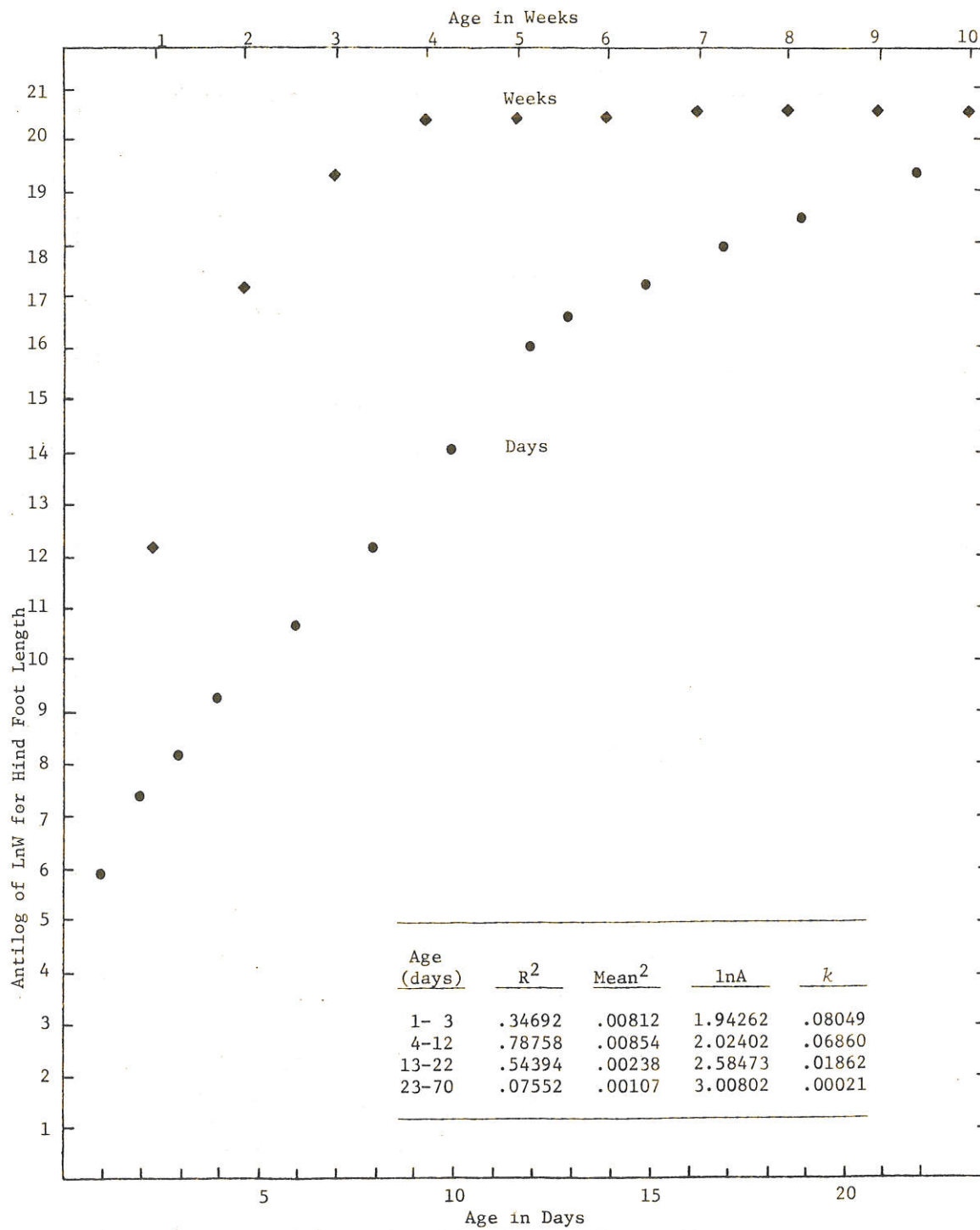


Figure 10. Growth curve for hind foot length of *Peromyscus maniculatus*.

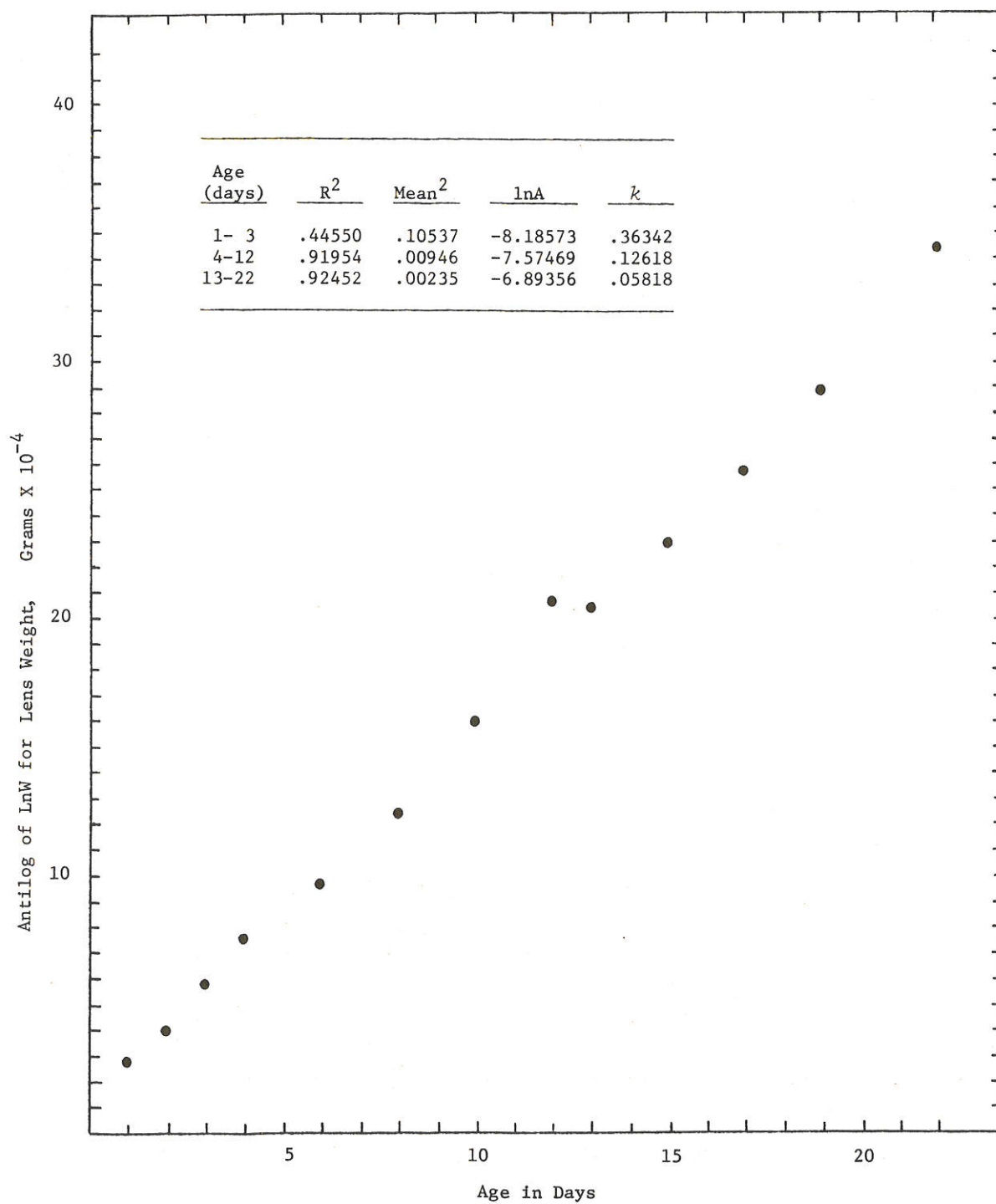


Figure 11. Growth curve for dried eye lens weight of *Peromyscus maniculatus*.

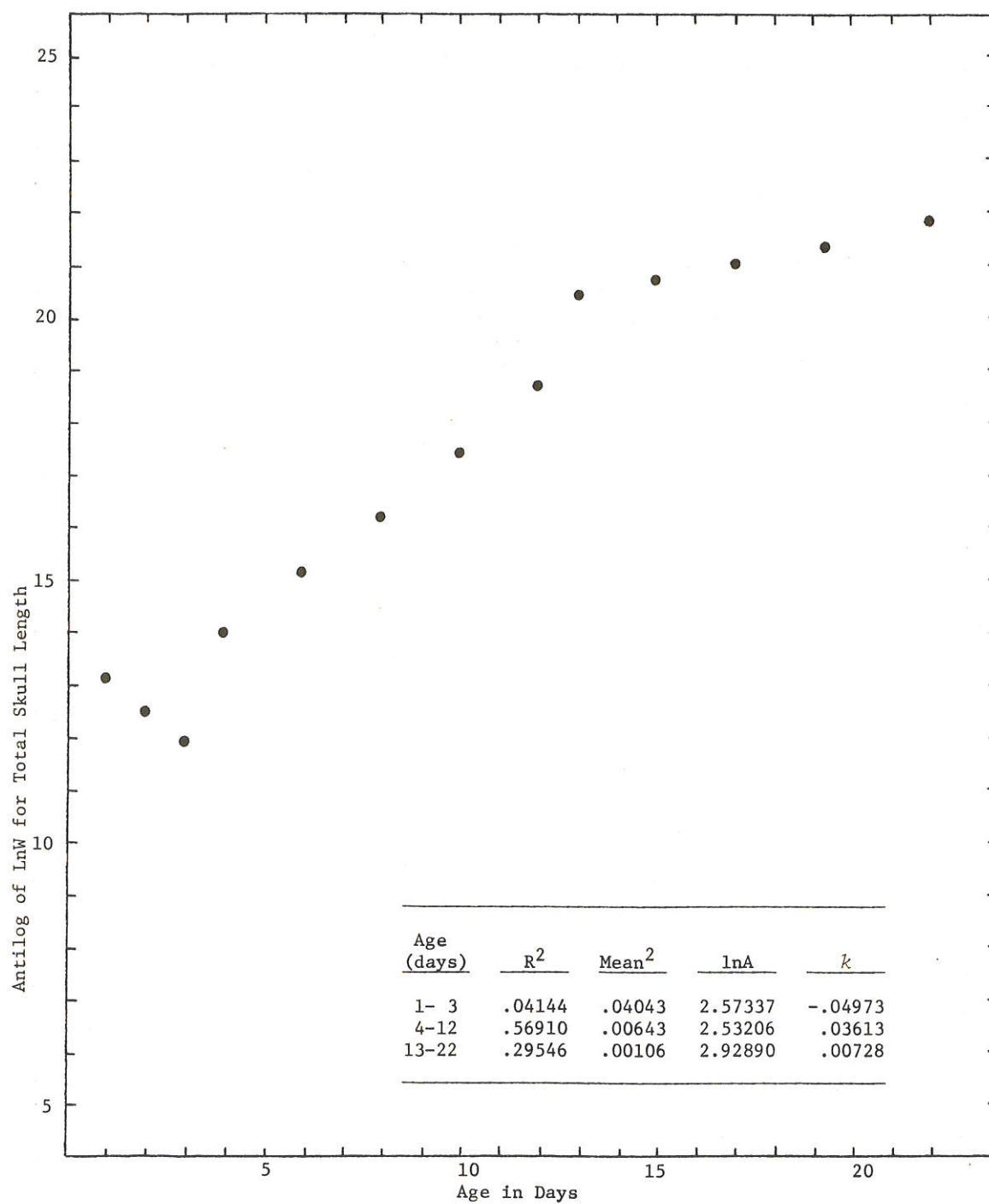


Figure 12. Growth curve for total skull length of *Peromyscus maniculatus*.

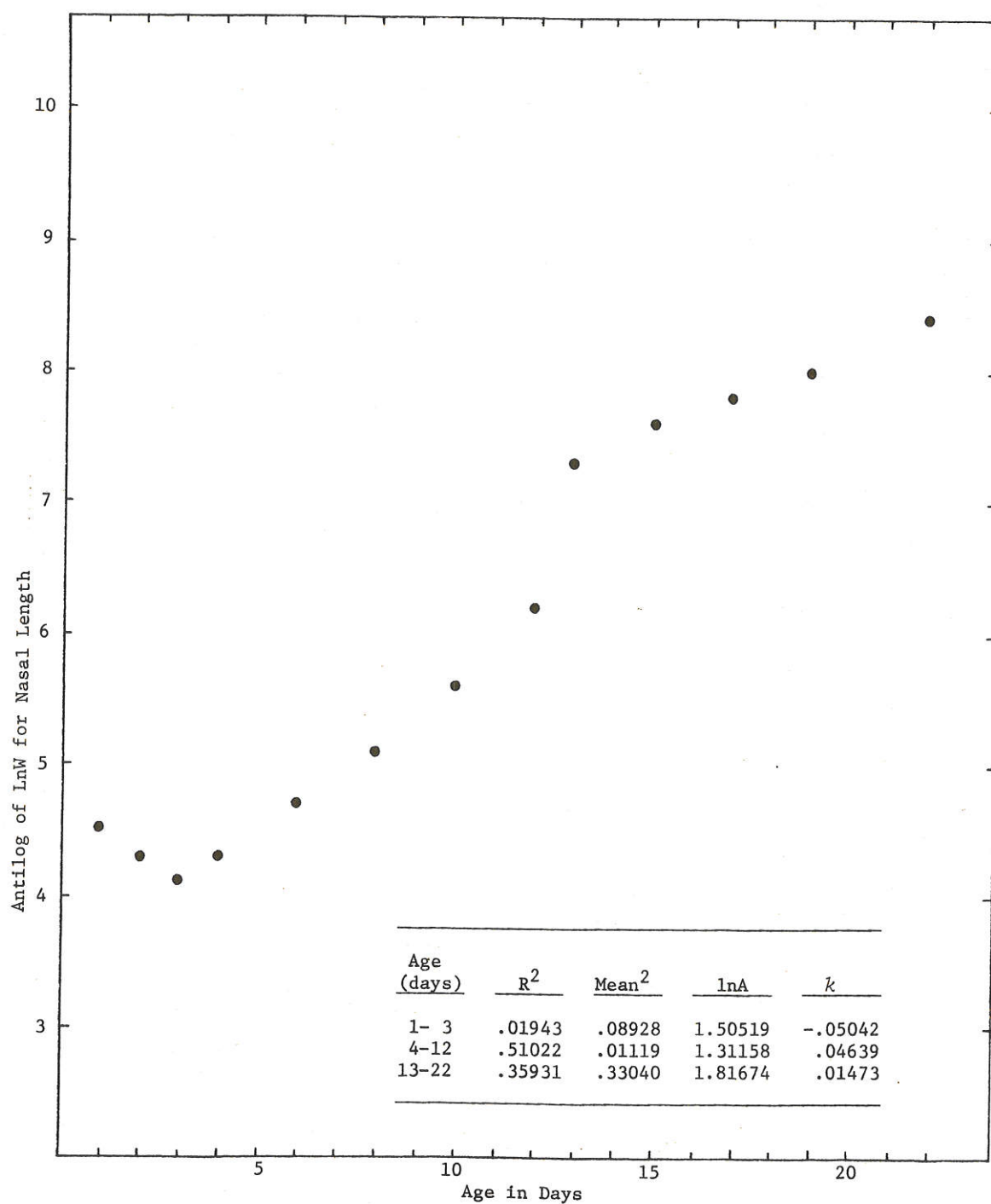


Figure 13. Growth curve of nasal length in *Peromyscus maniculatus*.

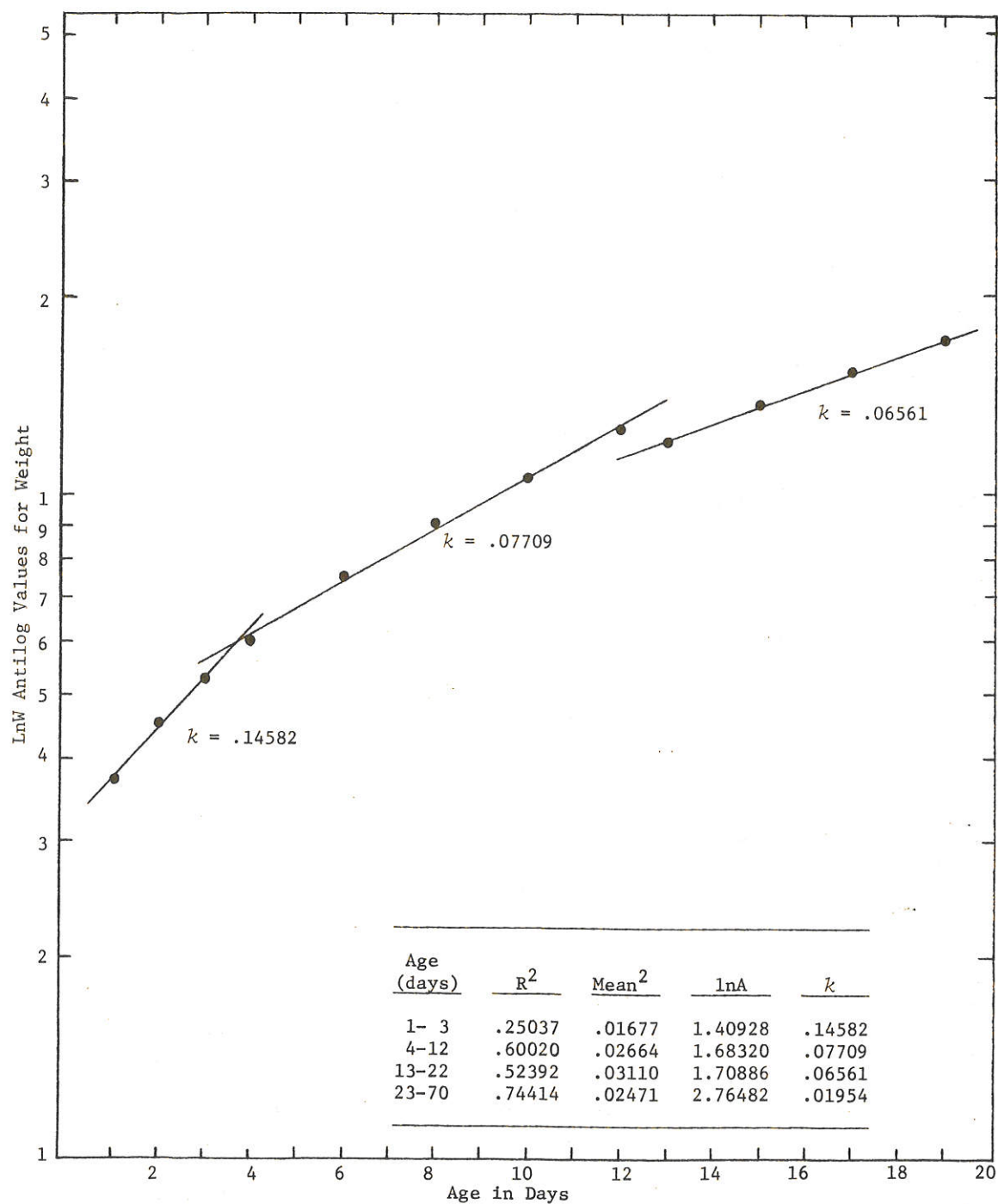


Figure 14. Instantaneous relative growth rates for *Dipodomys ordii* weight on semi-log plot to illustrate k (see Figure 1).

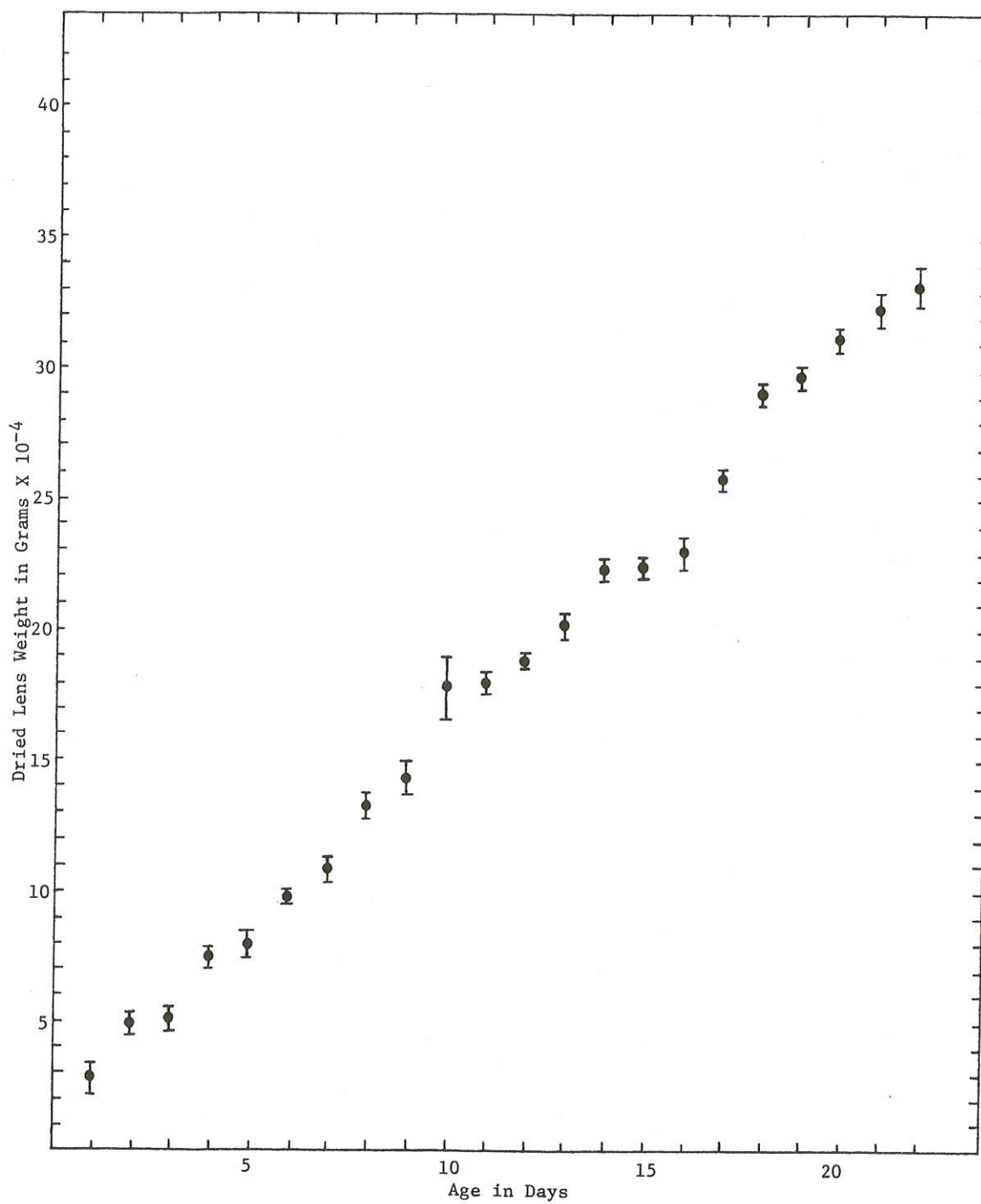


Figure 15. Mean dried eye lens weights with their respective standard errors ($p=.95$) for *Peromyscus maniculatus*.

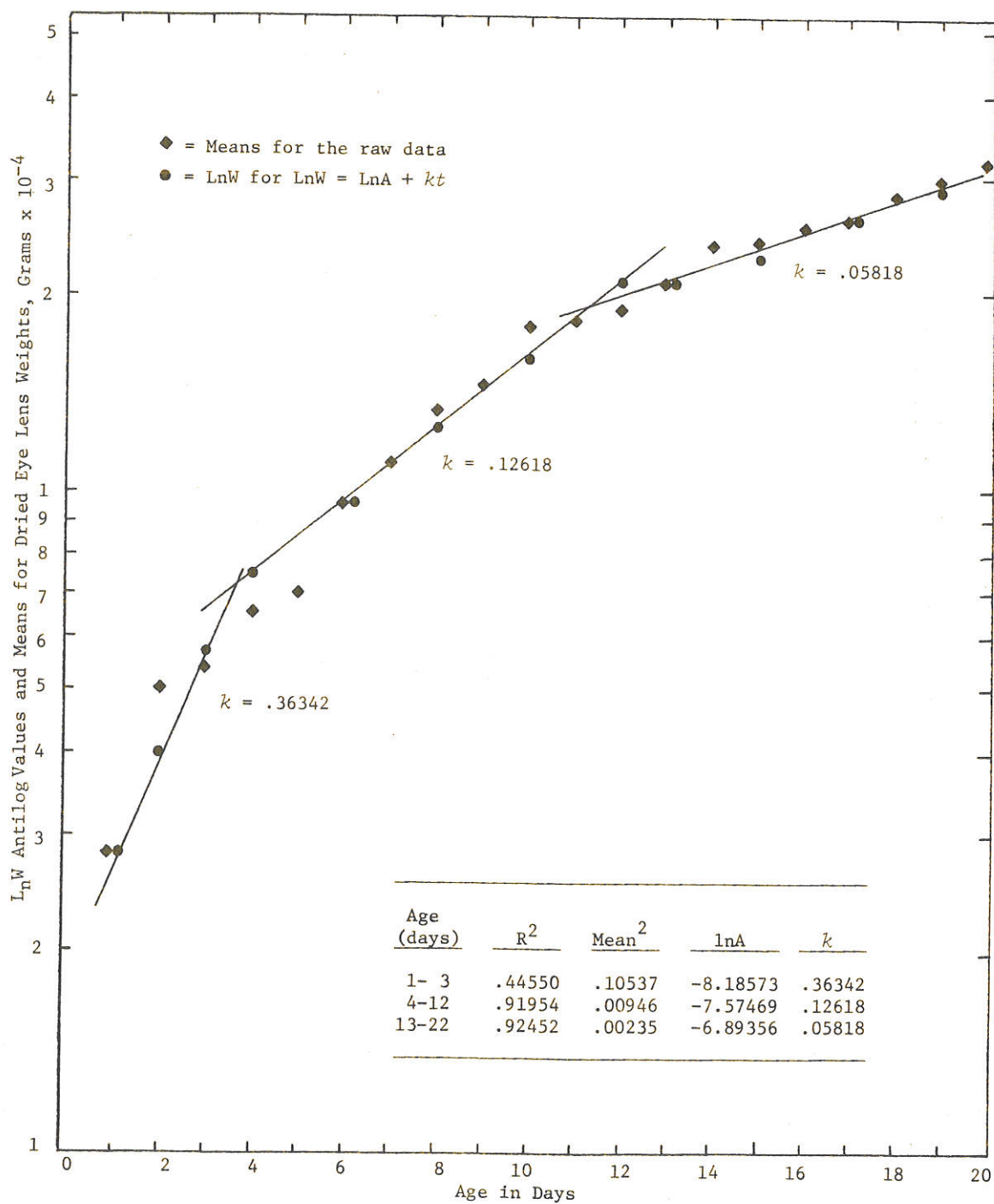


Figure 16. Instantaneous relative growth rates for *Peromyscus maniculatus* lens weights on plot to illustrate k (see Figures 11 and 15).

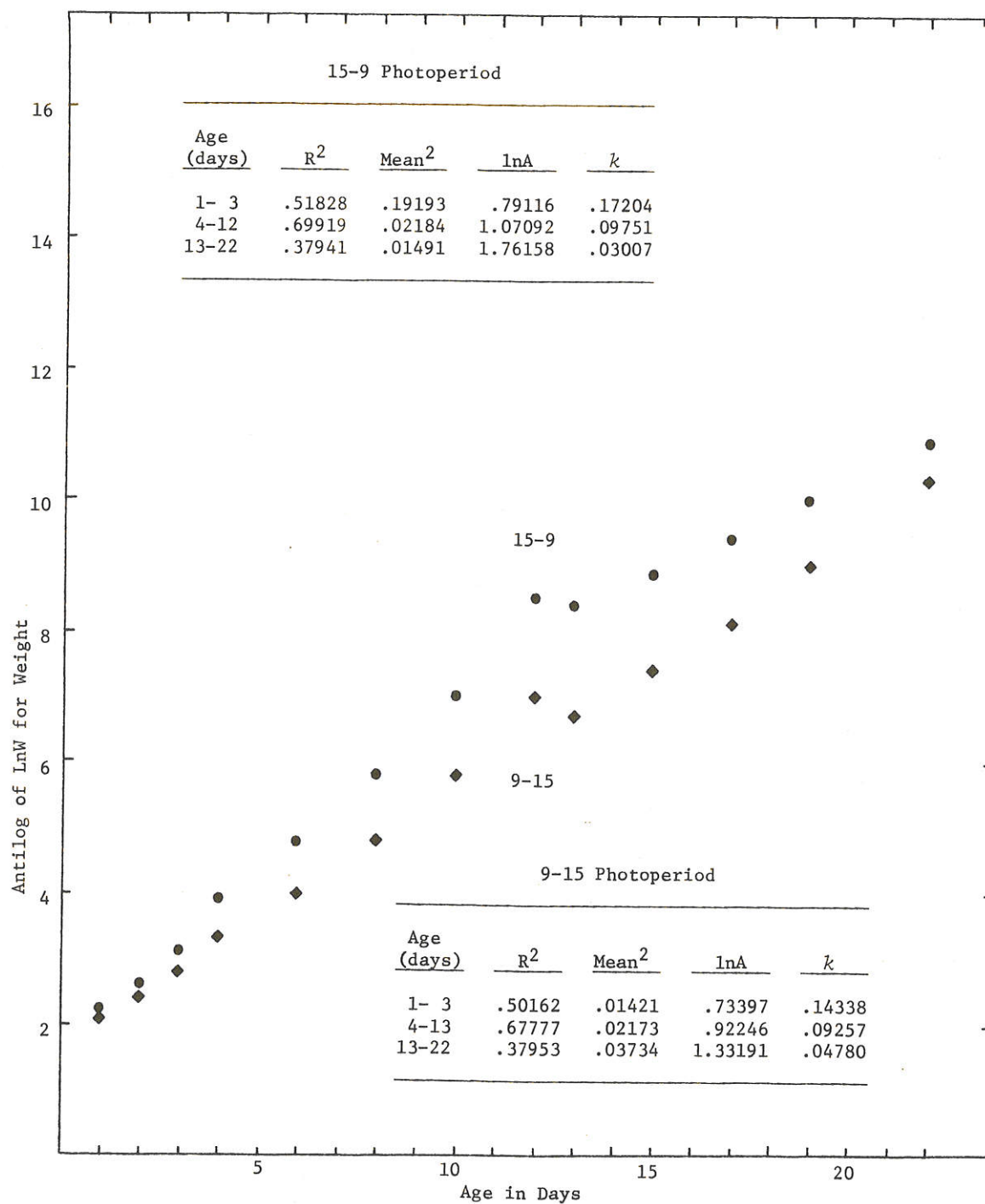


Figure 17. Growth curves for weight of *Peromyscus maniculatus* retained at photo-periods of 15 hr light and 9 hr dark (upper plot) and 9 hr light and 15 hr dark (lower plot).

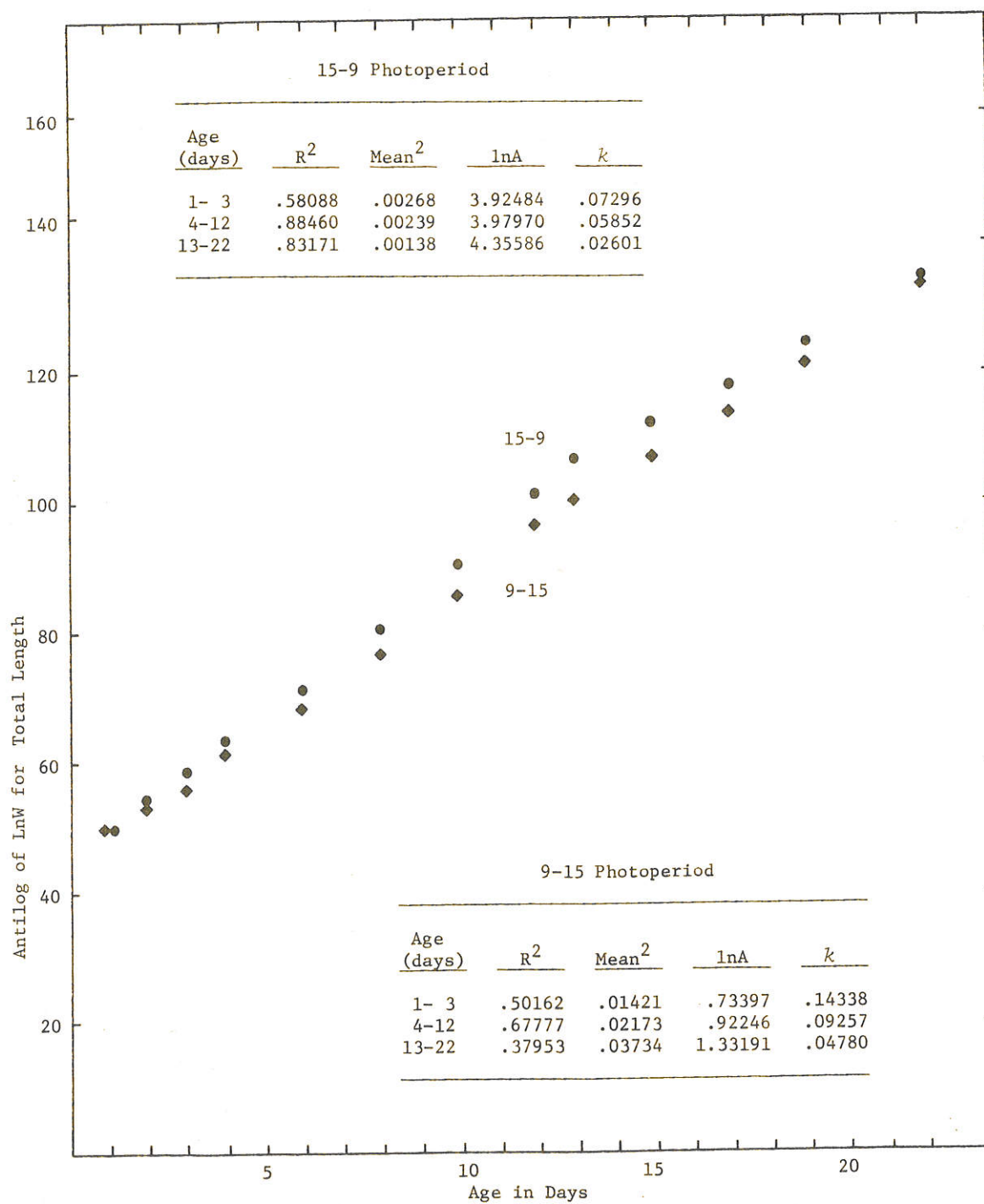


Figure 18. Growth curves for total length of *Peromyscus maniculatus* retained at photoperiods of 15 hr light and 9 hr dark (upper plot) and 9 hr light and 15 hr dark (lower plot).

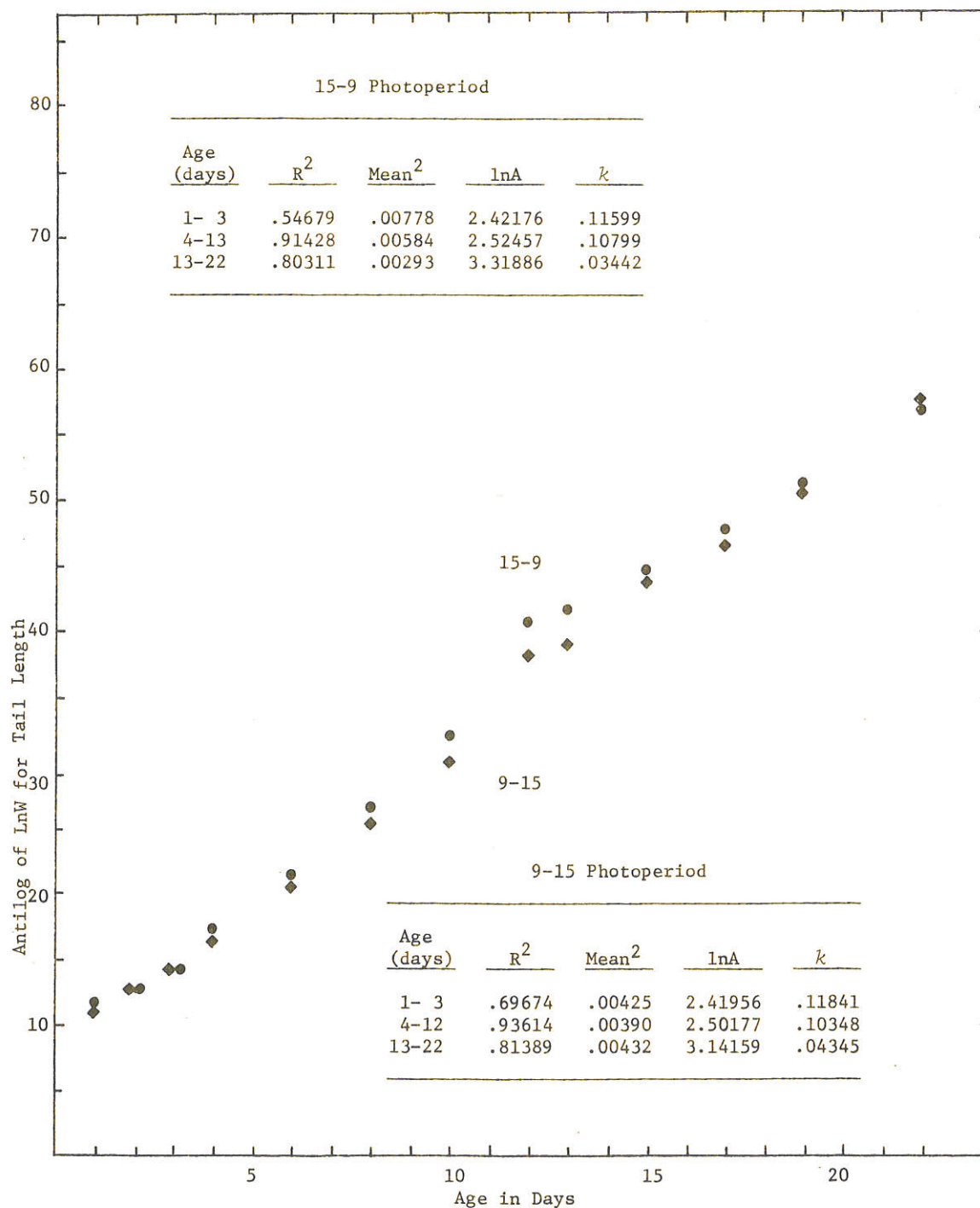


Figure 19. Growth curves for tail length of *Peromyscus maniculatus* retained at photo-periods of 15 hr light and 9 hr dark (upper plot) and 9 hr light and 15 hr dark (lower plot).

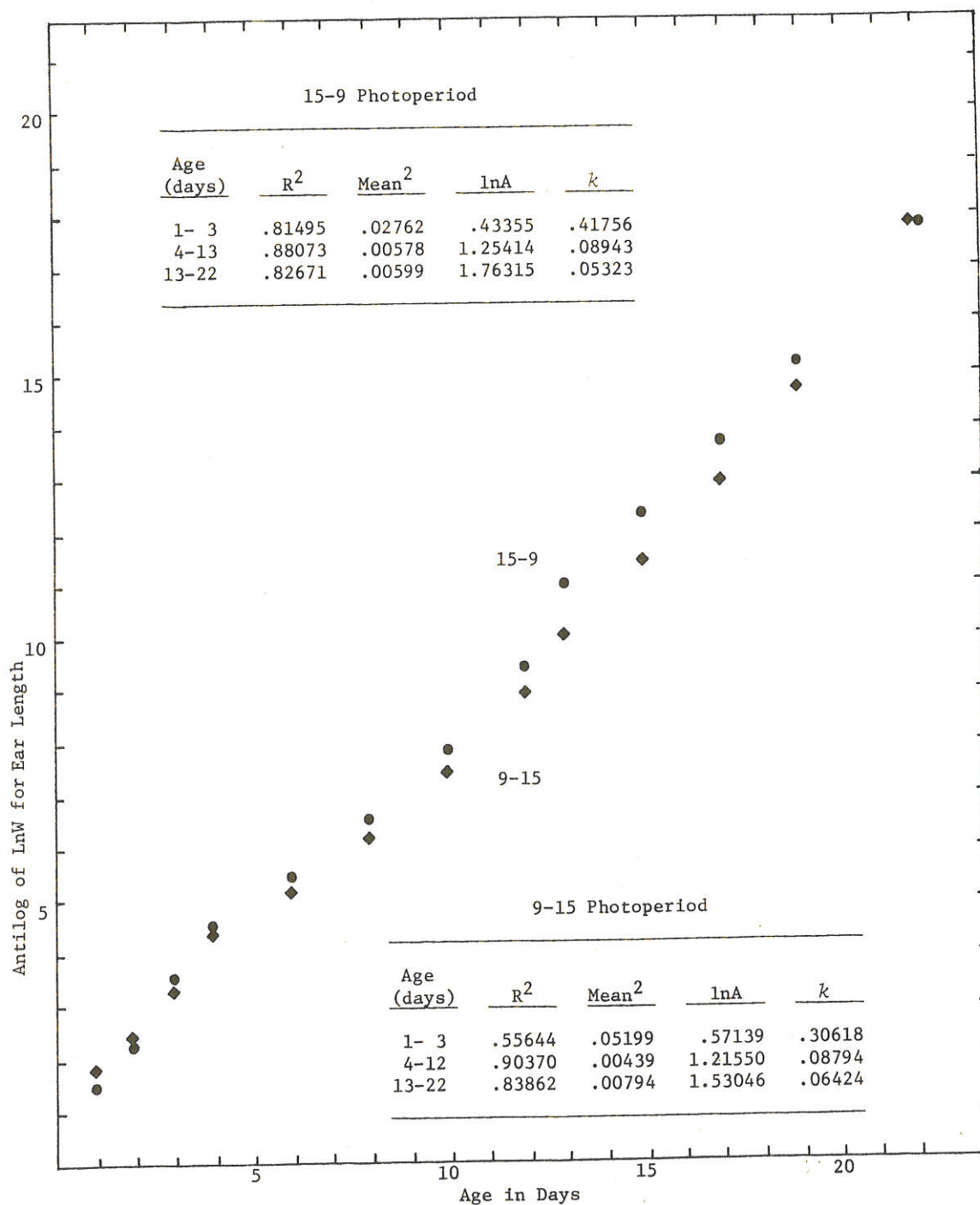


Figure 20. Growth curves for ear length of *Peromyscus maniculatus* retained at photo-periods of 15 hr light and 9 hr dark (upper plot) and 9 hr light and 15 hr dark (lower plot).

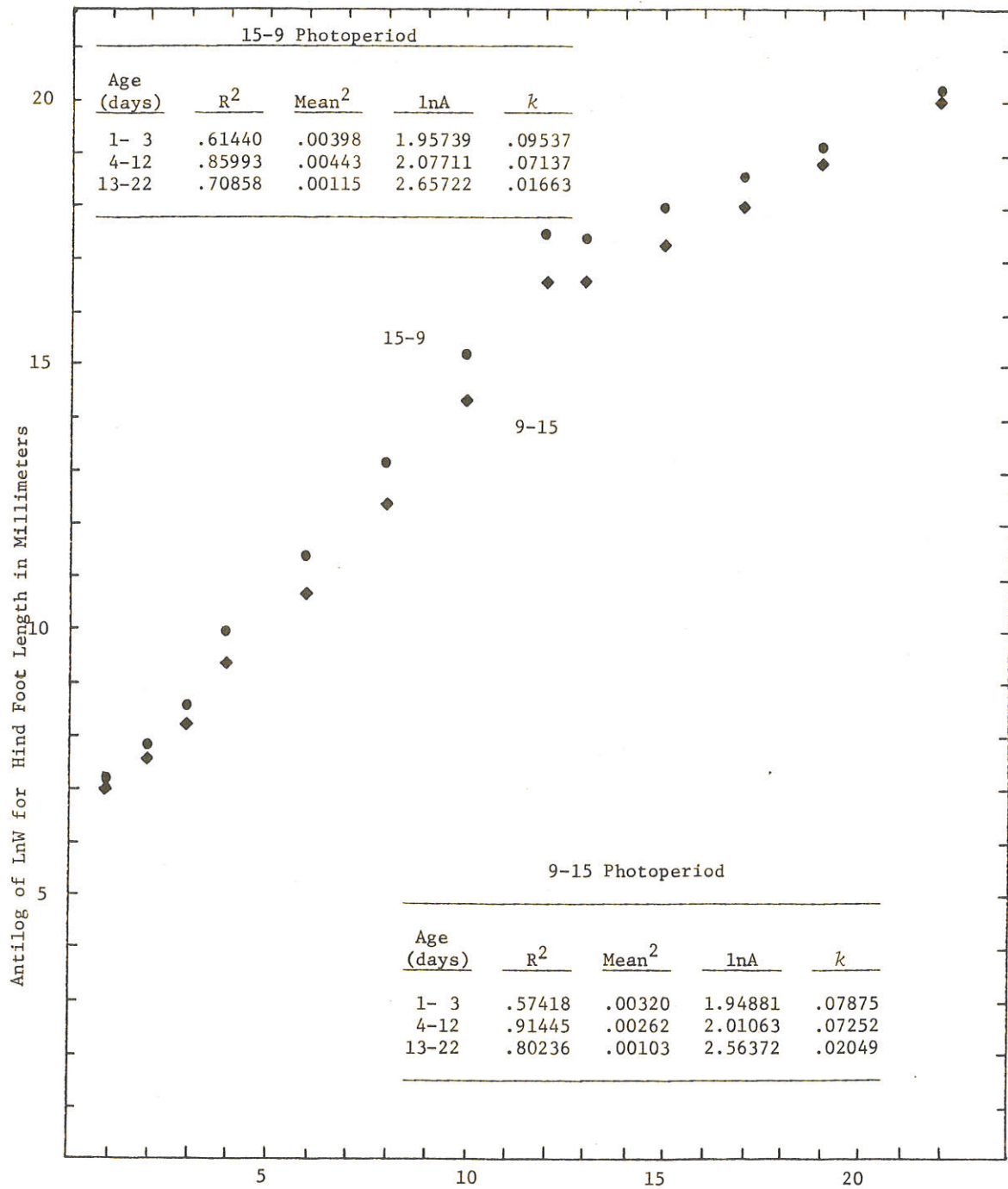


Figure 21. Growth curves for hind foot of *Peromyscus maniculatus* retained at photo-periods of 15 hr light and 9 hr dark (upper plot) and 9 hr light and 15 hr dark (lower plot).

Birth and death rates

Results of the rearing experiments for *P. maniculatus* and *D. ordii* in the laboratory are presented in Tables 2 and 3, respectively. There appears to be a reduction in litter size as the number of litters increases (Table 2), but this requires larger sample sizes to confirm. Field data cover a rather short time span; thus, they are yet sparse and analyses will require more collection replications (Tables 4 and 5).

Table 2. Mean number of young *Peromyscus maniculatus* born in the laboratory per successive litter

Litter Number													
	1	2	3	4	5	6	7	8	9	10	11	12	Total
*Litters Sexed	34	25	11	8	4	2	2	2	2	1	1	1	93
Mean Number Males	2.29	1.96	2.36	1.88	3.00	3.00	2.50	3.00	2.00	3.00	2.00	3.00	2.25
Mean Number Females	1.94	2.80	2.91	2.63	2.75	2.50	2.00	1.50	2.50	2.00	2.00	1.00	2.39
Total Litters	41	32	18	10	5	2	2	2	2	1	1	1	117
Mean Litter Size	4.22	5.00	4.78	4.20	5.60	5.50	4.50	4.50	4.50	5.00	4.00	4.00	4.62

*All litters born were not sexed.

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Table 3. Mean number of young *Dipodomys ordii* born in the laboratory

	Lab Reared and Bred	Field Reared and Lab Bred
Total Litters	7.0	3.0
Mean Number Males	1.3	1.3
Mean Number Females	1.8	1.7
Mean Litter Size	3.1	3.0

Table 4. Enclosure data for *Peromyscus maniculatus*

Population										
Date	Introduced		Recaptures		Field Mortality		Nativity		Total Present	
	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀
May 1972	15	15	15	15	0	0	0	0	15	15 = 30
Sept. 1972	0	0	4*	1	11	14	4	7	7	8 = 15

* One male died in trap.

Table 5. Enclosure data for *Dipodomys ordii*

Population										
Date	Introduced		Recaptures		Field Mortality		Nativity		Total Present	
	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀
August 1971	28	21	28	21	0	0	0	0	28	21 = 49
May 1972	6	3	7*	4	21	17	0	0	11	5 = 16
August 1972	0	4	4**	4	7	1	0	1	3	9 = 12

* Four animals (two of each sex) died in traps May 1972.

* One male died in trap in August 1972.

DISCUSSION

Most of the growth data analyzed thus far are for animals grown under standard laboratory conditions for both *P. maniculatus* and *D. ordii*. Although all of the r values are significant at the 0.95 level, one must consider two items in their interpretations: (1) the size of n , which when too large reduces the usefulness of r , and (2) what percentage of the variation must be accounted for before the correlation is considered to be biologically sound, and k can be accepted as a reliable estimate of the instantaneous relative growth rate. When the curves are examined on Figures 1-13 and 17-21, the correlations seem rather precise within the prescribed time intervals; thus, one is inclined to be rather liberal in setting lower limits on R^2 . It was determined that $R^2 > 0.25$ should provide enough accountability to accept a correlation that is significant as well as k . This does not mean the k values for those analyses with $R^2 > 0.25$ are in error, it simply means the confidence is not as strong.

Perhaps the most interesting of all parameters measured, because of its implications in predicting population for biomass, is total body weight. There have been other attempts to correlate weight with age, but since many of them were concerned with predicting age, the results were not particularly satisfying. The present study is concerned more with the characterization of body weight increase *per se* and will attempt to age organisms with other parameters such as dried eye lens weight, which has $r = 0.9531$ when correlated with body weight. The k values for *D. ordii* weight should represent accurately the instantaneous relative growth rates for the four intervals from days 1-70 (Fig. 1), but it is likely that after 80 days, as the organisms reach adult size, k would be less reliable. The k values for *P. maniculatus* should be accurate for the three intervals from days 1-22 (Fig. 6), but beyond that they are questionable. The study has provided growth rates (weight) for these two species under standard laboratory conditions that should be considered representative for the time intervals prescribed, and generally includes the time when animals are actually growing. Following this period of active growth, variations in weight might be more a matter of responses to environmental stresses and changes rather than actual growth phenomena.

When environmental variables are altered, the effects seem to be reflected by shifts in k for *P. maniculatus*. If Figures 6 and 17 are contrasted, the k values appear as:

	<u>1-3 days</u>	<u>4-13 days</u>	<u>13-22 days</u>
15 hr light, 9 hr dark	.17204	.09751	.3007
12 hr light, 12 hr dark	.15828	.09159	.04137
9 hr light, 15 hr dark	.14338	.09257	.04780

Generally, it might be concluded that longer photoperiods will accelerate growth, but animals retained in shorter photoperiods while nursing will soon catch up after foraging begins. The precise reason for these early growth differences is not clear, although it might be as simple as the amount of time the female stays in the nest each day; thus, availing herself to the suckling young. If this reasoning is correct growth would be slower in the field whenever foraging time is increased. Whatever, it appears that their genetic limitations are met shortly after they are weaned and reach a trappable age. Similar kinds of results are evident for the other variables measured, such as total length (Fig. 7 and 18), tail length (Fig. 8 and 19), ear length (Fig. 9 and 20) and hind foot length (Fig. 10 and 21); although the differences are not usually as great as those for body weight.

Although data are also being gathered on the effects of varying food and temperature under laboratory conditions, they are not yet complete. It is likely that food will eventually turn out to be the most important, particularly when it is coupled with foraging time. To evaluate the effects of variations within the independent variables it will be necessary to refine estimates of k to smaller time intervals such as single days. In this regard, k becomes more sensitive and its daily responses to environmental changes can be determined. This should allow for better predictability and modelling.

Data from the field enclosures are as yet rather incomplete since there has not been enough time for repeated sampling and the kill-trapped animals have not yet been analyzed for reproductive activity and age. Once these data are obtained, the age structure in the enclosed population can be estimated. Once the ages of animals in the enclosures are known from birth, it will no longer be necessary to estimate age, but reproduction activity will continually be monitored to assess mortality from birth to their trappable age. Hopefully, this can be accomplished by counting placental scars and embryos. This procedure will provide both birth and death rates per age class under field conditions.

All of the above-mentioned procedures depend on reasonably accurate methods for determining age. It is hoped that the animals can be aged with one or more of the variables measured. Thus far, it appears that non-parametric analyses will provide this method and eye lenses are likely to provide the best data after the animal has reached three days of age. Regression analyses suggest a close correlation of eye lens weights and age up to 23 days, and curves beyond that point have been developed by Ecodynamics (1970) at Dugway, Utah.

One possible weakness of these analyses is an inability to assess k under field conditions. Originally, it was assumed that shifts in k under field conditions would

not differ significantly from those established in the laboratory, but preliminary analyses of data obtained while experimenting with independent variables (in this case, photoperiod) would suggest that the assumption may not be valid. The next year's work should provide data to clarify this point. It is still possible that variations in k may compensate for each other sufficiently to result in animals all being about the same size at age 22 -- shortly after they become trappable.

EXPECTATIONS

The work conducted during 1972 has been successful in accomplishing much toward completing the objectives of the 1971 progress report, and has pointed some directions that research efforts should take to essentially complete the original objectives of this study for *D. ordii* and *P. maniculatus*.

Although growth rates have been characterized for both species under standard laboratory conditions for age intervals of 1-3, 4-12, 13-22, and 23-70 days, k must now be determined on a daily basis for the comparative purposes needed to develop a predictive analyses. In addition, non-parametric methods of analyses are planned to facilitate age determinations from dried eye lens weights so that reproductive activity and preemergence mortality can be assessed.

Experimentation is planned to further determine the interactions of independent variables and growth (particularly temperature variations), and quantity and proximity of food to the nest as it related to foraging time. Effects of the independent variables will be assessed by comparing the k values.

Specimens that have been collected near the enclosures for the past two years plus those to be collected in May and August of 1973 will be measured according to the standard growth parameters established (except for body weight) in this study, and their age will be determined by using the dried eye lens weights.

Natality and growth studies will be continued under experimental laboratory conditions where environmental parameters, food and temperature, will be varied. Field-collected animals, in conjunction with the growth and age determinations, will be assessed for natality as well. Both number of embryos and placental scars will be used to determine probable litter size. These data will be used to determine probable reproductive activity for animals included in the enclosures.

Life table data will continue to be gathered, as the *D. ordii* enclosure will be monitored for 10 days in May and again in August to determine field mortality, natality, and longevity; and the *P. maniculatus* enclosure will be studied for 10 days in both May and September.

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A submodel using the data of the first three objectives will be generated to describe the demography of the two species and hopefully provide some predictive capability.

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1972 PROGRESS REPORT

DIETS, FOOD PREFERENCES AND REPRODUCTIVE
CYCLES OF SOME DESERT RODENTS

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Research Memorandum, RM 73-24

MAY 1973

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Report Volume 3
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ABSTRACT

This study considers the diets, seasonal food preferences, habitat selection, seasonal activity cycles, and reproductive cycles of *Perognathus amplus*, *P. penicillatus*, *P. baileyi*, *P. intermedius*, *Dipodomys merriami*, and *Peromyscus eremicus*.

The diets and food preferences were examined by a microscopic technique yielding relative frequencies of the dietary constituents. Cheek pouch contents of the heteromyids and stomach contents of all rodents indicate seasonal shifts in food usage. The rodents feed mainly on seeds, but some feed on insects during certain seasons.

Analysis of the plant communities involving line transects, permanent 1 sq. meter plots and soil samples (for seeds) were taken at the animal capture sites.

The activity (percent trapping success) of the rodents was determined, as well as the age structure of the populations and their reproductive condition. The parameters will indicate much about the population dynamics of the rodents as well as how they divide their resources.

The foods used frequently by the rodents, the availability of the food, relative density of seeds in the soil, phenology of major plants, activity of rodents, and age structure and reproductive condition of rodent populations are summarized and presented in graphic form.

INTRODUCTION

Knowledge of the diets and food preferences of a rodent community is essential to an understanding of the ecological and energetic relationships of that community. The purpose of this study was to identify the diets of five desert rodent species and relate the diets to reproduction of the rodents and to food resources in the desert. Many of the dynamic aspects of the desert are dependent on the timing of seed production by annuals. The seeds provide a major portion of the diets of the rodents, as well as much of the new seasonal, above ground, vegetational biomass. It is hoped to establish the relationships between the phenology of desert plants, seed production, rodent reproduction, and rodent diets and preferences. This should provide a base from which to move into the study of other aspects of desert ecology, such as the use of seeds by birds and insects, and the impact of rodents on seasonal production of vegetation.

OBJECTIVES

1. To measure reproductive cycles of six species of desert rodents (*Perognathus amplus*, *P. intermedius*, *P. penicillatus*, *P. baileyi*, *Dipodomys merriami*, and *Peromyscus eremicus*) as functions of the weather and of phenology and productivity of vegetation at the Silverbell Site.
2. To determine seasonal activity patterns of desert rodents.
3. To measure phenology, standing crop, seed utilization, and composition of the vegetation at regular intervals throughout the year.
4. To measure the species composition of the diets of the five rodent species.
5. To relate dietary composition to the available food base and to determine the degree to which availability and preference determine foods consumed.
6. To calculate preference indices for the dietary components of each of the five mammalian species.

METHODS

Since June 1970, the principal investigators and the research assistants have spent a total of 684 man-days in the field. From June through August, semi-monthly samples of mammals were taken; monthly samples were taken during the winter and spring. When possible, a minimum of 50 individuals of each species of rodent under study were being taken during each sampling period.

Collection of phenological data (DSCODES A3UBB01 and A3UBB03)

Phenological data can be valuable in studying seasonal relationships between producers and consumers in any given biome. The bimodal pattern of rainfall in the Sonoran Desert (as defined by Shreve, 1951) is accompanied by a bimodal response of annuals present in this desert.

Early in the process study, it was determined that the rodents under investigation were primarily utilizing seeds collected from annual plants in the study area. Accordingly, phenological data were kept on all vegetation in the area to determine at what time(s) of the year peak production of fruits and seeds occurred, and when certain key plants set seed. Since green material was detected in some of the rodent stomachs, the dates that perennial species began to leaf out were also recorded.

The scheme used in gathering and organizing phenological data was adapted from Leith (1970). The vegetation was divided into four groups; herbs, shrubs, cacti, and trees. The observations made for each plant were: 1) vegetative stage; 2) production of culms; 3) flower and inflorescence buds; 4) flowering; 5) unripe seeds and fruits; 6) ripe seeds and dispersal; 7) yellowing of leaves; 8) leaves present; 9) plant not observed. The last two categories were added to Leith's scheme to include an important phenological event in the lives of perennial plants (8) and to include plants present in the study area but not always observed on a monthly basis (9).

Semi-monthly observations were made during the summers of 1970 and 1971 and monthly observations for the remainder of 1970-1971. Between 44-56 permanent vegetation plots were observed for each of the above time intervals, at which time field notes were made on the phenological conditions of the plant species observed. A number of "marker" plants were used to determine the status of that species' population in the study area. Also, the person recording vegetation at capture sites for the mammals noted significant phenological events for the plants present (e.g., *Larrea* flowering).

Data were then transferred from field notes and vegetation sheets to tables listing all the species present in the study area. Plants in flower were collected and preserved for the purpose of double checking the field data.

Analysis of permanent plots (DSCODE A3UBB03)

A series of 20 permanent meter-square plots were established in an area of the Sonoran Desert near Tucson, Arizona. These plots were approximately 30 m apart and marked with steel spikes and aluminum tags. Each plot was observed at least once a

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month. Observations were made on the number and kinds of annual plants present. Any change in the physical appearance of the plot (e.g., new ant hill) was also noted. The phenological status of each species of annual plant was recorded according to the method of Leith (1970).

Data from field notes were transferred to coding forms provided by the International Biological Program. Printouts of data received included the sample date, plot number, habitat, species taxon code, and absolute density of each species. These printouts were used to calculate seasonal differences in density and diversity of annual plants within the permanent plots.

Climatological data were furnished by the University of Arizona's Institute of Atmospheric Physics. Weather summaries utilized were those for Cortaro, Arizona (el. 610 m) and Silverbell, Arizona (el. 792 m). The permanent plots were located at an elevation of 701 m, approximately midway between the two weather stations. Climatograms (Tables 1 and 2) indicate the average monthly temperature (C) and monthly rainfall (mm).

Collection of seed data (DSCODE A3UBB02)

A major reason for collecting seed samples is that rodents under study are using seeds as main sources of food. They appear to be picking seeds from the soil long after the parent plants are dead. Ten random soil samples were collected semi-monthly during the summers of 1970 and 1971 and 10 samples were collected monthly throughout the rest of 1970 and 1971. Beginning in June of 1971, 10 samples of soil were collected at capture sites for each of the five species of rodents being studied. This technique will yield data on the quantity and quality of seeds available to the rodents.

Collection of soil samples

One-tenth m soil samples were collected to depths of 0-2, 2-4, 4-6 cm. The method consisted of randomly tossing a 1/10 m ring and collecting the soil enclosed by the ring. Each layer of soil was removed with a trowel and stored in a cloth bag for transportation to the laboratory. The date of collection, location of sample and name of collector were recorded for each sample. Data were also recorded on annuals present inside the sampling ring and the four nearest shrubs and/or trees to the sample sites.

Cain (1938) considers the number of samples (or plots) is adequate when a 10% increase in sample area, or in number of samples, yields an increase in number of species equal to 10% of the total. By calculating this percent increase it was determined that seven samples would be adequate. Ten samples per rodent species, per sampling period were taken.

Table 1. Monthly precipitation (centimeters) on rocky hills on creosote flats, recorded at Silverbell and Cortaro weather stations, respectively

	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Total
Rocky Hills													
1970-71	Trace	3.58	4.55	8.20	0.71	0.51	1.27	.08	1.50	Trace	.53	0	20.93
1971-72	Trace	2.29	15.88	7.32	7.98	0.28	2.90	3.78	2.03	1.27	0.91	0.74	45.38
Creosote Flats													
1970-71	0	1.78	3.20	8.81	0	0.41	1.14	1.80	2.24	0	1.19	0	20.57
1971-72	0	2.39	24.94	1.83	4.78	1.68	6.07	1.75	1.47	.97	0	1.70	47.58

Table 2. Mean monthly air temperatures and mean minimum air temperatures (C) on rocky hills and on creosote flats, recorded at Silverbell and Cortaro weather stations, respectively

		Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May
Rocky Hills													
1970-71	Avg.	30.0	31.0	---	26.8	20.5	---	---	---	13.9	12.1	18.2	---
	Avg. Min.	23.1	24.9	22.4	21.1	14.6	10.3	5.4	4.9	7.9	10.7	11.2	---
1971-72	Avg.	28.5	---	27.5	27.7	---	---	9.0	14.0	11.5	---	20.8	---
	Avg. Min.	21.9	---	21.2	21.5	---	---	4.0	8.8	5.0	---	13.5	---
Creosote Flats													
1970-71	Avg.	29.8	32.5	30.8	25.9	18.7	15.3	11.5	10.5	12.0	16.5	18.5	20.6
	Avg. Min.	20.4	24.8	23.4	17.6	9.1	5.4	1.8	.72	2.3	8.6	8.9	8.6
1971-72	Avg.	28.0	32.3	28.5	26.1	18.0	13.7	8.9	8.9	10.8	12.8	21.2	22.4
	Avg. Min.	17.8	24.6	21.6	17.5	8.5	4.8	0.9	-1.0	2.0	3.0	10.5	12.9

Extracting seeds from soil

Each soil sample was poured through a Tyler Soil Sieve with 0.495 mm openings and with 32 mesh to the inch. This size sieve was small enough to capture all of the smallest seeds except those of the Orchidaceae and the Solanaceae (personal communication, R. Hevly). The soil and seeds not passing through the sieve were returned to the original sample bags.

The soil-seed extracts were then put separately into a 2000 ml beaker and tap water was added until the material was thoroughly wetted. Ten ml of hydrochloric acid (10%) was added to this mixture in order to: 1) break up the caliche soil particles so that the seeds were released from the soil, and 2) bubble the seeds to the surface of the solution.

After bubbling had stopped, the remaining solution was poured through a 150 mm Buchner funnel fitted with Whatman filter paper (#1) on top of a 2000 ml suction flask. Air was pulled from the flask at a pressure of 20 psi with a vacuum pump. The water was then removed from the sample leaving a mixture of seeds and very fine soil on top of the filter paper. The filter paper was then air dried and placed in the original sample bag. The rocks and large soil particle mixture which was not dissolved by the acid was discarded, because examination of ten samples (Tables 3 and 4) showed that less than 15% of the seeds remained in this sediment. Table 4 also shows that 77% of the total seeds in the samples are removed by using the technique on only the 0.2 cm layer. Because of the time and effort necessary to extract the remaining seeds, efforts were concentrated on the upper (0-2 cm) layer.

Each sample was then re-sieved to remove the remaining fine soil. The seeds were then placed on a piece of graph paper and examined at magnification X10 with a binocular microscope. The seeds were separated into groups by genera, counted, and the number of each genus recorded on separate data sheets. Both known and unknown seeds were glued to a paper reference slide for identification or verification.

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Table 3. Total number of seeds recovered from 10 soil samples at three depths (July, 1970)

Depth	Rec. ^{*1}	Rem. [*]	Rec. ²	Rem.	Rec. ³	Rem.	Rec. ⁴	Rem.	Rec. ⁵	Rem.
0-2 cm	310	0	466	225	175	0	175	0	249	17
3-4 cm	30	0	8	0	0	0	11	0	18	0
5-6 cm	8	0	0	0	27	2	3	0	5	0
Totals	348	0	474	225	202	2	189	0	272	17
	6		7		8		9		10	
0-2 cm	233	0	64	5	37	0	437	97	145	73
3-4 cm	12	2	11	0	9	1	76	0	16	0
5-6 cm	2	0	7	0	2	0	4	0	3	0
Totals	247	2	82	5	48	1	517	97	164	73

* Rec. = Recovered, Rem. = Remained

Table 4. Seed distribution and recovery methods for seeds recovered from 10 soil samples (July, 1970)

1. Total number of seeds recovered = 2960
2. Number of seeds recovered by flotation = 2537
3. Percent of seeds recovered by flotation = 85.7%
4. Total number of seeds in top 0-2 cm layer = 2708
5. Percent of seeds in top 0-2 cm by flotation = 91%
6. Number of seeds recovered from top 0-2 cm by flotation = 2291
7. Percent of all seeds recovered by flotation in top 0-2 cm layer = 77.3%

Methods of sampling vegetation at capture sites

At most of the rodent capture sites, the vegetation was sampled using the line-intercept method. A 20 ft. steel tape was placed on the ground with the 10 ft. mark directly over the capture site. Alternate 1 ft. areas were considered a sample area. Within that 1 ft. area, all of the plants that touched the line or were within 1 cm of the line were recorded. These data are being used to calculate the relative frequency, relative density and relative dominance for each species. In addition, all cacti, shrubs and trees that intercepted the line were recorded. These data will be converted into a percent cover value for each species of plant.

A series of 44 permanent plots have been established in the study area. These include 20 plots in the creosote bush (*Larrea divaricata*) flats, 12 plots along washes, and 12 in the rocky hills. Each plot is circular and is 1 m² in area.

Monthly sampling of vegetation in these plots provides information from which absolute frequency and absolute density values can be calculated.

Diets of mammals (DSCODE A3UVC01)

The diets of the rodents are being studied by microscopically examining the stomach contents of specimens. The contents of each stomach are washed and mixed thoroughly in warm water. One microscope slide is made of material from each stomach using Hertwig's clearing solution (Baumgartner and Martin, 1939), and preparations are partially dried in a drying oven at 60 C. Twenty systematically located fields under 100-power magnification are studied on each slide. Food items are identified on the basis of distinctive epidermal features, using, for comparison, series of reference slides of known plant material (Davis, 1959; Croker, 1959; Storr, 1961). Each plant species present in each microscopic field is recorded and frequency percentages (the number of fields in which a plant species occurred out of 100 fields) are recorded for each specimen. Frequency percentages are then converted to particle density per field (using a Table by Fraker and Brischle, 1944). Relative dry weights of the food items are then accurately estimated by using the relative densities of the species (Sparks and Malechek, 1968). Similar procedures have been used in recent studies by Ward and Keith (1962).

Impact of rodents on seeds

In order to determine the number of seeds ingested per night by each rodent species, the relative density of those items over 1% for a two year period were used. Those items not over 1% were lumped into a miscellaneous category. Averages of those over 1% were extrapolated to the miscellaneous calculations. Relative density is proportional to dry weight of each seed species ingested (Sparks and Malechek, 1968), and was therefore multiplied by the calories per gram of each seed species. These products were summed and converted to relative figures. The relative figures (= relative contribution in calories by each seed species) were multiplied by the number of calories required by each rodent species per day, depending on the weight of the rodents. These requirements were determined from the literature or calculated on the basis of body weight using a metabolism formula ($\text{kcal/day} = 70 + 4w^{.75}$). The products were the relative contribution of absolute calories by each seed species. These were divided by the number of calories per seed to yield the number of seeds ingested per night. The calculations per seed were summed to give the the total number eaten per night. The calories per gram of the seeds species were determined by Dr. James MacMahon at Utah State University.

2.3.2.7.-10

The assumptions made to determine the number of seeds used by the rodents include:

1. The rodents were 90% metabolically efficient (Schreiber and Johnson, 1972)
2. Rodent densities are those given by Cockrum (Thames et al., 1972) for the Silverbell Site.
3. Metabolism while in torpor = one third of active metabolism.
4. The weight used to calculate the number of calories required by each rodent species were representative of the population, including young animals.
5. The percent of the year active by each rodent species represents trapping data for two years, and is assumed to reflect the relative amount of time active.

Reproductive cycles (DSCODE A3UBE21, A3UBE22)

Body weights, lengths, pelage coloration, and tooth wear were used as criteria for distinguishing between adult, subadult, or juvenile animals. Counts of embryos and of placental scars were used to determine litter size; the timing of litter, the presence of recent placental scars, and the conditions of the mammary gland provided indications of the number of litters per year. Careful measurements were made of the horn and body of the uterus and length and width of ovaries in the females. Females were determined to be reproductively active if they were pregnant, lactating or in estrous, as determined by the condition of the vaginal orifice. The standard measurements of the male include the length and width of the testis and the length of the caudal epididymis and seminal vesicle. The caudal epididymis and seminal vesicle were also periodically checked for the presence of sperm. Animals with sperm in the caudal epididymis or seminal vesicle were considered reproductively active. Scrotal testes, elongated seminal vesicle, and general coloration of the reproductive organs were also good indicators of reproductive condition.

RESULTS AND DISCUSSION

Since field work began in June 1970, 89,229 trap nights (a trap night equals one trap set for one night) have been logged and 5,409 rodents representing 13 species have been taken. The six most abundant rodents in the study area and the numbers of each that have been taken are listed in Table 5. Although most of the trapping was done in the desert flats dominated by creosote bush (*Larrea divaricata*), traps were also set in the rocky hills during each sampling period. The hills form an important and widespread habitat in the study area. Of the six predominant species listed in Table 3, only *P. amplus*, *P. penicillatus*, and *D. merriami* are common in the creosote bush flats.

Table 5. Species, age and sex composition of total animals trapped at the Silverbell Site from June 1970 to June 1972. Reproductive data were calculated for only the first six species DSCODE—A3UBE21, A3UBE22

	Total Animals	Percent Male	Adult	Subadult	Juvenile
<i>Dipodomys merriami</i>	1572	53.8	1443	116	13
<i>Perognathus amplus</i>	1410	49.6	1085	282	43
<i>Perognathus intermedius</i>	1212	47.0	1039	151	22
<i>Peromyscus eremicus</i>	534	52.2	419	98	17
<i>Perognathus baileyi</i>	438	45.5	376	57	5
<i>Perognathus penicillatus</i>	187	57.2	157	26	4
<i>Neotoma albigula</i>	31				
<i>Onychomys torridus</i>	6				
<i>Spermophilus tereticaudus</i>	6				
<i>Reithrodontomys megalotis</i>	6				
<i>Spermophilus harrisi</i>	4				
<i>Mus musculus</i>	2				
<i>Sigmodon hispidus</i>	1				

Sampling of vegetation (DSCODE A3UBB01 and A3UBB03)

Vegetative data from 3740 capture sites (91% of the total capture sites) and seed content data from 414 soil samples have been recorded. To facilitate analyses, the data are being transferred to coding sheets and placed on file at the computer center. Although relatively little vegetative data have been analyzed to date (one computer program is in operation), certain points merit comment.

Vegetation: The results for a year and a half of phenological data are shown in Table 6. The percentages were calculated by dividing the total number of plants with ripe seeds and dispersing seeds, by the total number of plants in the study area. Note that there is a different "n" number for each set of plants.

Table 6. Percent of herb species (n=66), shrub species (n=23), cacti (n=11), and tree species (n=5) with ripe and dispersing seeds over an 18-month period

Month	Herbs (% of plants)	Shrubs (% of plants)	Cacti (% of plants)	Trees (% of plants)
	% of plants with ripe and dispersing seeds			
June 1970	20	20	50	60
July 1970	20	22	50	60
August 1970	20	22	30	20
September 1970	10	10	40	20
October 1970	30	10	30	20

Continued

Table 6. Continued

Month	Herbs	Shrubs	Cacti	Trees
	(% of plants)	(% of plants)	(% of plants)	(% of plants)
% of plants with ripe and dispersing seeds				
November 1970	30	10	20	20
December 1970	12	0	20	20
January 1971	4	0	20	0
February 1971	0	0	20	0
March 1971	0	0	0	0
April 1971	0	0	0	0
May 1971	0	0	0	0
June 1971	0	5	10	0
July 1971	0	10	20	20
August 1971	0	10	0	20
September 1971	20	20	10	20
October 1971	30	40	30	20
November 1971	30	30	30	40
December 1971	20	10	30	40

When the study was initiated in July of 1970, the density and diversity of the annual vegetation was comparatively high. Fifteen species were recorded, with three species averaging 90 or more plants per sq. m (Table 7). In October, after the summer rains had occurred, eleven species were observed with only one plant (*Plantago insularis*) having an average density of 90 or more. By March of 1971, after an interval of extreme dryness, the diversity had dropped to seven species, and only *Plantago* had an average density of 25 plants per sq. m.

During the second year of the study, maximum diversity in the plots was recorded in December, 1971. Nine species were found, but only two (*Plantago* and *Bouteloua aristidoides*) had densities above six plants per sq. m (Table 8). Maximum diversity was also found in February, 1972, when nine species were identified and four plants had average densities of two or more plants per sq. m. Minimum diversity and density occurred in June of each year which approximates the driest part of the year in the Sonoran Desert.

As indicated in Tables 1 and 2, 1970-1971 was a comparatively "dry" year in the study area. The summer rains ended abruptly in September of 1971. Rain gauges at the site did not record any rainfall from December 18, 1970, until July 27, 1971. Thus, summer rains occurred during 1970, but winter rains did not fall on this part of the desert during 1971.

In contrast, 1971-1972 was a comparatively "wet" year. Summer rains began in July, reached their highest levels in August, and leveled off in September. However, measurable rainfall did continue through December, 1971. No appreciable difference was noted in average temperatures for the two weather stations over the period of observation.

Table 7. Permanent plots (DSCODE A3UBB03)

Average Density/10m ² of Annual Plants 1970-1971											
	J	July	A	S	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr. May
<i>Festuca octoflora</i>	109.0				.9	5.9	4.0	.2	.8	.2	
<i>Plantago insularis</i>	314.8				97.9	66.7	53.1	62.7	38.3	19.4	13.4 25.4
<i>Pectocarya platycarpa</i>	94.2					.2	1.0	.8	2.2	3.2	1.2 1.4
<i>Lepidium medium</i>	2.1				.1	.1	.5	.2	.4	.1	.2
<i>Plagiobothrys arizonicus</i>	3.4					.2	.3	.3	.1	.1	.1
<i>Lesquerella gordonii</i>	.8					.1					
<i>Chaenactis stevioides</i>	.2										
<i>Eriophyllum lanosum</i>	8.9										
<i>Bouteloua aristidoides</i>	.9				5.6	.3	4.0	4.7	4.6	2.2	2.2 1.2
<i>Cryptantha micrantha</i>	1.9				.2			.1	.1		.1
<i>Thelypodium lasiophyllum</i>	3.7					.5	.2	.4	.3	.3	.2 .2
<i>Eriastrum diffusum</i>	1.7										
<i>Erodium cicutarium</i>	14.8										
<i>Chorizanthe rigida</i>	.2				.1		.1				
<i>Allionia incarnata</i>	.1				2.9	1.0	1.0	.4	.2	.1	
<i>Senecio monoensis</i>					.2	.2	.2	.1			
<i>Senecio longilobus</i>					.2						
<i>Bouteloua barbata</i>					.3						
<i>Euphorbia albomarginata</i>					.7	.3	.5	.2	.5	.3	.2 .2
<i>Eriochloa spp.</i>							.1		.1		

Table 8. Permanent plots (DSCODE A3UBB03)

	Average Density/10m ² of Annual Plants											
	1971-1972											
	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May
<i>Festuca octoflora</i>						.2						
<i>Plantago insularis</i>	24.6	.1			1.5	10.2	6.6	15.3	14.5	6.2	8.8	8.1
<i>Pectocarya platycarpa</i>	.8	4.5							.8			
<i>Lesquerella gordonii</i>								.1	.1	.2		
<i>Bouteloua aristoides</i>	1.1	.4	5.0	6.1	7.6	7.3	7.1				5.9	5.9
<i>Senecio monoensis</i>			.1	.1	.1	.2	.1					
<i>Euphorbia albomarginata</i>	.4	.2	.5	.3	.5	.2	.3					
<i>Thelypodium lasiophyllum</i>	.2											
Grass spp. (unk.)		.7									2.0	
<i>Poa bigelovii</i>					.1	.1	.1					
<i>Bouteloua barbata</i>			.4	.9	.9	.5	.4					
<i>Erodium cicutarium</i>					.7	3.0	2.9	6.9	6.9	2.6	1.9	1.1
<i>Tridens pulchellus</i>							.1	.1	.1			
<i>Tidestromia</i> sp.							.1					
<i>Plagiobothrys arizonicus</i>									.1			
<i>Lotus</i> spp.									2.7	.1		
<i>Monoptilon bellioides</i>									.1			

Seeds in soil (DSCODE A3UBE02)

Tables 9-14 present data on seeds in the soil which are available to the rodents. Only those seeds species comprising more than 1% of the relative density of the samples are listed by species (MISCSP). Absolute densities are presented and relative densities for 1971-1972 for capture sites of each rodent species. A composite Table (9) is given for the first year of the study during which data were collected at random sites on the flats rather than at species-specific capture sites of rodents.

Calories per gram, seed weights, and calories per seed of the important seed species are presented in Table 15.

Comparisons of the seeds available to the rodent species are made in Tables 16 and 17.

Diets of rodents (DSCODE A3UVC01)

Preliminary data is available for the diets of live rodent species. These data are averaged for 1970-1971, 1971-1972, and 1970-1972, and are presented in Tables 18-22. Only those seed species making up more than 1% of the relative frequency of dietary items for the two-year period are included. Relative frequency figures are given for the stomach contents, relative densities for the cheek pouch contents. Percent usage figures indicate what percent of the rodents sampled used each species of seed.

Impact of rodents on seeds

The impact of the rodents on the seed reserves in terms of the number of seeds ingested is presented in Table 23.

Table 9. Densities of seeds in soil sample taken randomly in rodent habitat*

	Absolute Densities												Relative Density of Total		
	Jun	Jun	Jul (3)	Jul (10)	1971			1972					Total (83)	R.D.	
					Aug (1)	Aug	Sep	Oct (10)	Nov (10)	Dec (10)	Jan (10)	Feb (10)			Mar (10)
<i>Allonia</i>			113											113	2.7
<i>Eriochloa</i>		36	27											126	3.0
<i>Erodium</i>		4	65											209	5.0
<i>Festuca</i>		31	351											388	9.2
<i>Franseria</i>		15	54											73	1.7
<i>Larrea</i>		2	353											491	11.7
<i>Pectocarya</i>		125	1241											1759	41.8
<i>Plantago</i>		21	97											788	18.7
Miscellaneous species														262	6.2
Total		244	2448		2		470	225	231	170	181	125	113	4209	100.0
Average#2 seeds/m ²		813.3	2448		20		470	225	231	170	181	125	113	507.1	

* Numbers in parentheses are sample sizes (DSCODE A3UBB02).

Table 10. Densities of seeds in soil samples taken at capture sites of *Dipodomys merriami* *

	Absolute Densities												Relative Den- sity of Total					
	1971						1972						Total (167)	R.D.				
	May (19)	Jun (10)	Jun (14)	Jul (12)	Jul (9)	Aug (6)	Aug (11)	Sep (9)	Oct (9)	Nov (10)	Dec (10)	Jan (12)			Feb (8)	Mar (10)	Apr (8)	May (10)
<i>Allionia</i>	10	3	2	1	2		7		3	1	27	5	1	3	4	21	89	2.3
<i>Chaenactis</i>	22	11	5	2			40		2	2		4	2	4	1		95	2.5
<i>Erodium</i>	29	4	16	20	4	8	15		5	23	1	1		9	5	6	146	3.8
<i>Erigeron</i>	21	4	9	11		4	38	17		8	1	2			6	11	132	3.4
<i>Larrea</i>	21	53	22	55	5	1	16	14	2	8	13	62	15	84		32	403	10.5
Legume	2						4	34	11	4	21	10	1	19	4	7	107	2.8
<i>Pectocarya</i>	391	263	254	258	14	24	150	185	21	11	11	44	5	6	4	9	1650	42.9
<i>Plantago</i>	25	29	29	95	31	7		2	4	4	2	4	2	6		9	249	6.5
<i>Tridens</i>	25	5	9	1		1	3	36	7	30	260	74	184	6	41	2	685	17.8
Miscellaneous species	32	10	5	14	14	1	6	19	7	10	5	65	1	13	14	61	286	7.5
Total	578	382	350	457	70	46	279	307	62	101	341	271	211	150	79	158	3842	100.0
Average # seeds/m ²	304.2	382	250	380.8	77.8	76.7	253.6	341.1	69.9	101	341	225.8	263.8	150	98.8	158	230.1	

* Numbers in parentheses are sample sizes (DSCODE A3UBB02).

Table 11. Densities of seeds in soil samples taken at capture sites of *Pterognathus amplius**

	1971												Absolute densities				1972			Relative Density of Total	
	May (20)	Jun (10)	Jun (15)	Jul (13)	Jul (11)	Aug (12)	Aug (12)	Sep (11)	Oct (12)	Nov (11)	Dec (2)	Jan	Feb (4)	Mar (9)	Apr (11)	May (10)	Total (173)	R.D.			
<i>Allionia</i>	35			2	4			1	18	4			2			6	72	2.1			
<i>Carnegiea</i>	1									1				1		63	68	2.0			
<i>Chaenactis</i>	5	17	2	12	10	10	12	5	4	2	1			9	3	3	95	2.8			
<i>Erodium</i>	32	3	15	11	3	6	13		10	22				1	7	7	130	3.9			
<i>Franseria</i>	22	14	20	4	1	17	11	10	2	6	1			1	7	8	124	3.7			
<i>Larrea</i>	40	60	39	81	7	14	6	9	1	26			2	42	7	9	343	10.2			
<i>Legume</i>	2		1	1		2	1	7	27	4				23	19		96	2.9			
<i>Pectocarya</i>	222	173	381	123	89	33	73	118	5	11	4			105	50	13	1400	41.8			
<i>Plantago</i>	5	18	15	77	8	37	2						3	12		13	190	5.7			
<i>Tridens</i>	57	12	12			1	1	170	18	20	15		111	17	141	8	583	17.4			
Miscellaneous species	53	9	27	32	44	4	20	45	6				5	5	5	12	248	7.5			
Total	474	306	514	343	166	124	129	365	91	96	21		123	216	239	142	3349	100.0			
Average # seeds/m ²	273	306	342.6	263.8	150.9	103.3	107.5	331.8	75.8	62.7	105.0		307.5	240	217.3	142	193.6				

*Numbers in parentheses are sample sizes (DSCODE A3UBB02).

Table 12. Densities of seeds in soil samples taken at capture sites of *Perognathus batleyi*. *

	1971 Absolute Densities												Relative Density of Total					
	May (11)	Jun (10)	Jun (14)	Jul (12)	Jul (1)	Aug (4)	Aug (2)	Sep (5)	Oct (12)	Nov	Dec (9)	Jan (8)	Feb (7)	Mar (5)	Apr (2)	May (7)	Total (109)	R.D.
<i>Allionia</i>	2	10										9		34		2	57	2.1
<i>Boerhaavia</i>				2	1						24		3				30	1.1
<i>Erodium</i>		11	10	21				1	.1			2		1			47	1.8
<i>Euphorbia</i>				16		12	11	9	36		27	1	2	15	1	18	36	1.3
<i>Franseria</i>	13	16	33	14		2		6	1			9	5	3	2	12	194	7.4
<i>Larrea</i>	8	36	29	14								19	9	5	5	3	118	4.4
Legume									11			7	1	13		3	55	2.1
<i>Pectocarya</i>	138	262	481	347		31		26	37			4	1	36	5	11	1382	52.0
<i>Plantago</i>	3	30	14	86		7	1		7					3		5	160	6.0
<i>Tridens</i>	12		7					38	21			113	55	92	4	33	375	14.1
Miscellaneous species	30	13	28	5	4	2	1	32	17		7		7	3	52	1	202	7.7
Total	206	378	602	491	5	54	13	112	131		58	164	82	205	69	88	2656	100.0
Average # seeds/m ²	187.3	378	430	409.2	5	135	65	224	109.2		64.4	205	117.1	410	345	125.7	243.7	

* Numbers in parentheses are sample sizes (DSCODE A3UBB02):

Table 13. Densities of seeds in soil samples taken at capture sites of *Perognathus intermedium**

	1971												Absolute Densities					1972		Relative Densities of Total	
	May (6)	Jun (11)	Jun (10)	Jul (10)	Jul (10)	Aug (11)	Aug (10)	Sep (9)	Oct (12)	Nov (9)	Dec (10)	Jan (7)	Feb (11)	Mar (6)	Apr (10)	May (12)	Total (153)	R.D.			
<i>Allionia</i>	25	6				4	2	1		3	76	13	17	8	53	2	50	1.7			
<i>Boerhaavia</i>			4	13				2						1			179	6.2			
<i>Chaenactis</i>	5	8	4	5			1	6	1					1		5	36	1.3			
<i>Encelia</i>	10	2	7		6	6							5		4	5	36	1.3			
<i>Erodium</i>		4	1	3	1		1		5	8							33	1.1			
<i>Euphorbia</i>			2			8	2	39		13		17		5		4	91	3.1			
<i>Franseria</i>	7	8	6	26	28	16		7	2	69	14	54	8	7	7	29	288	10.0			
<i>Larrea</i>	27	46	7	17	6	6	1	6	1	65	3		3	14	5	5	208	7.2			
<i>Legume</i>					12		2	6	25	7	2	11	21	44	13	1	142	4.9			
<i>Lesquerella</i>	11				1	1			1					5		9	28	1.0			
<i>Pectocarya</i>	46	217	150	68	71	69	8	113		16	4	6	33	48	26	28	904	31.4			
<i>Plantago</i>	35	11	7	27	3	4	4		3	3						9	106	3.7			
<i>Tridens</i>	35					4	2	34	38	15	41	1	152	8	86	9	425	14.8			
Miscellaneous species	5	6	1	16	54	12	57	38	3	4	13	48	34	21	31	8	351	12.3			
Total	206	308	185	166	196	130	80	252	80	204	153	150	273	162	220	112	2877	100.0			
Average # seeds/m ²	343.3	280	185	166	196	118.2	80	280	66.7	226.7	153	214.3	248.2	270	220	93.3	188				

* Numbers in parentheses are sample sizes (DSCODE A3UBB02).

Table 14. Densities of seeds in soil samples taken at capture sites of *Peromyscus eremicus**

	1971 Absolute Densities												Relative Densities of Total					
	May (5)	Jun (2)	Jun (2)	Jul (6)	Jul (9)	Aug (2)	Aug (1)	Sep	Oct	Nov (7)	Dec (10)	Jan (9)	Feb (3)	Mar	Apr (12)	May	Total (68)	R.D.
<i>Boerhaavia</i>				2	7	1					153	33	3		63		262	17.5
<i>Carnegiea</i>	2			2	1	1				11	30				1		48	3.2
<i>Daucus</i>				79						1	11	10	4		15		120	8.0
<i>Encelia</i>	3	1	5		8	13				3					9		32	2.1
<i>Euphorbia</i>					1					2	5	117	1		10		142	9.5
<i>Franseria</i>	11	5		5	5	2	1			6	3	22	5		15		75	5.0
<i>Larrea</i>	4			3	5		2			1	1				7		23	1.5
<i>Pectocarya</i>	5	2	2	160	231	1				18	7	27	6		48		505	33.8
<i>Plantago</i>				22													22	1.5
<i>Tridens</i>	1	3								21	19	8	40		35		127	8.5
Miscellaneous species	6			26	17		1			22	22	23	12				137	9.4
Total	32	11	8	299	275	18	4			85	251	240	71		203		1493	100.0
Average # seeds/m ²	64	55	40	498.3	305.6	90	40			121.4	251	266.7	236.7		169.2		219.6	

* Numbers in parentheses are sample sizes (DSCODE A3UBB02).

Table 15. Calories per g, seed weights in mg, and calories per seed for those seed species important to the rodents*

Plant species	Calories/gram	Seed Wt. (mg)	Calories/seed
<i>Acacia constricta</i>	4,912 (1.4%)	19.05	444.29
<i>Boerhaavia</i> spp.	4,487 (2.5%)	1.70	7.61
<i>Crucifer</i>	4,589 (.02%)	1.76	8.08
<i>Eriochloa grandiflora</i>	5,026 (.82%)	1.36	6.84
<i>Erodium cicutarium</i>	5,505 (1.2%)	1.62	8.89
<i>Euphorbia</i> spp.	2,521 (.37%)	0.35	0.88
<i>Festuca octaflora</i>	4,132 (1.9%)	0.49	2.00
<i>Larrea divaricata</i>	4,966 (.34%)	2.29	11.35
<i>Lepidium medium</i>	4,479 (10.67%)	0.50	2.24
<i>Lesquerella gordonii</i>	5,297 (1.7%)	0.94	4.95
<i>Opuntia</i> spp.	4,652 (2.1%)	15.06	70.06
<i>Pectocarya platycarpa</i>	4,048 (.64%)	0.66	2.65
<i>Plantago insularis</i>	4,170 (2.2%)	0.93	3.84

*Numbers in parentheses are percent deviations

Table 16. Relative densities of seeds in the soil on flats at capture sites of *Dipodomys merriami* and *Perognathus amplus*—DSCODE A3UBB02

Seed species	1970-71	1971-72	
	Composite	<i>D. merriami</i>	<i>P. amplus</i>
<i>Erodium cicutarium</i>	5.0	3.8	3.9
<i>Franseria dumosa</i>	1.7	3.4	3.7
<i>Larrea divaricata</i>	11.7	10.5	10.2
<i>Pectocarya platycarpa</i>	41.8	42.9	41.8
<i>Plantago insularis</i>	18.7	6.5	5.7
<i>Tridens pulchellus</i>	0.0	17.8	17.4
Total	78.9	84.9	82.7

Table 17. Relative densities of seeds in the soil on hills at capture sites of *Perognathus intermedius* and *Perognathus baileyi*—DSCODE A3UBB02

Seed species	<i>P. intermedius</i>	<i>P. baileyi</i>
<i>Allionia incarnata</i>	1.7	2.1
<i>Boerhaavia</i> spp.	6.2	1.1
<i>Erodium cicutarium</i>	1.1	1.8
<i>Euphorbia</i> spp.	3.1	1.3
<i>Franseria dumosa</i>	10.0	7.4
<i>Larrea divaricata</i>	7.2	4.4
Legume	4.9	2.1
<i>Lesquerella gordonii</i>	1.0	0.0
<i>Pectocarya platycarpa</i>	31.4	52.0
<i>Plantago insularis</i>	3.7	6.0
<i>Tridens pulchellus</i>	14.8	14.1
Total	85.1	92.3

Table 18. First year, second year, and two-year summaries of stomach contents, cheek pouch contents, and percent usage of those items occurring at a frequency greater than 1% for *Dipodomys merriami* (DSCODE A3UVC01)

	Rf Stomach			Usage Stomach			Rd Pouches			Usage Pouches		
	70-71	71-72	70-72	70-71	71-72	70-72	70-71	71-72	70-72	70-71	71-72	70-72
<i>Acacia</i>	1.58	1.32	1.47	10.16	8.52	9.39	0.81	1.39	1.06	5.88	6.49	6.17
<i>Eriochloa</i>	1.88	3.72	2.62	9.45	11.76	10.53	1.06	7.14	3.65	0.89	5.07	2.85
<i>Erodium</i>	9.46	9.43	9.45	30.84	25.96	28.56	4.36	3.08	3.82	4.81	3.65	4.27
<i>Euphorbia</i>	6.85	12.88	9.29	24.95	29.61	27.13	0.06	7.16	4.01	2.26	2.84	3.22
<i>Festuca</i>	1.86	0.47	1.30	12.30	2.43	7.69	0.90	0.34	0.65	0.36	0.20	0.28
<i>Insect</i>	15.62	19.18	17.06	65.60	58.82	62.33	0.09		0.05	1.25		0.66
<i>Larrea</i>	8.58	9.68	9.02	46.70	39.55	43.35	27.88	0.57	24.04	38.68	0.20	35.48
<i>Lesquerella</i>	1.15	1.27	1.20	8.73	7.10	7.97	0.16	2.17	1.02	0.89	1.42	1.14
<i>Opuntia</i>	1.75	3.86	2.60	12.47	12.17	12.33	0.08	0.89	0.70	0.89	3.04	3.22
<i>Pectocarya</i>	26.35	12.51	20.76	73.44	31.44	53.80	10.88	1.30	6.80	14.26	2.43	8.73
<i>Plantago</i>	17.38	12.53	15.42	58.47	33.67	46.87	36.77	32.00	34.74	33.69	16.23	25.52
<i>Tridens</i>	1.10	1.62	1.31	10.87	6.29	8.73	2.84	1.00	2.06	1.07	0.81	0.95
<i>Crucifer</i>	0.60	2.70	1.45	6.95	10.55	8.63	1.67	7.12	3.99	9.80	11.16	10.44
Total	94.16	91.17	90.35				87.47	64.16	85.59			

Table 19. First year, second year, and two-year summaries of stomach contents, cheek pouch contents, and percent usage of those items occurring at a frequency greater than 1% for *Perognathus amplus*---DSCODE A3UVC01

	Rf Stomach			Usage Stomach			Rd Pouches			Usage Pouches		
	70-71	71-72	70-72	70-71	71-72	70-72	70-71	71-72	70-72	70-71	71-72	70-72
<i>Acacia</i>	(339)	(375)	(714)				(223)	(212)	(435)			
<i>Erodium</i>	2.01	1.90	1.96	10.62	10.67	10.64	1.70	1.22	1.44	2.65	4.53	3.64
<i>Euphorbia</i>	11.69	14.79	13.22	38.94	37.60	38.24	0.36	0.99	0.70	3.24	2.93	3.08
<i>Insect</i>	1.86	2.21	2.47	16.12	9.33	12.60	0.21	4.88	3.32	1.77	1.07	6.44
<i>Larrea</i>	2.68	4.66	3.66	21.24	20.27	20.73	0.10	0.28	0.20	0.88	0.53	0.70
	34.93	30.09	32.55	76.70	60.27	68.07	34.03	31.97	32.91	45.72	42.13	43.84
Miscellaneous												
species	0.71	1.32	1.01	9.44	8.80	9.10		0.02	0.01		0.27	0.14
<i>Opuntia</i>	1.14	2.44	1.78									
<i>Pectocarya</i>	22.74	15.10	18.97	7.08	8.27	7.70	0.01	0.07	0.04	0.29	0.80	0.56
<i>Plantago</i>	14.18	12.75	13.47	56.05	37.33	46.22	3.02	9.98	6.80	7.96	10.40	9.24
<i>Crucifer</i>	1.39	4.06	2.71	48.08	33.60	40.48	46.01	28.60	36.55	33.63	21.33	27.17
				13.86	17.33	15.69	5.97	7.31	6.70	11.80	12.27	12.04
Total	93.33	89.32	91.80				91.41	85.32	88.67			

Table 20. First year, second year, and two-year summaries of stomach contents, cheek pouch contents, and percent usage of those items occurring at a frequency greater than 1% for *Perognathus baileyi*—DSCODE A3UVC01

	Rf Stomach			Usage Stomach			Rd Pouches			Usage Pouches		
	70-71	71-72	70-72	70-71	71-72	70-72	70-71	71-72	70-72	70-71	71-72	70-72
<i>Acacia</i>	(186)	(144)	(330)				(89)	(55)	(144)			
<i>Boerhaavia</i>	3.57	3.22	3.42	13.98	12.50	13.33	4.40	5.56	4.88	3.23	5.57	4.24
<i>Eriochloa</i>	1.33	11.49	5.55	5.38	20.14	11.82	0.04	2.49	1.06		2.08	1.21
<i>Eriochloa</i>	0.99	2.49	1.61	3.76	4.17	3.94		23.36	9.72		2.08	0.91
<i>Eriochloa</i>	1.82	0.98	1.47	5.91	2.78	4.55						
<i>Festuca</i>	1.57	0.32	1.05	9.14	2.78	6.36	0.11		0.06	0.54		0.30
<i>Fouquieria</i>	2.09	7.54	4.36	6.99	12.50	9.39	0.67	1.71	1.10	1.08	2.78	1.82
<i>Insect</i>	9.41	8.27	8.93	37.63	22.92	31.21	0.15		0.09	1.61		0.91
<i>Larrea</i>	8.13	6.72	7.54	31.18	27.08	29.39	8.58	7.68	8.21	6.99	9.78	8.18
<i>Opuntia</i>	16.39	23.73	19.21	42.48	43.06	42.42		3.89	3.80		6.25	8.18
<i>Pectocarya</i>	25.51	23.82	21.47	61.83	50.00	47.88	24.52	44.86	29.70	23.12	13.89	16.97
<i>Plantago</i>	8.28	8.10	8.17	30.11		25.76	29.36		20.43	8.60		6.97
<i>Tridens</i>	11.30	0.30	6.60				8.06		4.71			
Total	90.39	96.99	89.38				75.89	89.55	83.76			

Table 21. First year, second year, and two-year summaries of stomach contents, cheek pouch contents, and percent usage of those items occurring at a frequency greater than 1% for *Perognathus intermedius*-----DSCODE A3UVC01

	Rf Stomach			Usage Stomach			Rd Pouches			Usage Pouches		
	70-71	71-72	70-72	70-71	71-72	70-72	70-71	71-72	70-72	70-71	71-72	70-72
<i>Acacia</i>	(371)	(412)	(783)				(113)	(129)	(242)			
<i>Boerhaavia</i>	3.58	3.12	3.35	14.8	12.14	13.41	1.51	2.53	2.08	2.2	4.61	3.45
<i>Cercidium</i>	0.47	11.54	6.00	1.9	21.60	12.26	.08	11.57	6.35		2.91	1.66
<i>Eriochloa</i>	2.68	0.87	1.77	7.6	3.40	5.36	0.26	0.47	0.38	1.4	1.46	1.40
<i>Erodium</i>	0.36	4.37	2.37	1.1	8.01	4.73	1.55	14.06	8.42	0.5	3.64	2.17
<i>Festuca</i>	0.56	1.87	1.22	4.0	4.61	4.34						
<i>Fouquieria</i>	10.29	2.54	6.41	26.4	6.55	15.84	18.21	4.88	8.21	2.4	1.70	1.15
<i>Insect</i>	1.99	2.43	2.21	5.4	4.13	4.73	5.30	0.06	5.07	1.1	0.49	1.40
<i>Larrea</i>	13.25	19.08	16.16	43.9	42.96	43.42			.03			0.26
	19.22	8.71	13.92	49.9	22.82	35.50	25.85	16.99	20.99	11.6	8.50	9.96
Miscellaneous species	1.53	1.14	1.34	19.9	11.41	15.45		0.16	.09		0.24	0.13
<i>Opuntia</i>	17.08	15.86	16.44	50.7	37.86	43.94		1.09	1.99		3.64	4.73
<i>Pectocarya</i>	14.00	7.70	10.68	41.2	20.39	43.81	25.49	3.86	19.52	5.1	2.67	10.22
<i>Tridens</i>	6.62	9.34	7.98	12.1	18.20	15.33	5.83	5.66	5.74	1.6	1.70	1.66
Total	91.63	88.57	89.85				84.08	61.33	78.87			

Table 22. First year, second year, and two-year summaries of stomach contents and percent usage of those items occurring at a frequency greater than 1% for *Peromyscus eremicus*—DSCODE A3UVC01

	Rf Stomach			Usage Stomach		
	70-71 (239)	71-72 (244)	70-72 (483)	70-71	71-72	70-72
<i>Acacia</i>	1.06	1.13	1.09	11.30	8.20	9.71
<i>Boerhaavia</i>	0.60	15.72	7.96	5.86	35.25	20.66
<i>Fouquieria</i>	5.07	2.73	4.06	13.39	7.38	10.54
Insect	56.80	59.70	58.29	94.56	96.31	95.45
<i>Larrea</i>	1.07	1.43	1.24	9.21	11.89	10.54
Miscellaneous species	2.00	1.29	1.65	21.76	12.30	16.94
<i>Opuntia</i>	16.41	10.14	13.32	51.05	29.92	40.29
<i>Pectocarya</i>	5.96	1.56	3.58	20.92	3.69	11.57
<i>Tridens</i>	3.37	0.81	2.12	11.30	6.97	9.09
Total	92.34	94.51	93.31			

Table 23. Seed usage by individuals and populations

Rodent Species (wt)	Seeds/Day	Seeds/Year Individual*	Seeds/Year Population**	Total For Sympatric Species/Year/Ha.
<i>Dipodomys merriami</i> (40g)	4053	1,411,470 (340 active 25 torpor)	8,609,967 @6.1/ha.	12,648,077/ha.
<i>Perognathus amplus</i> (11g)	1244	351,140 (241 active 124 torpor)	4,038,110 @11.5/ha.	
<i>Perognathus baileyi</i> (26g)	1824	590,304 (303 active 62 torpor)	944,486 @1.6/ha.	2,512,802/ha.
<i>Perognathus intermedius</i> (13g)	845	257,101 (274 active 91 torpor)	1,568,316 @4.5/ha.	

*Figures in parentheses indicate days active and in torpor

**Figures of density of rodents/ha taken from E. L. Cockrum in Thames et al., 1972.

ACTIVITY PATTERNS

Dipodomys merriami

Activity of *D. merriami* during the first year declined to its lowest level during July and August, the hottest part of the summer. A similar pattern was noted for *Dipodomys agilis* in southern California by MacMillen (1964). With the onset of summer rains and a second peak of reproduction, *D. merriami*'s activity reached its peak in November 1970. After the November peak, the activity leveled off, declining slightly in the spring, perhaps in response to the emergence of the other rodents (Table 24).

Table 24. Monthly trapping success for *Dipodomys merriami*—DSCODES A3UBE21,22

Month	Trap Nights	Animals Taken	% Success*
1970			
Jun	5741	145	2.5
Jul	5424	65	1.2
Aug	4590	49	1.0
Sep	2200	49	2.2
Oct	1900	97	5.1
Nov	1100	81	7.3
Dec	2400	76	3.2
1971			
Jan	2145	65	3.0
Feb	2125	79	3.7
Mar	1000	41	4.1
Apr	2225	61	2.7
May	2400	94	3.9
Jun	3670	93	2.5
Jul	4044	113	2.8
Aug	4325	91	2.1
Sep	1880	30	1.6
Oct**	1950	14	0.7
Nov	1000	29	2.9
Dec	990	49	4.9
1972			
Jan	875	52	5.9
Feb	840	68	8.1
Mar	900	63	7.0
Apr	998	12	1.2
May	600	56	9.3

* Trapping success equals $\frac{\text{number of animals trapped}}{\text{number of trap nights}}$.

** Rained all one night.

The activity of kangaroo rats during the second year (June 1971-June 1972) was significantly different from that of the first. The summer was not so hot (See Table 2) and consequently there was not a drastic decline in activity as in the previous summer. With the onset of autumn rains, more food was available, reproduction intensified, densities increased, and there was an increase in activity. There was a decline in activity again in the spring (April), repeating the trend of the previous year.

Dipodomys merriami was the largest rodent studied and apparently the best adapted to withstand the cooler winter months. A Spearman rank correlation co-efficient indicated a correlation at the .05 level between average body weight and surface inactivity for the winter months of the six species studied. Winter is generally considered a stressful time for rodents and many react through hibernation or torpor with consequent weight loss. This is not true for *D. merriami*, especially in years with adequate food supply. Activity of *D. merriami* (as indicated by trapping percentages) actually increased during the cooler months (Fig. 1), agreeing with the findings of Chew and Butterworth (1964) for this same species. As other rodents hibernated or reduced their activity, the kangaroo rat was able to expand its range and was trapped around the bases of the rocky hills previously occupied by pocket mice but not by kangaroo rats.

Perognathus baileyi

Perognathus baileyi was the fifth most abundant species in the area (Table 5). Its distribution was confined to an ecotonal area between the creosote flats and the rocky hills. Because of the limited habitat this species occupies, monthly trapping percentages may have been biased as ecotonal areas were not systematically trapped.

Although an accurate pattern of activity for *P. baileyi* is probably not represented by this data, seasonal trends can be noted (Fig. 2). The month in which the greatest number of animals were trapped (Table 25) was September 1970, immediately after heavy summer rains. Population densities were also high during October 1970. Population densities appeared fairly consistent throughout the remaining months of the first year with only a slight tapering off during winter months. Reynolds and Haskell (1949) also reported consistent numbers of Bailey pocket mice active during winter months. Apparently because of the large size of *P. baileyi*, it could withstand cold temperatures.

Table 25. Monthly trapping success for *Perognathus baileyi*—DSCODES A3UBE21,22

Month	Trap Nights	Animals Taken	% Success*
1970			
Jun	2766	51	1.8
Jul	2327	36	1.5
Aug	2230	34	1.5
Sep	1200	66	5.5
Oct	1300	53	4.1
Nov	2400	30	1.3
Dec	700	14	2.0
1971			
Jan	1045	2	0.2
Feb	1100	4	0.4
Mar	800	3	0.4
Apr	800	5	0.6
May	800	13	1.6
Jun	3720	12	0.3
Jul	2710	36	1.3
Aug	2634	16	0.6
Sep	1050	12	1.1
Oct	800	8	1.0
Nov	750	0	0
Dec	800	10	1.3
1972			
Jan	875	0	0
Feb	625	12	1.9
Mar	875	12	1.4
Apr	600	2	0.3
May	1000	7	0.7

* Trapping success equals $\frac{\text{number of animals trapped}}{\text{number of trap nights}}$.

The two months during the second year (November and January) in which no *P. baileyi* were trapped does not give evidence of dormancy (Fig. 2). Trapping in areas not inhabited by *P. baileyi* during these two months may be the explanation for lack of specimens. Aside from these two months, activity during the second year (Fig. 2) appeared stable as indicated by a consistent 1.1 trapping percentage. It is interesting and unusual that there were no increases in trapping percentages during the months of reproduction and when young animals augmented the population.

Perognathus intermedius

Activity in *P. intermedius* during the first year (Fig. 3) showed a response to lower winter temperatures. During three winter months (December, January, and February) in

the first year, no *P. intermedius* were trapped. A peak in activity was recorded in July 1970 following an intense reproductive period in the spring. This peak was characterized by a large number of postpartum females and percent young in the sample (Table 26). There was a gradual decrease of numbers of animals active for the two months prior to their winter's dormancy (October, November, 1970) and a gradual increase in activity during the spring following the dormant period (March, April, 1971).

Table 26. Monthly trapping success for *Perognathus intermedius*—DSCODES A3UBE21,22

Month	Trap Nights	Animals Taken	% Success
1970			
Jun	2766	187	6.4
Jul	2327	110	6.8
Aug	2230	136	4.7
Sep	1200	58	4.8
Oct	1300	32	2.5
Nov	2400	6	0.3
Dec	700	0	0
1971			
Jan	1045	0	0
Feb	1100	0	0
Mar	800	11	1.4
Apr	800	13	1.6
May	800	37	4.6
Jun	3720	102	2.7
Jul	2710	147	5.4
Aug	2634	57	2.2
Sep	1050	42	4.0
Oct	800	20	2.5
Nov	750	31	4.1
Dec	800	27	3.4
1972			
Jan	875	65	7.4
Feb	625	25	4.0
Mar	875	36	4.1
Apr	600	55	9.0
May	1000	15	1.5

* Trapping success equals $\frac{\text{number of animals trapped}}{\text{number of trap nights}}$.

Activity patterns in the two years of the study differed. In the second year there was no period in which no animals were taken (Table 26 and Fig.3). Temperatures were milder, rainfall plentiful and food more abundant during the second year; perhaps these conditions enabled *P. intermedius* to remain active all winter. April, 1972 was the month that yielded the highest trapping success of *P. intermedius* (9.0 %). This percentage is significant in that trapping percentages for the other five species were exceedingly low during this same month (Tables 1-4 and 6-7).

Although *P. intermedius* has not been reported to hibernate or become torpid during stressful environmental conditions, other species of *Perognathus* of approximately the same size become dormant during stressful periods. *Perognathus longimembris* and *P. formosus* are usually inactive above the ground for varying periods in the cooler autumn, winter and early spring (Chew and Butterworth, 1964; French et al., 1967). Some individuals of both species were found above ground during mild weather during these seasons, suggesting that these dormant pocket mice are sensitive to rapid temperature changes. Torpidity in *P. fallax* has been noted by MacMillen (1964) and discussed in more detail by Bartholomew and Cade (1957). Chew and Butterworth (1964) have evidence that hibernation in *P. longimembris* significantly enhanced its survival. Our data suggest that dormancy in *P. intermedius* occurs only in winter months when the food supply may be limited.

Peromyscus eremicus

Activity during the first year was remarkably consistent from month to month, with an overall trapping percentage around 1.2. No animals were trapped during September 1970, but in this month we did not trap in appropriate habitat for *P. eremicus*. The highest trapping success of the first year was 2.5% in June. In the following months, trapping percentages were lower but consistent (Fig. 4). This data contrasts with that of Lewis (1972) who trapped approximately 145 km to the north of our study site during 1967 and 1968.

Trapping during the second year revealed a striking contrast to the first year in the relative numbers of *P. eremicus* present (Fig.4). During the summer months, trapping percentages were low, presumably due to low population numbers as the result of prolonged adverse environmental conditions. After intense summer rains, however, trapping percentages increased almost linearly from 0.4% in October, 1971 to a peak of 10.2% in February of 1972. Following the peak in February, there was a drastic decline in trapping success, and by May, 1972 no cactus mice were trapped during 1,000 trap nights in a suitable habitat.

The tremendous increase in cactus mice during the second winter could be the result of a combination of two factors: 1) the reduction in surface activity of the sympatric *P. intermedius* (Fig. 3) thus reducing suppression through competition, and 2) addition of young to the population (78% of 34 females trapped in November and December were reproductive) (Fig. 5).

The apparent population crash in the spring of the second year may have been the result of limited food. The high numbers of *P. eremicus* might have further been affected by the emergence of *P. intermedius* from winter dormancy.

MacMillen (1965) reports estivation in *P. eremicus* under adverse environmental conditions. Likewise, Lewis (1972) attributes his summer months of decreased trapping success to estivation of *P. eremicus*, explaining that estivation in cactus mice might be a response to a combination of aridity and high ambient temperatures. Lindeborg (1952) and MacMillen (1964) have shown *P. eremicus* to be better adapted to xeric conditions than other *Peromyscus*.

Summer estivation did not appear to occur among the cactus mice in our study area (Table 27 and Fig. 4). There were decreased percentages of animals trapped during the summer of the second year even after the summer rains began. This was, however, probably indicative of decreased population densities rather than estivation, as the preceding months were particularly stressful in terms of paucity of new vegetation.

Table 27. Monthly trapping success for *Peromyscus eremicus*—DSCODES A3UBE21,22

Month	Trap Nights	Animals Taken	% Success*
1970			
Jun	2766	69	2.5
Jul	2327	33	1.4
Aug	2230	27	1.2
Sep**			
Oct	1300	23	1.8
Nov	2400	21	0.9
Dec	700	4	0.6
1971			
Jan	1045	6	0.6
Feb	1100	20	1.8
Mar	800	13	1.6
Apr	800	5	1.0
May	800	8	1.6
Jun	3720	3	0.1
Jul	2710	25	0.9
Aug	2634	10	0.4
Sep	1050	1	0.1
Oct	800	3	0.4
Nov	750	29	3.9
Dec	800	35	4.4

Continued

Table 27. Continued

Month	Trap Nights	Animals Taken	% Success*
1972			
Jan	875	54	6.2
Feb	625	64	10.2
Mar	875	59	6.7
Apr	600	22	3.7
May	1000	0	0

* Trapping success equals $\frac{\text{number of animals trapped}}{\text{number of trap nights}}$.

** Traps not set in appropriate habitat.

Peroznathus penicillatus

Peroznathus penicillatus was not abundant in our study area and was restricted to arroyos. Trapping procedures that involved only occasionally trapping the ranges of *P. penicillatus* accounted for their scarcity in the samples of certain months. Seasonal activity patterns, size variation, and breeding characteristics can be interpreted with some degree of confidence, however, even though our total sample size was low (Table 28).

Dormancy during winter is typical of *P. penicillatus*. Arnold (1942) found *P. penicillatus* to be inactive during several winter months. Reynolds and Haskell, (1949), likewise, failed to trap this species from December to February in southern Arizona and speculated that it was in hibernation. Hudson (1964) found that under laboratory conditions, *P. penicillatus* became torpid in winter. In our study, the above-ground activity of *P. penicillatus* was also reduced through the winter season (Fig. 6 and Table 28). In the first year there were two months (November and December, 1970) in which no *P. penicillatus* were trapped. Trapping during the second year yielded three months (January, March and April, 1971) when no animals were taken.

Trapping during the seasons other than the winter, showed similar patterns for the two years. Late spring and early summer appeared to be a time of increased activity. Surface activity of *P. penicillatus* declined during both of the summers, probably in response to hotter, drier conditions. Following summer rains, there was an increase in activity with September, 1970 yielding the highest percentage of animals trapped and October, 1971 being the most productive of fecund animals.

Table 28. Monthly trapping success for *Perognathus penicillatus*—DSCODES A3UBE21,22

Month	Trap Nights	Animals Taken	% Success*
1970			
Jun	2766	33	1.2
Jul	2327	7	0.3
Aug	2230	9	0.4
Sep	1200	18	1.5
Oct	1300	5	0.4
Nov	2400	0	0
Dec	700	0	0
1971			
Jan	1045	1	0.1
Feb	1100	1	0.1
Mar	800	1	0.1
Apr	800	1	0.1
May	800	11	1.4
Jun	3720	27	0.7
Jul	2710	19	0.7
Aug	2634	12	0.5
Sep	1050	15	1.0
Oct	800	13	1.6
Nov	750	2	0.3
Dec	800	2	0.3
1972			
Jan	875	0	0
Feb	625	1	0.2
Mar	875	0	0
Apr	600	0	0
May	1000	9	0.9

* Trapping success equals $\frac{\text{numbers of animals trapped}}{\text{number of trap nights}}$.

Perognathus amplus

Perognathus amplus is not equally active above ground at all seasons. Trapping percentages for *P. amplus* were at their highest level during June, 1970, the first month of the study (Fig. 7). The highest temperatures of the year (Fig. 7), recorded in July, were accompanied by a sharp decline in surface activity of *P. amplus*. This temporary reduction in surface activity by most of the individuals suggests that high ambient temperatures are stressful to small pocket mice and that periodic torpor is employed. There was an increase in activity again during the cooler and more humid period of late summer and fall. As temperatures dropped in the winter, so did the activity of *P. amplus*. The species suspended surface activity for a four-month period (December through March).

The activity of *P. amplus* during the second year (June 1971-June 1972) was significantly different from that of the first. The summer was not as hot and consequently the reduced activity was not so pronounced as in the previous summer. In the autumn of 1971, following late summer rains, surface activity increased such that trapping percentages were 1.9%, as compared to 0.2 for November 1970. During only one month of the second year (January 1972) were no specimens of *P. amplus* trapped. The highest trapping percentages (5.7%) during the second year for *P. amplus* were in March 1972 (Table 29).

The rainfall pattern was distinctly different for the two years and correspondingly so were the trapping data for *P. amplus*. Apparently individuals of this species forage on the surface of the ground only when conditions are ideal. Surface activity may be reduced through a state of torpor, estivation or hibernation. There could be, however, activity within the burrow with the animals living on stored food materials.

Table 29. Monthly trapping success for *Perognathus amplus*—DSCODE A3UBE21,22

Month	Trap Nights	Animals Taken	% Success*
1970			
Jun	5741	398	6.9
Jul	5424	111	2.0
Aug	4590	164	3.6
Sep	2200	83	3.8
Oct	1900	18	0.9
Nov	1100	2	0.2
Dec	2400	0	0
1971			
Jan	2145	0	0
Feb	2125	0	0
Mar	1000	0	0
Apr	2225	16	0.7
May	2400	37	1.5
Jun	3670	164	4.5
Jul	4044	136	3.4
Aug	4325	115	2.7
Sep	1880	19	1.0
Oct	1950	33	1.7
Nov	1000	19	1.9
Dec	990	2	0.2
1972			
Jan	875	0	0
Feb	840	3	0.4
Mar	900	51	5.7
Apr	998	22	2.2
May	600	17	2.8

* Trapping success equals $\frac{\text{number of animals trapped}}{\text{number of trap nights}}$.

Perognathus amplus was the smallest rodent studied and apparently the most affected by cold temperatures. Laboratory studies of metabolic rates and activity patterns for *P. amplus* have not been conducted; however, studies have been done on related desert species (i.e., *P. californicus*, *P. longimembris*) which have approximately the same body weight (Chew et al., 1965; Chew and Butterworth, 1964; Bartholomew and Cade, 1957; Hayden, 1965). These authors have shown that smaller pocket mice (approximately 10 g) have a decreased metabolic rate with torpor ensuing if food is limited and/or ambient temperatures are decreased. French et al., (1967) suggested that reduced activity during stressful times of the year aids in the survival and longevity of pocket mice.

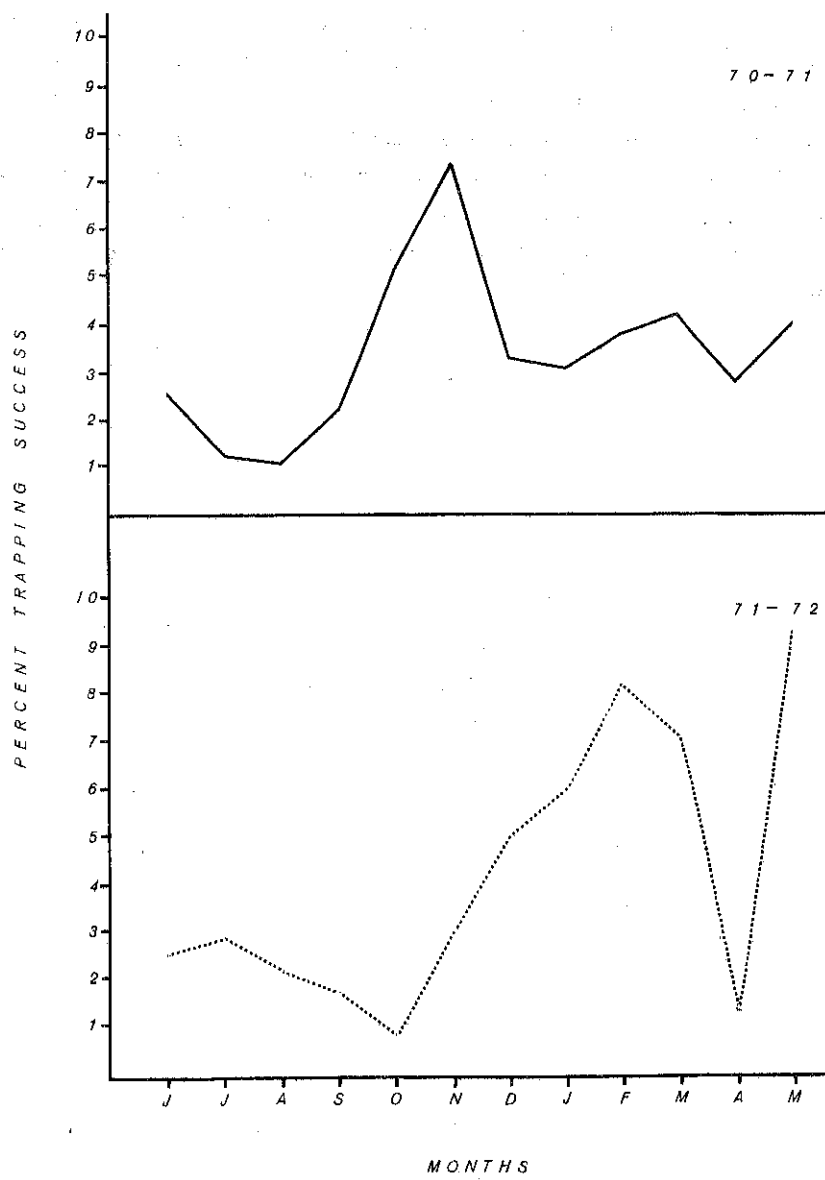


Figure 1. Percent trapping success of *Dipodomys merriami*. (DSCODE A3UBE21, BE22)

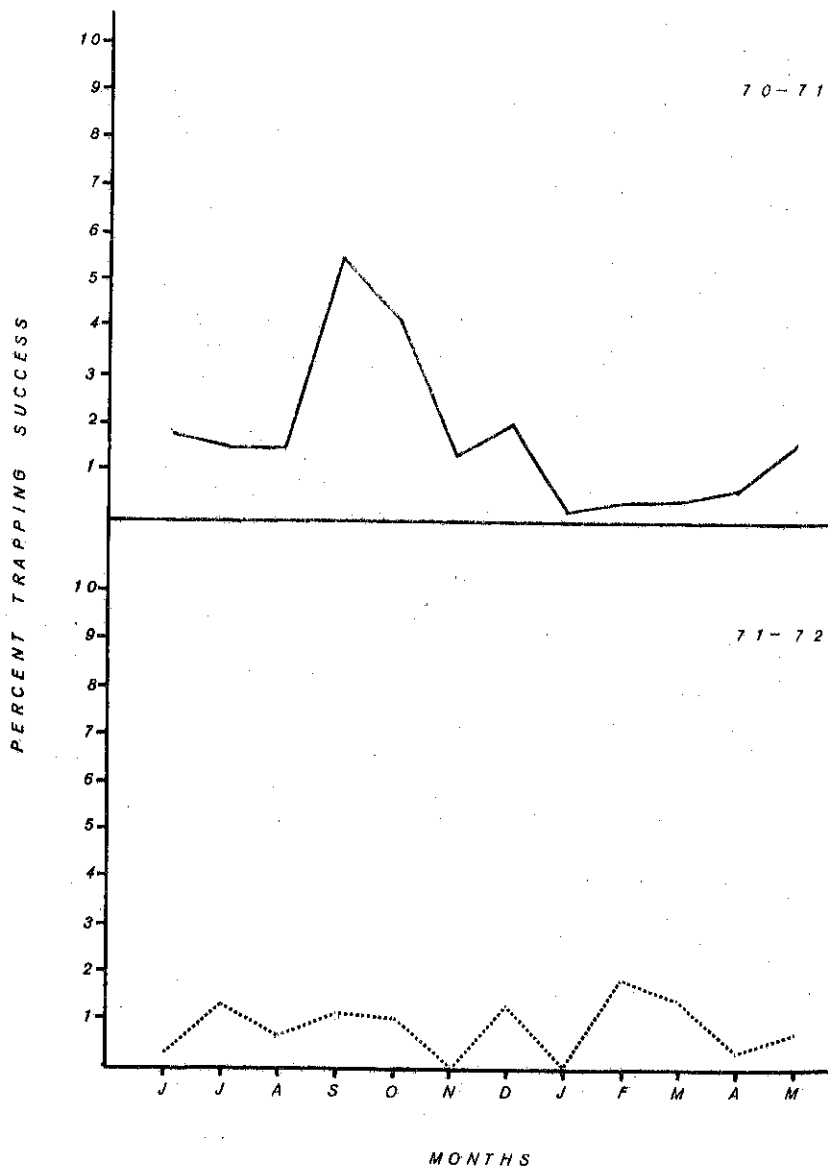


Figure 2. Percent trapping success of *Perognathus baileyi*. (DSCODES A3UBE21, BE22)

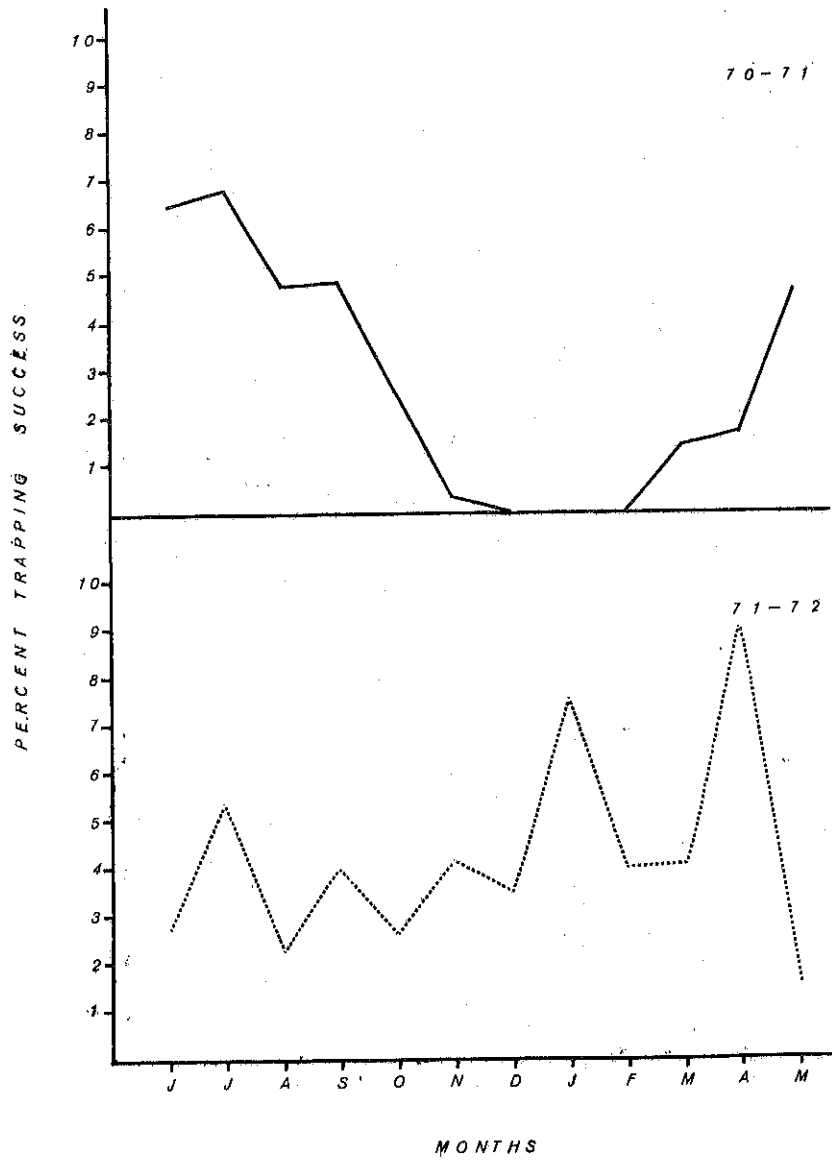


Figure 3. Percent trapping success of *Perognathus intermedius*. (DSCODES A3UBE21, BE22)

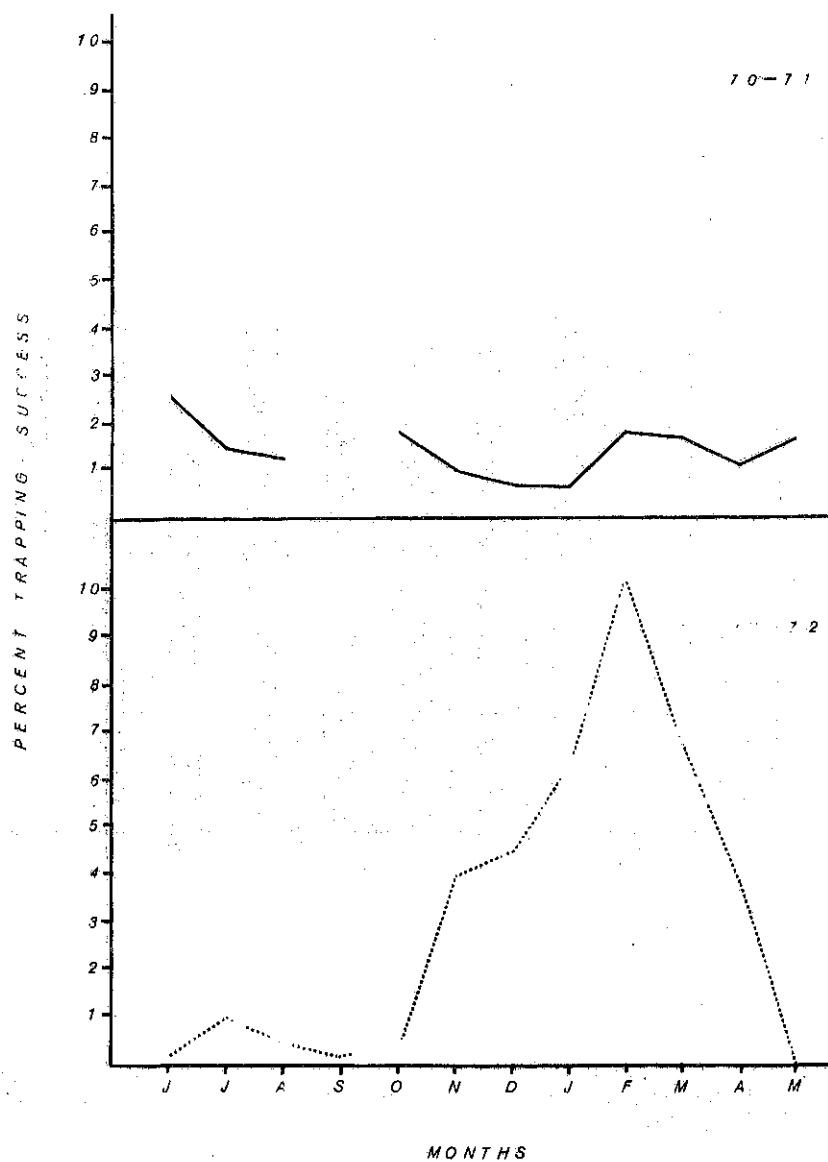


Figure 4. Percent trapping success of *Peromyscus eremicus*. (DSCODES A3UBE21, BE22).
 * Traps not set in appropriate habitat.

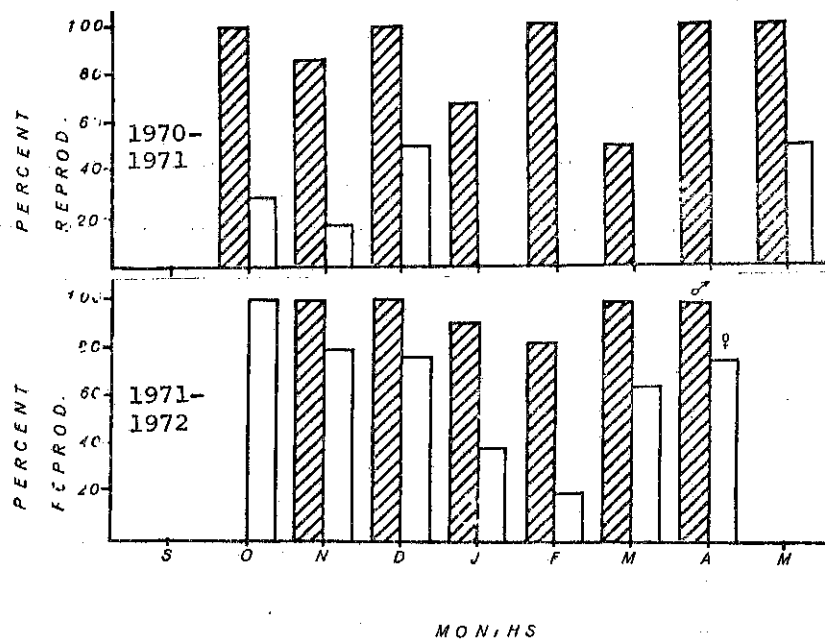


Figure 5. Summary of fecundity of adult male and female *Peromyscus eremicus*. Graph represents September through May of both years. (DSCODES A3UBE21, BE22)

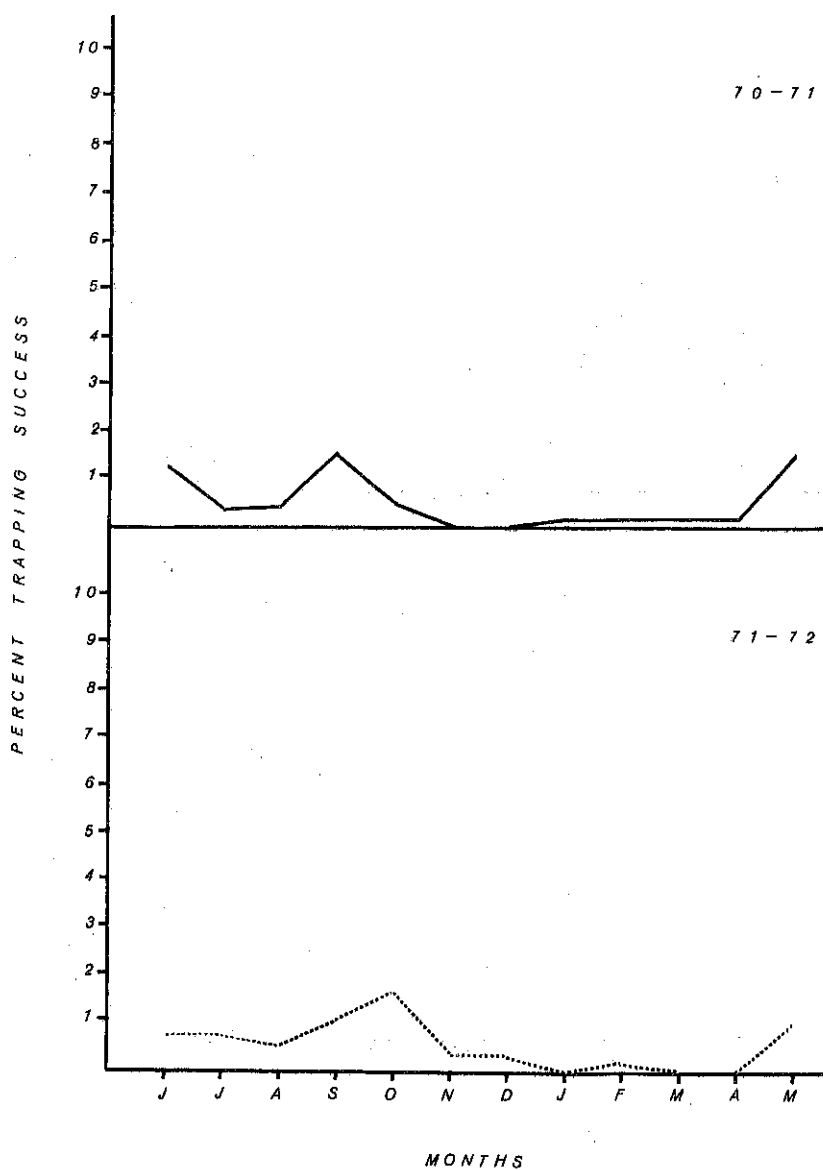


Figure 6. Percent trapping success of *Perognathus penicillatus*. (DSCODES A3UBE21, BE22)

2.3.2.7.-44

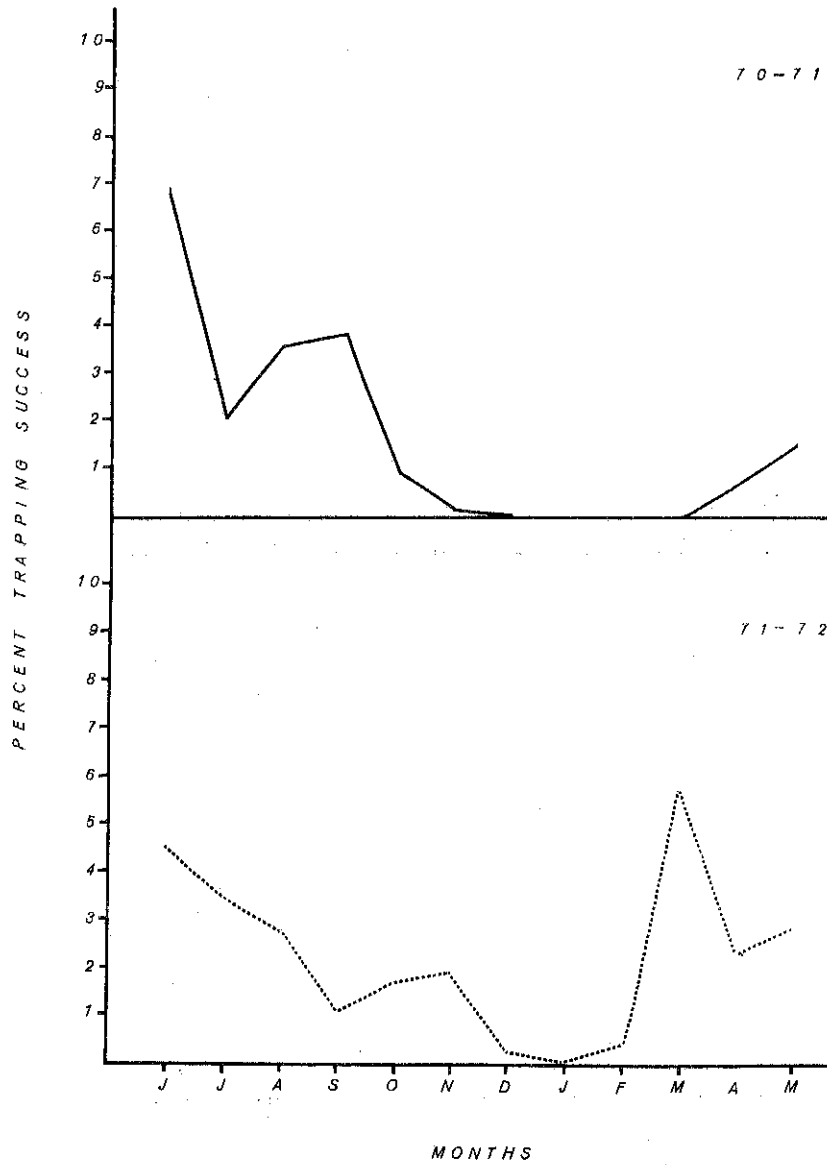


Figure 7. Percent trapping success of *Perognathus amplus*. (DSCODES A3UBE21, BE22)

SIZE, SEX, AND AGE RATIOS
(DSCODES A3UBE21, BE22)

Dipodomys merriami

Dipodomys merriami has a rapid early development (Butterworth 1961), being weaned at 17-22 days postpartum. Allometric ontogenic growth in foetal kangaroo rats partially contributes to rapid postnatal development (Van De Graaff, 1973). Young kangaroo rats rapidly gain weight and are between 20.5 and 26.5 g within three to six weeks (Chew and Butterworth, 1964). *Dipodomys merriami* attains 82% of its adult size within 15 days after birth and achieves its average adult weight within 150 to 180 days (Butterworth, 1961). Chew and Butterworth (1959), under laboratory conditions, reported estrus in *D. merriami* at 24 to 33 days of age. Trapping percentages of young kangaroo rats are low because juveniles mature rapidly (Chew and Butterworth, 1964).

A very small number of kangaroo rats (.83%) were juvenile (Table 30) and, likewise, few (7.1%) were subadult. Five of the 13 juveniles were trapped during the first half of June, 1970. The sex ratio for both juveniles and subadults was near 50:50 (Table 30).

Adult kangaroo rats accounted for 91.6% of the total animals trapped over the two-year period. Of the adult animals, 53.6% were males (Table 30), showing little departure from a 50:50 ratio. The slightly higher percentage of males may be indicative of their more aggressive behavior or larger home ranges. Blair (1943) found that *D. merriami* males occupied 4.07 ± 0.24 acres and females 3.88 ± 0.51 acres. York (1949) likewise found males to have larger home ranges (2.58 ha) than females (1.37 ha).

Table 30. Total semimonthly, and monthly sex and age ratio of 1,572 *Dipodomys merriami*—DSCODE A3UBE21,22

Month	Adults			Young			% Young
	Males	Females	%Males	Males	Females	%Males	
1970							
Jun 10	54	46	54.0	20	11	64.5	23.7
Jun 20	5	9	35.7	0	0	--	0
Jul 10	11	8	57.9	3	2	60.0	20.8
Jul 20	16	17	48.5	3	5	37.5	19.5
Aug 10	18	12	60.0	1	2	33.3	9.1
Aug 20	5	10	33.3	1	0	100.0	6.3
Sep	25	22	53.2	0	2	0	4.1
Oct	46	46	50.0	3	2	60.0	5.2
Nov	45	32	58.4	3	1	75.0	4.9
Dec	41	30	57.7	3	2	60.0	6.6

Continued

Table 30. Continued

Month	Adults			Young			% Young
	Males	Females	%Males	Males	Females	%Males	
1971							
Jan	36	29	55.4	0	0	--	0
Feb	33	44	42.9	1	1	50.0	2.5
Mar	24	17	58.5	0	0	--	0
Apr	31	30	50.8	0	0	--	0
May	41	48	46.1	1	4	20.0	5.3
Jun 10	18	15	54.5	0	0	--	0
Jun 20	28	27	50.9	1	4	20.0	8.3
Jul 10	27	19	58.7	0	1	0	2.1
Jul 20	34	26	56.7	4	2	66.6	9.1
Aug 10	16	11	59.3	0	0	--	0
Aug 20	34	28	54.9	1	1	50.0	3.1
Sep	16	13	55.2	1	0	100.0	3.3
Oct	10	3	77.0	0	1	0	7.1
Nov	15	11	57.7	1	2	33.3	10.3
Dec	24	18	57.1	4	3	57.1	14.3
1972							
Jan	28	17	62.2	4	3	57.1	13.5
Feb	33	28	54.1	6	1	85.7	10.3
Mar	30	26	53.6	3	4	42.9	11.1
Apr	6	4	60.0	1	1	50.0	16.7
May	24	23	51.1	6	3	66.6	16.1
Total	774	669	53.6	71	58	55.0	8.2

Adult males were approximately 3 g heavier than adult females (Table 31) and approximately 4 mm longer. Males that were considered reproductively active were likewise heavier (up to 6 g heavier) than non-reproductive adult males. There was a direct correlation between the amount of spermatozoa present in the caudal epididymis and the weight of the animal. Those adult animals with no sperm present (N=90) had an average weight of 38.95 g; those having moderate amounts (N=137) had a mean weight of 41.79 g; those having large amounts (N=356) had a mean weight of 43.28 g (Table 32).

Three-hundred adult females in breeding condition (mean weight 41.54 g) were appreciably heavier than 80 non-breeding adult females (mean weight 34.26 g). Pregnant females (N=193), having a mean weight of 42.36 g, were heavier than any other category of females. The condition of lactating apparently did not pose severe metabolic strains on females. Weights of 87 lactating females diminished an average of 1.68 g from their fecund weight and remained heavier than those in estrus or those with placental scars (Table 33).

Table 31. Body measurement statistics of 1,572 *Dipodomys merriami**

Measurement	Males		
	Adult	Subadult	Juvenile
Total length	245.8±8.7(770)215-268	224.1±14.8(63)184-253	193.8±12.2(8)175-212
Tail length	140.4±7.1(770)117-177	130.3±12.2(63)99-155	113.9±9.7(8)105-133
Hind foot	36.0±1.1(774)28-39	35.3±1.6(63)25-38	34.6±1.1(8)33-36
Ear	12.0±0.8(774)8-15	11.0±0.7(63)9-12	10.5±1.2(8)9-12
Weights	41.4±4.3(774)27.8-55.2	29.4±4.6(63)20.9-36.2	17.4±2.5(8)13.5-20.0
Bacula length	11.3±0.9(774)7.4-13.1	8.5±1.0(63)5.7-10.8	6.8±0.7(8)5.7-7.8
	Females		
	Adult	Subadult	Juvenile
Total length	241.2±9.1(668)211-263	223.3±15.6(53)180-260	195.4±28.0(5)157-223
Tail length	137.6±7.2(668)116-160	129.8±12.8(53)96-147	115.0±17.7(5)92-130
Hind foot	35.5±1.0(669)32-39	35.0±0.8(53)32-36	34.4±0.6(5)34-35
Ear	11.8±0.8(669)8-15	11.1±0.8(53)9-13	9.8±1.1(5)8-11
Weights	39.9±4.6(669)27.6-57.8	27.9±4.1(53)18.2-35.6	18.6±4.8(5)12.0-24.7

*The mean number is given, followed by the standard deviation, the size of the sample (in parentheses), and the range. Lengths are expressed in mm, weights in g. DSCODE A3UBE21, 22.

Table 32. Mean body weights (g) and bacula measurements (mm) of various ages and reproductive categories of 845 *Dipodomys merriami**

	N	Body Weight		Baculum	
		Mean	Range	Mean	Range
Juvenile	8	17.36	13.50-20.00	6.79	5.65-7.75
Subadult	63	29.43	20.90-46.30	8.49	5.70-10.80
Adult					
No spermatozoa	90	37.20	27.80-48.90	9.95	7.40-12.15
Small amounts	137	38.95	30.50-47.70	10.88	8.60-12.55
Moderate amounts	191	41.79	32.20-51.00	11.50	9.10-12.90
Large amounts	356	43.28	35.10-55.20	11.70	10.00-13.10

*i.e., spermatazoa content in caudal epididymes.

Table 33. Breeding characteristics of adult female *Dipodomys merriami*—DSCODE A3UBE22

Month	Sample Size No.	No.	%	Gravid		No.	%	Postpartum	
				Weight Mean±S.D.	Embryos Mean±S.D.			Weight Mean±S.D.	Placental Scars Mean±S.D.
1970									
Jun 10	46	31	67	39.5±4.2	2.0±0.2	6	13	35.7±1.9	1.8±0.4
Jun 20	9	5	56	38.7±2.9	2.0	3	33	36.9±3.8	2.0
Jul 10	8	4	50	43.8±6.6	2.0	2	25	34.4±0.7	2.0
Jul 20	17	2	12	38.6±4.2	2.0	9	53	36.8±2.2	2.0
Aug 10	12	2	17	39.9±8.3	1.5±0.7	8	67	36.9±4.0	2.0±0.5
Aug 20	10	2	20	36.6±2.6	2.0	6	60	40.0±4.7	2.0
Sep	22	9	41	42.5±4.5	2.3±0.5	4	18	42.0±1.7	2.0
Oct	46	2	4	40.6±3.5	2.0	27	59	38.6±2.5	2.0
Nov	32	0	0			27	84	37.3±2.7	2.0
Dec	30	0	0			23	77	38.1±3.5	2.0
1971									
Jan	29	0	0			24	83	37.2±3.1	2.0
Feb	44	8	18	43.1±5.0	2.0	26	59	37.6±2.6	2.0
Mar	17	0	0			13	76	35.3±2.8	2.0
Apr	30	4	13	39.4±2.4	2.0	18	60	36.9±2.4	2.0
May	48	9	19	38.2±2.2	1.9±0.3	25	52	33.0±1.1	2.0
Jun 10	15	1	7	39.2	1.0	8	53	35.8±3.8	2.0
Jun 20	27	1	4	38.7	1.0	16	59	36.4±2.5	2.0±0.4
Jul 10	19	2	11	39.1±0.5	2.0	13	68	36.4±2.2	2.0±0.4
Jul 20	26	7	27	42.6±3.7	2.0	14	54	38.2±2.4	1.9±0.4
Aug 10	11	5	45	39.7±3.7	2.0	1	9	42.3	2.0
Aug 20	28	23	82	44.2±3.6	2.2±0.5	0	0		
Sep	13	6	46	43.4±3.3	2.2±0.4	2	15	41.2±0.1	2.5±0.7
Oct	3	2	67	42.2±0.3	2.0	0	0		
Nov	11	6	55	46.9±3.1	2.3±0.5	0	0		
Dec	18	2	11	40.1±6.2	2.0	4	22	39.6±2.4	2.0
1972									
Jan	17	10	59	43.2±5.4	2.0	1	6	40.7	2.0
Feb	28	16	57	44.1±5.3	1.9±0.4	4	14	41.4±2.6	2.0
Mar	26	22	85	45.1±5.4	2.1±0.3	0	0		
Apr	4	2	50	38.9±7.2	2.0	1	25	38.0	3.0
May	23	10	43	44.6±3.5	1.9±0.3	4	17	40.0±3.8	2.0
Total	669	193	29	42.4±4.9	2.0±0.4	289	43	37.4±3.0	2.0±0.2

Body weights of adult kangaroo rats sometimes fluctuated markedly (Figs. 8 and 9) throughout the study period and could be correlated to climatic conditions and reproductive phases. Chew and Butterworth (1964) reported a seasonal trend (in years of adequate food supply) of mean body weight of adult animals that indicated that conditions in winter and early spring were most conducive to general vigor of kangaroo rats. Figure 8 shows a similar pattern of body weight increase during the cooler months of this study period.

Males reached their lowest weights in early August, 1970, then increased through the last half of August after the summer rains, and reached their peak weight in late September. During the first year, both the adult males and adult females were strikingly lighter in weight (Fig. 8) than in the second year. Correspondingly, the amount of rainfall (Table 1), phenology of plants and available seeds were also drastically different in the two years. Indications of decline in body weights indicate that the hottest times of the year are stressful to kangaroo rats (Fig 9).

Perognathus amplus

No studies have been done to determine growth rates and development in *Perognathus amplus*; therefore, body weights and measurements at a given age are not known. Hayden and Gambino (1966) have measured growth and development of another small pocket mouse (8.5 g), *Perognathus longimembris*, therefore data are available for a species closely related to *P. amplus* and of comparable size.

Juveniles had an average weight of 6.30 g and accounted for 3.1% of the *P. amplus* trapped. Thirty-seven of the total juveniles (36%) were taken during the first half of June 1970. Fifteen juveniles were males (35%) and were slightly heavier (6.7 g) than the females (5.9 g).

Subadults accounted for 20% of the total *P. amplus* trapped (mean weight 7.57 g). Sixty-eight percent of the subadults were taken during the first half of June, 1970 (Table 34)

Table 34. Total semimonthly and monthly sex and age ratio of 1,410 *Peromyscus amplus*—DSCODE A3UBE21,22

Month	Adult			Young			
	Males	Females	% Males	Males	Females	% Males	% Young
1970							
Jun 10	60	66	47.6	111	119	48.3	64.6
Jun 20	14	12	53.9	7	9	43.8	38.1
Jul 10	24	26	48.0	4	10	28.6	21.9
Jul 20	24	15	61.5	2	6	25.0	17.0
Aug 10	54	62	46.6	2	6	25.0	6.5
Aug 20	21	14	60.0	1	4	20.0	12.5
Sep	42	36	53.8	1	4	20.0	6.0
Oct	11	7	61.1	0	0	--	0
Nov	1	1	50.0	0	0	--	0
Dec	0	0	--	0	0	--	--

Continued

Table 34. Continued

Month	Adult			Young			
	Males	Females	% Males	Males	Females	% Males	% Young
1971							
Jan	0	0	--	0	0	--	--
Feb	0	0	--	0	0	--	--
Mar	0	0	--	0	0	--	--
Apr	7	9	43.8	0	0	--	0
May	27	7	79.4	1	2	33.3	8.1
Jun 10	33	45	42.3	2	3	40.0	6.0
Jun 20	40	40	50.0	0	1	0	1.2
Jul 10	26	38	40.6	0	2	0	3.0
Jul 20	23	42	35.4	2	3	40.0	7.1
Aug 10	22	23	48.9	0	0	--	0
Aug 20	37	29	66.1	11	3	78.6	20.0
Sep	12	7	63.2	0	0	--	0
Oct	13	8	62.0	8	4	66.6	36.4
Nov	10	7	58.8	0	2	0	10.5
Dec	1	1	50.0	0	0	--	0
1972							
Jan	0	0	--	0	0	--	--
Feb	2	1	66.6	0	0	--	0
Mar	31	20	60.8	0	0	--	0
Apr	12	10	54.5	0	0	--	0
May	8	4	66.6	3	2	60.0	29.4
Total	555	530	51.2	145	180	44.6	23.0

Over the two-year period, adult *P. amplus* had an average body weight of 10.92 g. The males were slightly heavier (11.35 g) than the females (10.49 g). Males were, likewise, consistently heavier throughout the two-year study, even though there were seasonal weight fluctuations (Figs 10 and 11, Table 35)

There was a striking contrast in the body weights of adult animals between the two years of study. During June 1970, immediately following a reproductive period, adult *P. amplus* were heavier than at any other time of the first year. Their body weights were the lowest immediately preceding and immediately following winter dormancy (Fig 10).

In contrast to the previous June (1970), the average body weights of the adults were at their lowest level during June, 1971. The summer rains started and germination of plants occurred in August, 1971 and concurrently the average body weights of *P. amplus* greatly increased. Heavier animals (those weighing over 10 g) did not go into winter inactivity for so long as in the previous year. The increased body weights of *P. amplus* during the second year indicate that high availability of food is probably conducive to

increased surface activity in pocket mice. Trapping during four months of the first winter yielded no *P. amplus*, whereas in the second winter only during January were no *P. amplus* taken.

Increased body weight in *P. amplus* appears to be a prerequisite for successful reproduction. Adult males with large amounts of spermatozoa present (N=192) had an average body weight of 12.76 g, whereas adult males with no spermatozoa had a mean body weight of 10.27 g. Likewise, 66 females that were determined to be reproductively active had an average body weight of 12.57 g; in contrast, 302 non-reproductive females averaged 9.55 g in body weight. (Table 36).

Pregnant females (N=32) had the heaviest average body weight (13.14 g) of all other categories of *P. amplus*. The average body weight of lactating females (12.41 g) was not significantly lighter than that of pregnant individuals.

Perognathus baileyi (DSCODE A3UBE21,22)

Perognathus baileyi of different ages exhibited a wide range in body weights and lengths (Table 37). Five juveniles had an average body weight of 12.85 g. Although the average body length of these five juveniles was considerably less (164.1 mm) than that of 164 adults (210.8 mm), the hind foot length of the juveniles (25.45 mm) was nearly comparable to that of the adults (26.22 mm). This same allometric growth ratio of the hind foot to other parts of the body has been examined in other heteromyids and is probably of significant adaptive value (Van De Graaff, 1973).

Subadults accounted for 12.7% of the *P. baileyi* sampled. They had an average body weight of 18.27 g, an average body length of 186.7 mm, and an average hind foot length of 25.27 mm. The body length and weight increased greatly over that of juveniles, but the length of the hind foot remained virtually unchanged. During the first year, young animals occurred from June through September and constituted a significant portion of the sample (Table 38). In the second year, young animals were trapped from July through September and then not again until April 1972.

Cumulative data for the two years showed 211 adult females to have a mean body weight of 24.51 g and 165 adult males to have a mean body weight of 28.14 g. The interesting aspect of adult body weights in *P. baileyi* is the wide range (Table 39) within the adult categories. Analysis of this information, plus other data, implies that *P. baileyi* does not mature as rapidly as the other heteromyids and perhaps has a longer life expectancy.

Table 35. Body measurement statistics of 1,410 *Perognathus amplus**—DSCODE A3UBE21, 22

Measurement	Males		
	Adult	Subadult	Juvenile
Total length	146.5±8.3(544)118-178	136.4±7.2(130)119-156	125.1±6.2(15)117-137
Tail length	74.4±5.3(544)58-93	71.5±5.5(130)55-85	65.3±4.1(15)61-73
Hind foot	19.6±0.9(555)17-26	19.2±1.0(130)17-26	19.1±0.6(15)18-20
Ear	6.8±0.6(555)2-8	6.4±0.6(130)5-7	6.0±0.7(15)5-7
Weights	11.4±2.1(555)5.6-18.5	8.5±1.3(130)4.9-10.9	6.7±1.1(15)4.7-8.6
Bacula length	6.6±1.0(555)4.4-9.2	5.2±0.4(130)3.4-6.6	4.9±0.4(15)4.5-5.6
Females			
Total length	144.9±9.0(515)120-256	135.0±7.4(151)115-154	121.1±9.2(28)100-136
Tail length	74.0±4.8(515)58-90	71.1±5.6(151)53-85	62.8±7.3(28)44-73
Hind foot	19.4±0.9(530)13-24	19.0±0.8(152)17-21	18.0±1.1(28)14-19
Ear	6.7±0.6(530)5-9	6.3±0.5(152)5-7	5.9±0.6(28)5-7
Weights	10.5±1.9(530)6.8-19.3	8.3±1.1(152)5.9-11.2	5.9±0.6(28)4.9-7.2

*The mean number is given, followed by the standard deviation, the size of the sample (in parentheses), and the range. Lengths are expressed in mm, weights in g.

Table 36. Mean body weights (g) and bacula measurements (mm) of various ages and reproductive categories of 700 *Perognathus amplus**

	N	Body Weight		Baculum	
		Mean	Range	Mean	Range
Juvenile	15	6.68	4.70- 8.60	4.85	4.45-5.60
Subadult	130	8.45	6.90-10.90	5.24	3.40-6.44
Adult					
No spermatozoa	209	10.27	7.40-14.30	5.74	4.35-7.90
Small amounts	70	10.62	5.60-17.40	6.53	5.00-8.35
Moderate amounts	84	11.39	8.30-18.30	6.88	4.70-8.50
Large amounts	192	12.76	8.70-18.50	7.52	6.00-9.20

*i.e., spermatozoa content in caudal epididymes

Table 37. Body measurement statistics of 438 *Perognathus baileyi**—DSCODE A3UBE21,22

Measurement	Males		
	Adult	Subadult	Juvenile
Total length	210.8±14.0(164)106-240	184.1±14.0(29)143-205	164.3±16.7(4)148-181
Tail length	114.0±8.0(164)76-140	102.3±9.8(29)70-114	86.8±12.6(4)75-100
Hind foot	26.6±1.4(165)24-38	25.4±1.4(30)22-29	25.5±1.3(4)24-27
Ear	9.5±1.1(165)7-19	8.5±1.0(30)7-10	8.3±0.5(4)8-9
Weight	28.1±5.1(165)18.6-44.0	17.9±2.8(30)12.0-24.3	12.5±1.9(4)10.6-15.1
Bacula length	10.2±1.1(165)6.8-12.8	8.7±0.8(30)7.3-10.8	8.1±0.4(4)7.7-8.6
Females			
Total length	201.4±12.9(209)176-228	189.4±8.9(27)170-205	163±0(1)163
Tail length	109.2±6.5(209)86-125	105.7±6.3(27)95-119	95±0(1)95
Hind foot	25.8±1.0(211)21-29	25.1±1.9(27)20-29	25±0(1)25
Ear	9.2±0.8(211)7-11	9.1±0.7(27)8-11	7±0(1)7
Weight	24.5±3.4(211)16.6-38.4	18.6±2.8(27)13.7-23.7	14.4±0(1)14.4

*The mean number is given, followed by the standard deviation, the size of the sample (in parentheses) and the range. Lengths are expressed in mm, weights in g.

Table 38. Total semimonthly and monthly sex and age ratio of 438 *Perognathus baileyi*
DSCODE A3UBE21,22

Month	Adult			Young			
	Males	Females	% Males	Males	Females	% Males	% Young
1970							
Jun 10	1	8	11.1	5	3	62.5	47.1
Jun 20	6	17	26.1	6	5	54.5	32.4
Jul 10	2	1	66.6	1	1	50.0	40.0
Jul 20	11	14	44.0	1	5	16.7	19.4
Aug 10	4	10	28.6	4	5	44.4	39.1
Aug 20	5	4	55.6	0	2	0	18.2
Sep	23	37	38.3	3	3	50.0	9.1
Oct	24	29	45.3	0	0	--	0
Nov	12	15	44.4	2	1	66.6	10.0
Dec	6	8	42.9	0	0	--	0
1971							
Jan	1	1	50.0	0	0	--	0
Feb	3	1	75.0	0	0	--	0
Mar	3	0	100.0	0	0	--	0
Apr	3	2	60.0	0	0	--	0
May	7	5	58.3	1	0	100.0	7.7

Continued

Table 38. Continued

Month	Adult			Young			
	Males	Females	% Males	Males	Females	% Males	% Young
Jun 10	6	6	50.0	0	0	--	0
Jun 20	0	0	--	0	0	--	--
Jul 10	15	9	62.5	4	1	80.0	17.2
Jul 20	3	4	42.9	0	0	--	0
Aug 10	3	6	33.3	1	1	50.0	18.2
Aug 20	1	3	25.0	1	0	100.0	20.0
Sep	5	5	50.0	2	0	100.0	16.7
Oct	2	6	25.0	0	0	--	0
Nov	0	0	--	0	0	--	--
Dec	6	4	60.0	0	0	--	0
1972							
Jan	0	0	--	0	0	--	--
Feb	4	8	33.3	0	0	--	0
Mar	6	6	50.0	0	0	--	0
Apr	1	0	100.0	1	0	100.0	50.0
May	2	2	50.0	2	1	66.6	42.9
Total	165	211	43.9	34	28	54.8	14.2

Table 39. Mean body weights (g) and bacula measurements (mm) of various ages and reproductive categories of 199 *Perognathus baileyi**

	N	Body Weight		Baculum	
		Mean	Range	Mean	Range
Juvenile	4	12.47	10.60-15.10	8.10	7.70- 8.60
Subadult	30	17.91	12.00-24.30	8.66	7.25-10.80
Adult					
No spermatozoa	70	25.01	18.60-34.90	9.26	6.75-10.90
Small amounts	30	29.91	22.40-40.10	10.29	8.30-11.70
Moderate amounts	20	31.31	21.60-41.80	11.05	9.90-12.50
Large amounts	45	30.44	21.20-44.00	11.11	8.85-12.80

*i.e., spermatozoa content in caudal epididymes.

Males were consistently heavier than females (Fig.12), but both males and females had seasonal weight fluctuations. Adults were heaviest prior to and during reproductive periods and weighed less during the colder months of the year. (Fig.13).

Ninety-five adult male *P. baileyi* were found to be fertile. These fecund males had a mean body weight of 30.45 g, which was 5.44 g heavier than 70 adult non-fecund males. Readiness to mate apparently involves an increase in body weight (Table 39).

Only four females in estrus were taken; these had a mean body weight of 23.42 g, which is not significantly higher than the mean weight of 86 non-breeding females (22.55 g). Pregnant and lactating females were significantly heavier, averaging 28.43 g and 27.42 g respectively.

Perognathus intermedius DSCODE A3UBE21,22

Of those *P. intermedius* examined, 46.1% were males. Although this percentage reflects an even ratio of males to females, there were times of the year when males were distinctly more active than females (Table 40). Seemingly, during the cooler months of the winter, males had greater surface activity than females; in contrast, females were trapped in greater numbers during the summers. Adult males were slightly heavier (13.1 g) than adult females (12.7 g), Table 41, and perhaps were more sensitive to high temperatures than females, but could better tolerate colder temperatures.

Table 40. Total semimonthly and monthly sex and age ratio of 1,212 *Perognathus intermedius*—DSCODE A3UBE21, 22

Month	Adults			Young			
	Males	Females	% Males	Males	Females	% Males	% Young
1970							
Jun 10	19	49	27.9	9	12	42.9	23.6
Jun 20	27	38	41.5	14	19	42.4	33.7
Jul 10	11	17	39.3	13	13	50.0	48.1
Jul 20	11	29	27.5	11	5	68.8	28.6
Aug 10	18	29	38.3	16	7	69.6	32.9
Aug 20	29	34	46.0	1	2	33.3	4.5
Sep	25	30	45.5	1	2	33.3	5.2
Oct	20	12	62.5	0	0	--	0
Nov	4	2	66.6	0	0	--	0
Dec	0	0	--	0	0	--	--
1971							
Jan	0	0	--	0	0	--	--
Feb	0	0	--	0	0	--	--
Mar	8	3	72.7	0	0	--	0
Apr	6	7	46.2	0	0	--	0
May	26	11	70.3	0	0	--	0
Jun 10	20	18	52.6	0	0	--	0

Continued

Table 40. Continued

Month	Adults			Young			
	Males	Females	% Males	Males	Females	% Males	% Young
Jun 20	22	42	34.4	0	0	--	0
Jul 10	19	31	38.0	9	11	45.0	28.6
Jul 20	29	40	42.0	6	2	75.0	10.4
Aug 10	4	8	33.3	3	0	100.0	20.0
Aug 20	16	22	42.1	1	3	25.0	9.5
Sep	18	23	43.9	0	1	0	2.4
Oct	2	14	12.5	2	2	50.0	20.0
Nov	13	16	44.8	1	1	50.0	6.5
Dec	17	10	63.0	0	0	--	0
1972							
Jan	52	11	82.5	0	2	0	3.1
Feb	18	7	72.0	0	0	--	0
Mar	20	15	57.1	1	0	100.0	2.8
Apr	23	31	65.7	1	0	100.0	1.9
May	2	11	15.4	2	0	100.0	13.3
Total	479	560	46.1	91	82	52.6	14.3

Young animals comprised 14.1% of the *P. intermedius* trapped (1.7% juvenile and 12.4% subadult). The mean weight of the juveniles was 7.35 g and the mean weight of the subadults was 9.70 g. During the first year, young animals were trapped only throughout the summer months (Table 40), with a peak of 48.1% of the total sample of *P. intermedius* being young in the first portion of July 1970. Young animals were trapped in every month of the second year after June except during December and February.

Adult *P. intermedius* had a mean weight of 12.9 g. Body weights of adult males averaged 13.1 g (Table 41) which was only slightly heavier than adult females with a mean body weight of 12.7 g. Males were generally heavier than females (Fig. 15) throughout the non-reproductive periods, but females increased their weights and were often heavier than males during reproductive peaks.

Comparisons of body weights of *P. intermedius* during different seasons in two years indicated that the only time the weights of the animals approached the lower limits of their range was immediately prior to winter dormancy (November, 1970) and immediately after emergence (March, 1971). Perhaps decreased body weight due to paucity of food is a factor contributing to reduced surface activity.

As in the other heteromyids, there is a correlation in adult males between reproductive condition and body weight (i.e., spermatozoa present). Adult males with large

amounts of spermatozoa in the caudal epididymis (N=174) had a mean body weight of 13.99 g and 64 adult males with moderate amounts of spermatozoa had a mean body weight of 13.39 g. Adult *P. intermedius* with no spermatozoa observed in the caudal epididymis (N=172) weighed an average of 12.15 g (Table 42).

Table 41. Body measurement statistics of 1,212 *Perognathus intermedius**

Measurement	Males		
	Adult	Subadult	Juvenile
Total length	169.0±8.0(461)142-188	160.6±10.5(81)130-184	142.4±6.4(9)134-156
Tail length	91.3±6.5(461)67-110	91.0±7.8(81)67-104	80.7±3.3(9)75-87
Hind foot	20.4±0.8(479)18-23	19.9±0.7(82)18-22	20.0±1.0(9)19-22
Ear	7.2±0.5(479)6-9	6.6±0.6(82)5-9	6.3±0.5(9)6-7
Weight	13.1±1.8(479)9.2-20.6	9.9±1.4(82)6.7-14.0	7.5±1.5(9)6.0-9.9
Bacula length	11.3±1.2(479)7.9-13.6	8.8±0.7(82)6.0-10.3	7.8±0.6(9)6.9-8.9
Females			
Total length	167.4±8.0(533)122-188	158.0±9.3(69)139-177	142.0±12.8(13)116-159
Tail length	90.8±6.2(533)69-105	89.6±6.8(69)73-102	79.4±9.9(13)62-91
Hind foot	20.2±0.9(560)18-23	20.0±0.9(69)18-22	19.1±0.8(13)18-20
Ear	7.1±0.5(560)6-9	6.7±1.3(69)6-9	6.2±0.6(13)5-7
Weight	12.7±1.9(560)7.1-20.0	9.5±1.5(69)6.7-12.8	7.2±1.3(13)5.2-10.0

*The mean number is given, followed by the standard deviation, the size of the sample (in parentheses) and the range. Lengths are expressed in mm, weights in g (DSCODE A3UBE21,22)

Table 42. Mean body weights (g) and Bacula measurements (mm) of various ages and reproductive categories of 570 *Perognathus intermedius**

	N	Body Weight		Baculum	
		Mean	Range	Mean	Range
Juvenile	9	7.54	6.00- 9.90	7.79	6.90- 8.90
Subadult	82	9.93	6.70-14.00	8.80	6.00-10.30
Adult					
No spermatozoa	172	12.15	9.20-16.50	10.04	7.90-13.40
Small amounts	69	12.84	10.40-16.20	11.59	9.85-12.85
Moderate amounts	64	13.39	10.40-20.30	11.91	9.70-12.80
Large amounts	174	13.99	10.50-20.60	12.18	8.50-13.55

*i.e., spermatozoa content in caudal epididymes.

2.3.2.7.-58

Eighty-two pregnant females had a mean body weight of 14.82 g; this mean is higher than that for any other category of *P. intermedius*. Lactating females, likewise, were heavy (13.54 g, N=45), but the average body weights of 16 females in estrus (12.27 g) was not significantly heavier than 159 non-reproductive females (11.59 g).

Peromyscus eremicus (DSCODE A3UBE21,22)

The sex ratio in *P. eremicus* was close to 1:1 (Table 43). Davis and Davis (1947) reported sex ratios from large laboratory colonies of *P. eremicus* to be 53% males and Lewis (1972) reported a predominance of 66% males, ascribing the uneven ratio to a more aggressive behavior of males.

Brand and Ryckman (1968) in studying the postnatal development in *P. eremicus*, found that weaning begins on the 20th to 22nd day postpartum and is completed by the 25th day. They further observed post-juvenile molt beginning on the 34th to 37th day. Apparently there is only an approximate 10-day foraging period as juveniles which explains why such a low percentage of juveniles were sampled (2.1% from a sample of 534).

There were sexual differences in the body length and weights of the juveniles. The mean weight of juveniles was 10.06 g and the mean length was 148.58 mm. Eight juvenile females averaged exactly 1 g heavier than nine juvenile males. The females also averaged 2.19 mm longer than the males and had a slightly longer hind foot (Table 44).

The greatest number of subadults were taken during June and July of the first year, indicating a spring reproductive peak. Some young animals were taken in all but four months of the study (Table 43) and in two of those months (September, 1970, and May, 1972) there were no *P. eremicus* trapped. The uniform occurrence of young animals indicates continuous breeding in cactus mice. The combined mean subadult male and female body weight was 13.96 g and the combined mean body length was 164.75 mm. Although the body length and body weight significantly increased over juveniles, the mean hind foot length remained nearly the same.

Adults were represented by 419 specimens (78.5% of the population) that had an average body weight of 20.09 g. Of the six species studied, only in *P. eremicus* was the mean female weight heavier than that in the male, 20.76 g to 19.42 g respectively. There did not appear to be any pattern of body weight changes that could be correlated with environmental conditions (Figs. 16 and 17). Not only were the females heavier than the males, they also averaged 3.42 mm longer (males were 181.96 mm, females were 185.38 mm), while the mean hind foot lengths were essentially the same (19.53 mm).

Table 43. Total, semimonthly and monthly sex and age ratio of 534 *Peromyscus eremicus*—DSCODE A3UBE21,22

Month	Adult			Young			
	Males	Females	% Males	Males	Females	% Males	% Young
1970							
Jun 10	13	12	52.0	10	3	77.0	34.2
Jun 20	5	8	38.5	13	5	72.2	58.1
Jul 10	1	3	25.0	3	1	75.0	50.0
Jul 20	9	8	52.9	4	4	50.0	32.0
Aug 10	8	5	61.5	5	4	55.6	40.9
Aug 20	3	1	75.0	0	1	0	20.0
Sep	0	0	--	0	0	--	--
Oct	8	10	44.5	3	2	60.0	21.7
Nov	7	11	38.9	1	2	33.3	14.3
Dec	1	2	33.3	0	1	0	25.0
1971							
Jan	3	2	60.0	0	1	0	16.7
Feb	12	7	63.2	0	1	0	5.0
Mar	6	5	54.5	1	1	50.0	15.4
Apr	3	2	60.0	0	0	--	0
May	5	2	71.4	1	0	100.0	12.5
Jun 10	0	1	0	0	0	--	0
Jun 20	0	2	0	0	0	--	0
Jul 10	2	4	33.3	1	1	50.0	25.0
Jul 20	9	6	60.0	1	1	50.0	11.8
Aug 10	3	2	60.0	1	1	50.0	28.6
Aug 20	2	1	66.6	0	0	--	0
Sep	0	0	--	1	0	100.0	100.0
Oct	0	1	0	1	1	50.0	66.0
Nov	11	14	73.3	2	2	50.0	13.8
Dec	16	13	55.2	1	5	16.6	17.1
1972							
Jan	22	24	47.8	3	5	37.5	14.8
Feb	33	26	56.0	1	4	20.0	7.8
Mar	27	23	54.0	7	2	77.8	15.3
Apr	7	8	46.7	3	4	42.9	31.8
May	0	0	--	0	0	--	--
Total	216	203	51.6	63	52	54.8	21.5

Table 44. Body measurement statistics of 534 *Peromyscus eremicus**—DSCODE A3UBE21,22

Measurement	Male		
	Adult	Subadult	Juvenile
Total length	182.0±9.3(213)159-205	166.3±9.8(54)143-188	147.4±12.3(9)123-161
Tail length	93.1±7.4(213)71-117	86.2±8.1(54)64-103	75.9±7.5(9)62-85
Hind foot	19.5±0.7(216)17-21	19.1±0.8(54)17-20	18.8±1.4(9)17-20
Ear	17.8±1.1(216)15-21	17.1±1.1(54)12-19	16.4±1.9(9)14-20
Weight	19.4±2.3(216)11.7-28.0	14.2±1.7(54)10.0-17.8	9.6±2.2(9)6.3-12.2
Bacula length	8.9±0.8(216)5.8-10.4	7.0±0.9(54)5.5-8.8	5.5±0.5(9)4.8-6.3

Continued

Table 44. Continued

Measurement	Female		
	Adult	Subadult	Juvenile
Total length	185.0±11.5(202)143-220	163.2±10.8(43)136-183	149.6±11.1(8)135-165
Tail length	95.8±8.7(202)64-135	84.4±9.3(43)62-101	77.0±7.9(8)67-89
Hind foot	19.6±0.8(202)17-22	19.0±0.7(44)18-20	19.1±0.8(8)18-20
Ear	17.8±1.2(203)17-20	17.0±1.4(44)14-22	16.1±0.8(8)15-17
Weight	20.8±3.9(203)12.6-35.2	13.7±1.7(44)9.6-19.2	10.6±1.8(8)8.1-12.7

*The mean number is given, followed by the standard deviation, the size of the sample (in parentheses), and the range. Lengths are expressed in mm, weights in g.

As in the other rodents of the study, increased body weight accompanied breeding in *P. eremicus*. A very high percentage of adult males (49.07 %) were found to have large quantities of spermatozoa present in the caudal epididymis. These males had an average body weight of 20.44 g, 1.13 g more than that of 50 males with moderate amounts of spermatozoa (Table 45). Fertile adult males were heavier than non-fecund adult males (Table 45). Breeding females, likewise, were on the average heavier than were non-breeding females (19.15 g vs. 16.50 g). Pregnant females averaged slightly heavier than lactating females (Table 46). It was perhaps because of the high number of reproductive females (Table 47) in the population from month to month that the females weighed more than the males.

Table 45. Mean body weights (g) and bacula measurements (mm) of various ages and reproductive categories of 279 *Peromyscus eremicus* *

	N	Body Weight		Baculum	
		Mean	Range	Mean	Range
Juvenile	9	9.56	6.30-12.20	5.49	4.80- 6.30
Subadult	54	14.23	10.00-17.80	6.98	5.50- 8.80
Adult					
No spermatozoa	13	16.22	14.10-19.50	7.36	5.75- 9.60
Small amounts	43	18.01	14.90-21.70	8.51	6.25- 9.70
Moderate amounts	54	19.31	11.70-28.00	8.89	7.40-10.20
Large amounts	106	20.44	16.80-25.30	9.15	7.85-10.40

*i.e., spermatozoa content in caudal epididymes.

Table 46. Breeding characteristics of adult female *Peromyscus eremicus*—DSCODE A3UBE22

Month	Sample Size	No.	%	Gravid		No.	%	Postpartum	Placental Scars
	No.			Weight Mean±S.D.	Embryos Mean±S.D.			Weight Mean±S.D.	
1970									
Jun 10	12	8	67	24.3±3.3	2.6±0.5	3	25	21.5±1.9	3.3±0.6
Jun 20	8	2	25	19.4±4.5	2.0	2	25	21.7±2.3	3.0
Jul 10	3	3	100	21.3±1.6	2.0	0	0		
Jul 20	8	2	25	21.3±5.0	3.0	5	63	17.6±2.5	2.6±0.6
Aug 10	5	3	60	19.9±3.4	2.7±0.6	2	40	16.1±2.8	2.0
Aug 20	1	1	100	30.6	4.0	0	0		
Sep									
Oct	10	2	20	20.8±3.4	3.0±1.4	2	20	20.5±3.5	3.0
Nov	11	1	9	17.9	2.0	5	45	20.1±2.1	2.2±1.1
Dec	2	1	50	19.4	3.0	1	50	20.9	4.0
1971									
Jan	2	0	0			1	50	19.5	3.0
Feb	7	0	0			3	43	19.0±1.6	2.0±1.0
Mar	5	0	0			4	80	18.8±1.8	2.3±1.0
Apr	2	0	0			0	0		
May	2	0	0			0	0		
Jun 10	1	0	0			1	100	16.4	2.0
Jun 20	2	0	0			2	100	19.0±1.3	3.5±0.7
Jul 10	4	2	50	22.3±1.3	3.5±0.7	0	0		
Jul 20	6	1	17	22.0		3	50	20.0±1.2	3.0
Aug 10	2	2	100	22.5±2.1	2.5±0.7	0	0		
Aug 20	1	1	100	29.2	3.0	0	0		
Sep									
Oct	1	0	0			0	0		
Nov	14	8	57	24.3±2.9	2.8±0.7	3	21	20.8±1.4	2.3±0.6
Dec	13	7	54	23.5±5.6	3.0±0.6	0	0		
1972									
Jan	24	9	38	21.1±1.5	2.4±0.5	4	17	24.3±1.1	3.0
Feb	26	5	19	25.7±4.7	2.8±1.1	11	42	22.9±4.5	2.6±0.7
Mar	23	10	43	22.6±3.6	2.2±0.4	8	35	21.1±1.9	2.4±0.5
Apr	8	4	50	23.5±2.5	2.8±0.5	1	13	22.0	3.0
May									
Total	203	72	35	22.9±3.8	2.6±0.7	61	30	20.6±3.1	2.6±0.7

2.3.2.7.-62

Table 47. Summary of the reproductive cycles of *Peromyscus eremicus* based on 225 females (203 adults, 52 young) from June 1970 through May 1972—DSCODE A3UBE22

Month	Estrus	% Reproductive		% Non-reproductive	
		Pregnant	Lactating	Adult	Young
1970					
Jun 10	0	53.33	6.67	20.00	20.00
Jun 20	0	15.38	30.77	15.39	38.46
Jul 10	0	75.00	0	0	25.00
Jul 20	0	16.67	8.33	41.67	33.33
Aug 10	0	33.33	0	22.22	44.44
Aug 20	0	50.00	0	0	50.00
Sep	-	--	--	--	--
Oct	0	16.67	8.33	49.00	16.66
Nov	0	7.69	7.69	69.24	15.38
Dec	0	33.34	0	33.33	33.33
1971					
Jan	0	0	0	66.67	33.33
Feb	0	0	0	87.50	12.50
Mar	0	0	0	83.33	16.67
Apr	0	0	0	100.00	0
May	0	0	50.00	50.00	0
Jun 10	0	0	0	100.00	0
Jun 20	0	0	0	100.00	0
Jul 10	0	40.00	40.00	0	20.00
Jul 20	0	14.29	28.57	42.85	14.29
Aug 10	0	66.67	0	0	33.33
Aug 20	0	100.00	0	0	0
Sep	--	--	--	--	--
Oct	0	0	50.00	0	50.00
Nov	0	50.00	18.75	18.75	12.50
Dec	5.56	38.89	11.11	16.67	27.78
1972					
Jan	0	31.03	0	51.73	17.24
Feb	0	16.67	0	70.00	13.33
Mar	0	40.00	20.00	32.00	8.00
Apr	8.33	33.33	8.33	16.68	33.33
May	--	--	--	--	--

Perognathus penicillatus (DSCODE A3UBE21, 22)

Of those specimens of *P. penicillatus* examined, 57.2% were males. This is not a significant departure from a 1:1 ratio, especially considering the small sample size (Table 48).

Four juveniles accounted for 2.1% of the total sample of *P. penicillatus* and had a mean weight of 8.85 g and a mean total length of 143.50 mm (Table 49).

Table 48. Total semimonthly and monthly sex and age ratio of 187 *Perognathus penicillatus*—DSCODE A3UBE21,22

Month	Adult			Young			
	Males	Females	% Males	Males	Females	% Males	% Young
1970							
Jun 10	18	7	72.0	5	0	100.0	16.7
Jun 20	2	0	100.0	0	1	0	33.3
Jul 10	1	0	100.0	0	0	--	0
Jul 20	3	2	60.0	0	1	0	16.7
Aug 10	4	3	57.1	0	0	--	0
Aug 20	0	1	0	1	0	100.0	50.0
Sep	7	10	41.1	0	1	0	5.6
Oct	2	3	40.0	0	0	--	0
Nov	0	0	--	0	0	--	--
Dec	0	0	--	0	0	--	--
1971							
Jan	0	1	0	0	0	--	0
Feb	1	0	100.0	0	0	--	0
Mar	1	0	100.0	0	0	--	0
Apr	1	0	100.0	0	0	--	0
May	9	1	90.0	1	0	100.0	9.1
Jun 10	2	3	40.0	1	0	100.0	16.7
Jun 20	12	9	57.1	0	0	--	0
Jul 10	4	4	50.0	0	0	--	0
Jul 20	4	4	50.0	3	0	100.0	27.3
Aug 10	1	2	33.3	1	2	33.3	50.0
Aug 20	2	1	66.6	1	2	33.3	50.0
Sep	4	7	36.4	2	2	50.0	26.7
Oct	5	5	50.0	2	1	66.6	23.1
Nov	2	0	100.0	0	0	--	0
Dec	1	0	100.0	0	1	0	50.0
1972							
Jan	0	0	--	0	0	--	--
Feb	1	0	100.0	0	0	--	0
Mar	0	0	--	0	0	--	--
Apr	0	0	--	0	0	--	--
May	3	4	42.9	0	2	0	22.2
Total	90	67	57.3	17	13	56.7	16.0

Table 49. Body measurement statistics of 187 *Perognathus penicillatus**—DSCODE A3UBE21,22

Measurement	Male		
	Adult	Subadult	Juvenile
Total length	178.5±9.3(87)124-202	164.2±8.7(14)149-181	143.0±10.6(3)131-151
Tail length	95.2±5.4(87)82-105	90.6±7.1(14)80-104	78.0±12.5(3)65-90
Hind foot	23.0±1.3(90)20-26	22.3±1.6(14)19-24	22.0±2.0(3)20-24
Ear	7.9±0.7(90)7-10	7.3±0.7(14)6-8	6.7±1.2(3)6-8
Weight	16.8±2.7(90)10.0-25.0	12.5±2.4(14)9.4-16.5	8.4±0.3(3)8.1-8.6
Bacula	11.7±1.2(90)6.8-13.4	9.0±1.0(14)7.0-11.4	7.7±0.4(3)7.2-7.9
Female			
Total length	179.5±8.2(66)161-203	165.3±6.2(12)153-173	145.0±0(1)145
Tail length	96.8±5.3(66)84-112	90.5±5.5(12)82-98	79.0±0(1)79
Hind foot	23.7±1.4(67)22-29	22.4±0.7(12)21-23	23.0±0(1)23
Ear	8.2±0.8(67)6-11	7.8±0.6(12)7-9	7.0±0(1)7
Weight	17.0±2.2(67)13.0-23.3	13.7±3.1(12)10.0-20.0	10.2±0(1)10.2

*The mean number is given, followed by the standard deviation, the size of sample (in parentheses) and the range. Lengths are expressed in mm, weights in g.

One of the diagnostic characteristics of *P. penicillatus* is the large hind foot (Hall and Kelson, 1959). Juveniles had a mean hind foot length of 22.25 mm as compared to a mean hind foot length in 157 adults of 23.34 mm. The mean weight of juveniles was 52.4% that of adults. The mean total body length was 80.2% that of adults and the mean hind foot length was 95.3% that of adults. The disproportionately long hind limb in juveniles is of apparent adaptive value for locomotion.

Twenty-six subadults had a mean body length of 164.73 mm, a mean body weight of 13.05 g, and accounted for 13.9% of the total *P. penicillatus* trapped.

Young animals were trapped from June through September of the first year (Table 48). During the second year, however, young animals were trapped throughout the summer except in July, 1971. One young animal was trapped in October, 1971 and another in December 1971. No further young were taken until May, 1972.

Over the two-year period, 157 adult *P. penicillatus* had a mean weight of 16.89 g. The mean body weight of 67 females (17.04 g) was slightly higher than that of 90 males (16.75 g). In contrast, the average body length of females (\bar{x} =179.45 mm) and males (\bar{x} =178.47 mm) were essentially the same (Fig. 18).

Fertile males of *P. penicillatus* were approximately the same weight as non-fertile males. The reproductive males had a mean body weight of 16.88 g while non-fecund males had a mean body weight of 16.23 g (Table 50).

Adult female *P. penicillatus* did show increased body weight with fecundity. Eight lactating females had a mean body weight of 18.12 g which is heavier than any other category of male or female. Pregnant females (N=8) had a mean body weight (\bar{x} =17.85 g) slightly less than lactating females, but their mean body weight was still 1.94 g heavier than that of 17 non-reproductive females.

Table 50. Mean body weights (g) and bacula measurements (mm) of various ages and reproductive categories of 107 *Perognathus penicillatus**

	N	Body Weight		Baculum	
		Mean	Range	Mean	Range
Juvenile	3	8.40	8.10- 8.60	7.65	7.15- 7.90
Subadult	14	12.45	9.40-16.50	9.01	7.00-11.40
Adult					
No spermatozoa	19	16.23	10.00-21.10	10.03	6.80-12.70
Small amounts	13	17.58	12.10-25.00	11.46	10.10-12.80
Moderate amounts	17	16.19	12.90-20.70	12.11	11.00-12.90
Large amounts	41	16.95	13.50-24.80	12.47	11.20-13.40

* i.e., spermatozoa content in caudal epididymes.

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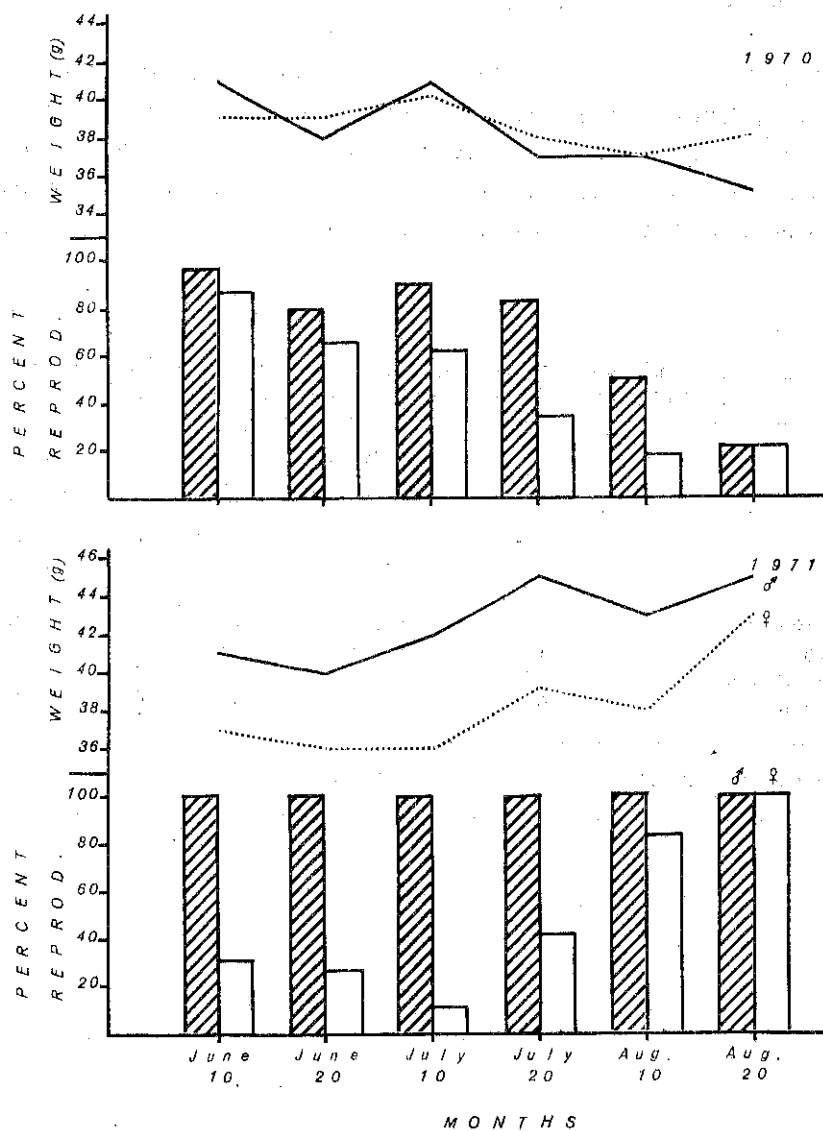


Figure 8. Summary of comparative weight fluctuations and fecundity of adult male and female *Dipodomys merriami*. Graph represents the six summer trapping periods of both years. (DSCODES A3UBE21, BE22)

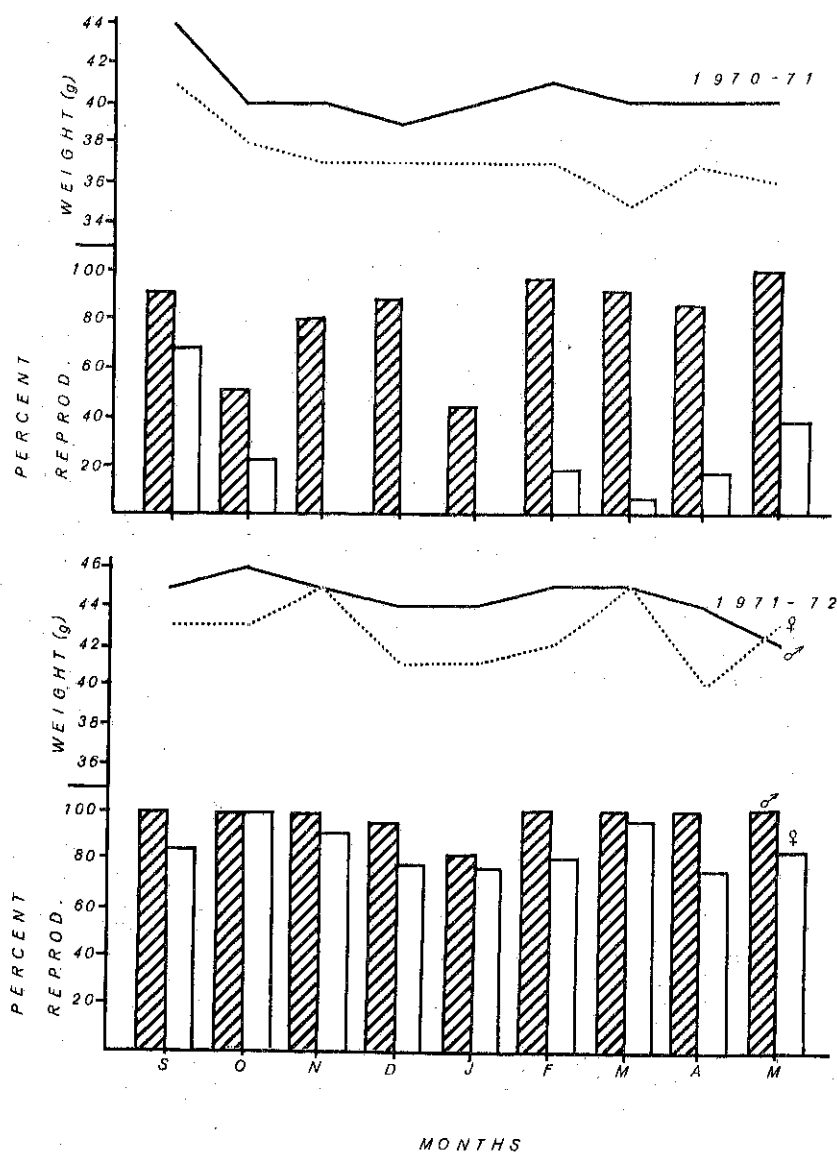


Figure 9. Summary of comparative weight fluctuations and monthly fecundity of adult male and female *Dipodomys merriami*. Graph represents months of September through May of both years. (DSCODES A3UBE21, BE22)

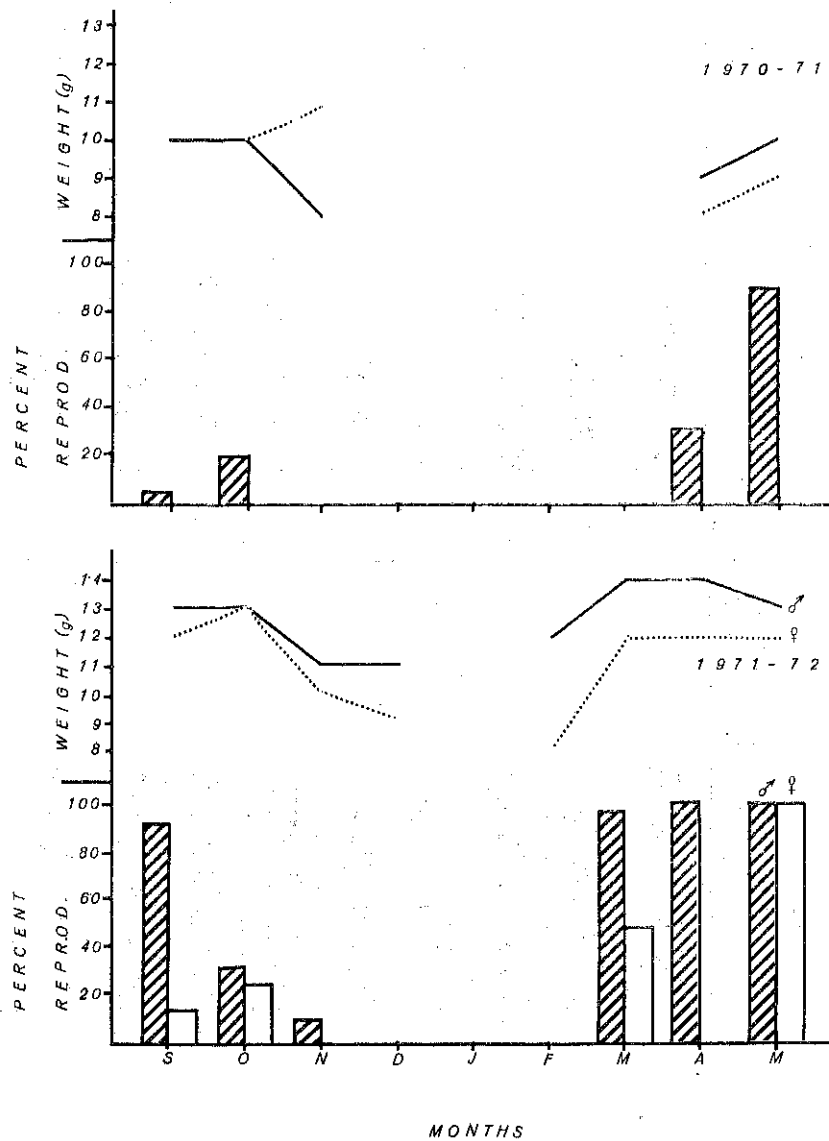


Figure 10. Summary of comparative weight fluctuations and monthly fecundity of adult male and female *Perognathus amplus*. Graph represents months of September through May of both years. Gaps in weight lines indicate lack of specimens. (DSCODES A3UBE21, BE22)

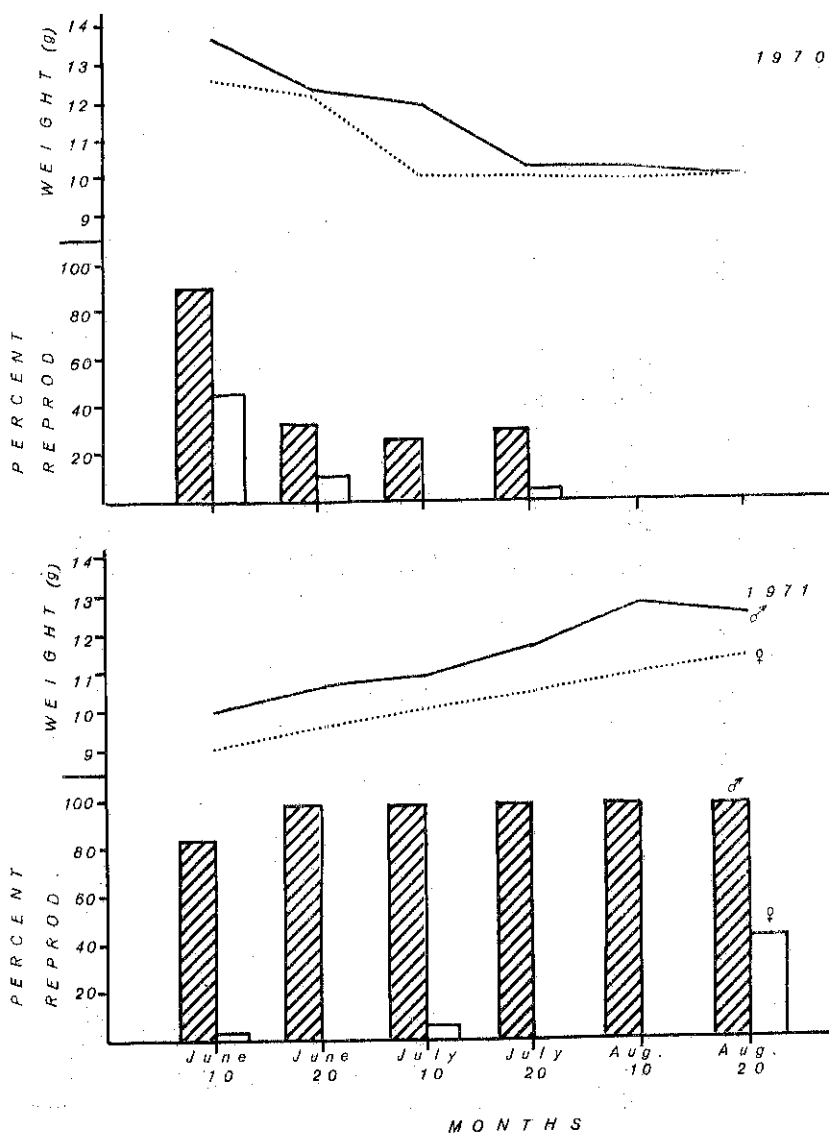


Figure 11. Summary of comparative weight fluctuations and fecundity of adult male and female *Perognathus amplus*. Graph represents the six summer trapping periods of both years (DSCODES A3UBE21, BE22)

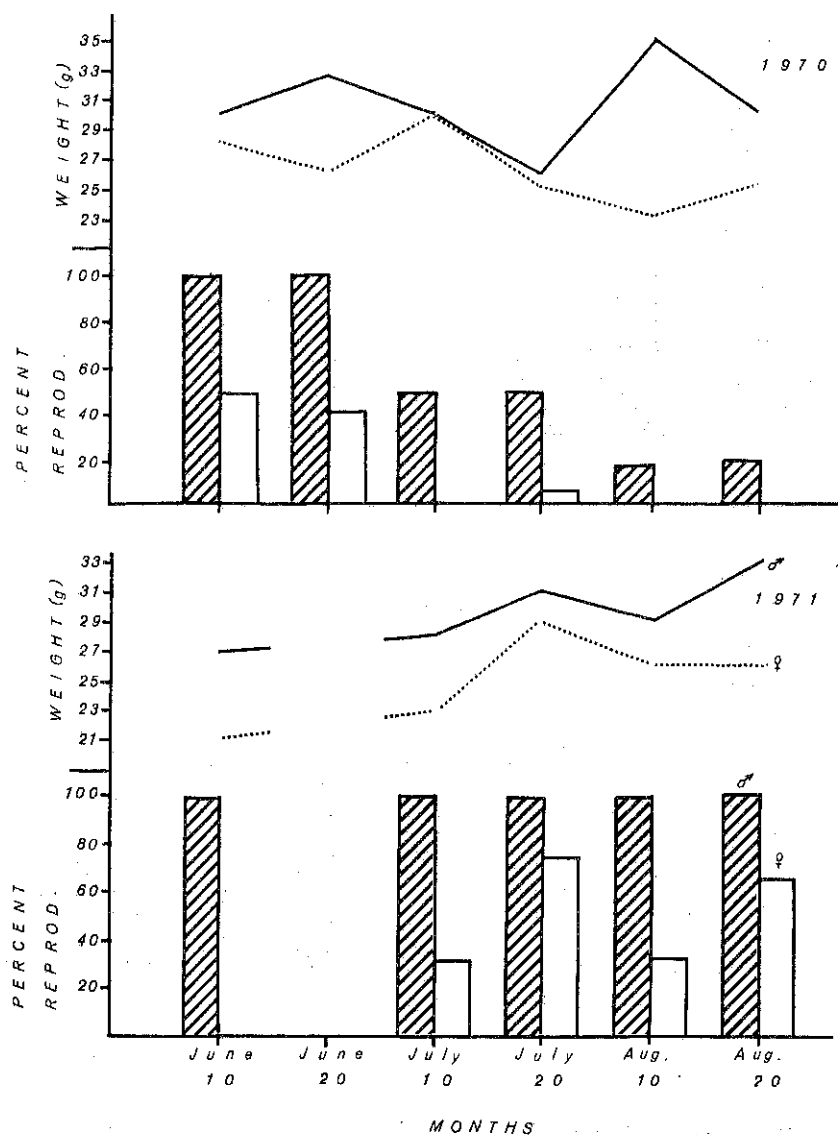


Figure 12. Summary of comparative weight fluctuations and fecundity of adult male and female *Perognathus baileyi*. Graph represents the six summer trapping periods of both years. Gaps in weight lines indicate lack of specimens. (DSCODES A3UBE21, BE22)

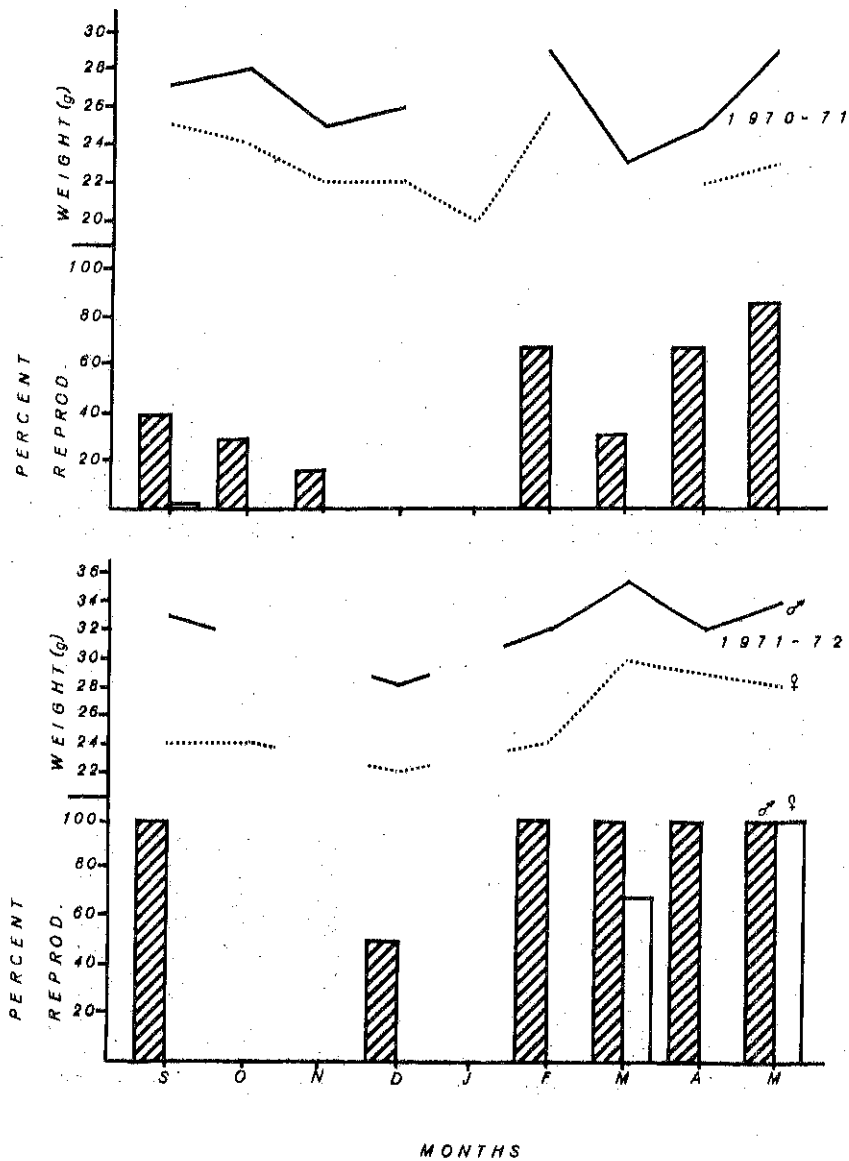


Figure 13. Summary of comparative weight fluctuations and monthly fecundity of adult male and female *Perognathus baileyi*. Graph represents months of September through May of both years. Gaps in weight lines indicate lack of specimens. (DSCODES A3UBE21, BE22)

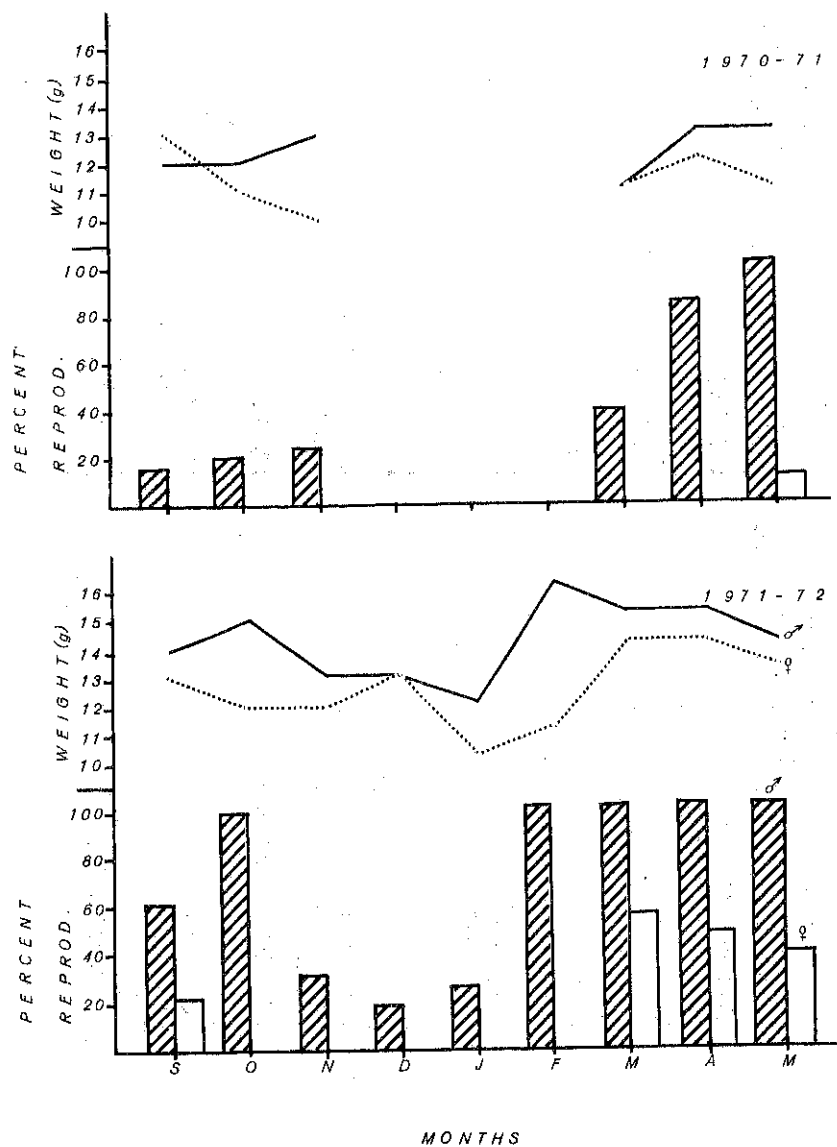


Figure 14. Summary of comparative weight fluctuations and monthly fecundity of adult male and female *Perognathus intermedius*. Graph represents months of September through May of both years. Gaps in weight lines indicate lack of specimens. (DSCODES A3UBE21, BE22)

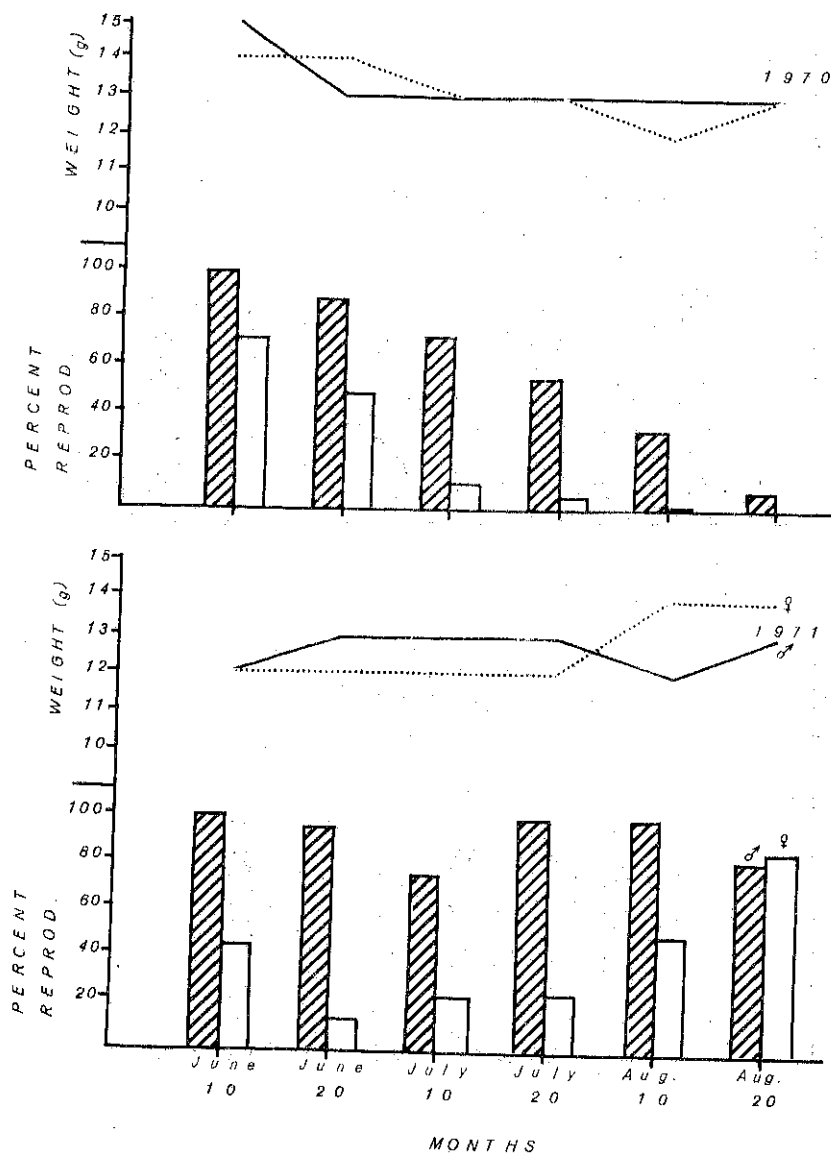


Figure 15. Summary of comparative weight fluctuations and fecundity of adult male and female *Perognathus intermedius*. Graph represents the six summer trapping periods of both years. (DSCODES A3UBE21, BE22)

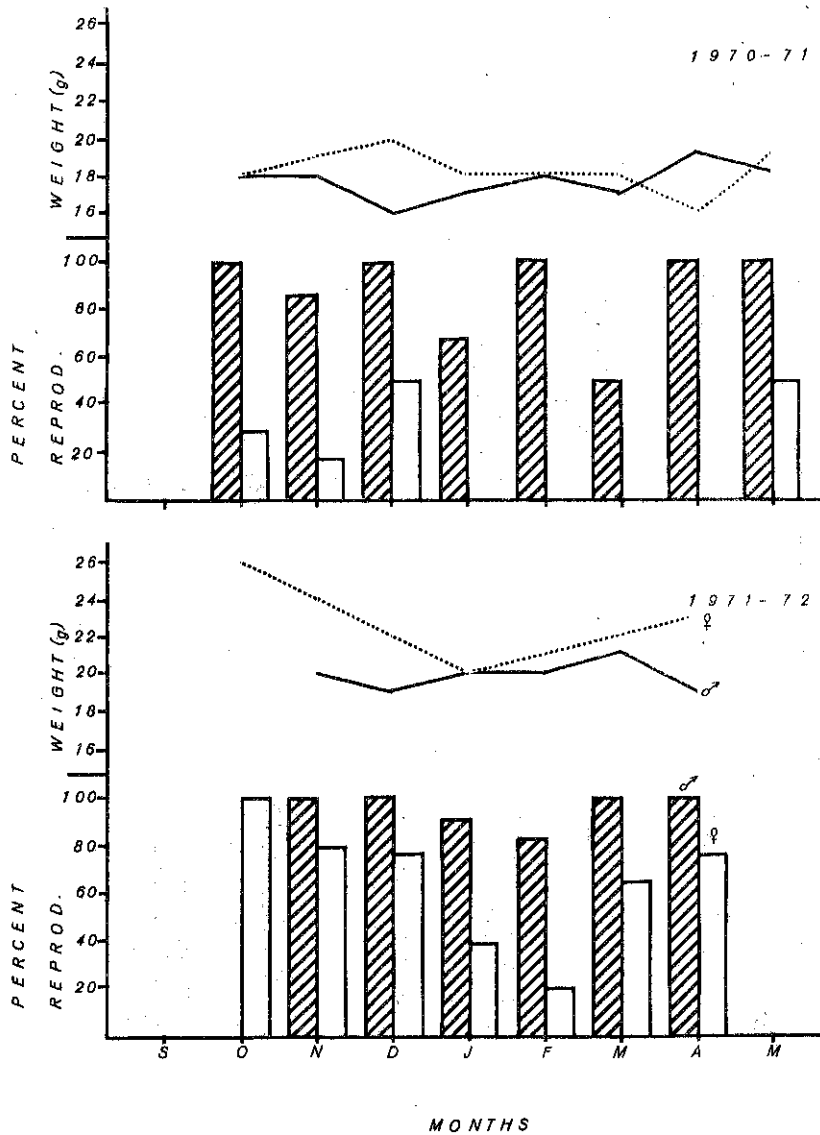


Figure 16. Summary of comparative weight fluctuations and monthly fecundity of adult male and female *Peromyscus eremicus*. Graph represents months of September through May of both years. Gaps in weight lines indicate lack of specimens. (DSCODES A3UBE21, BE22)

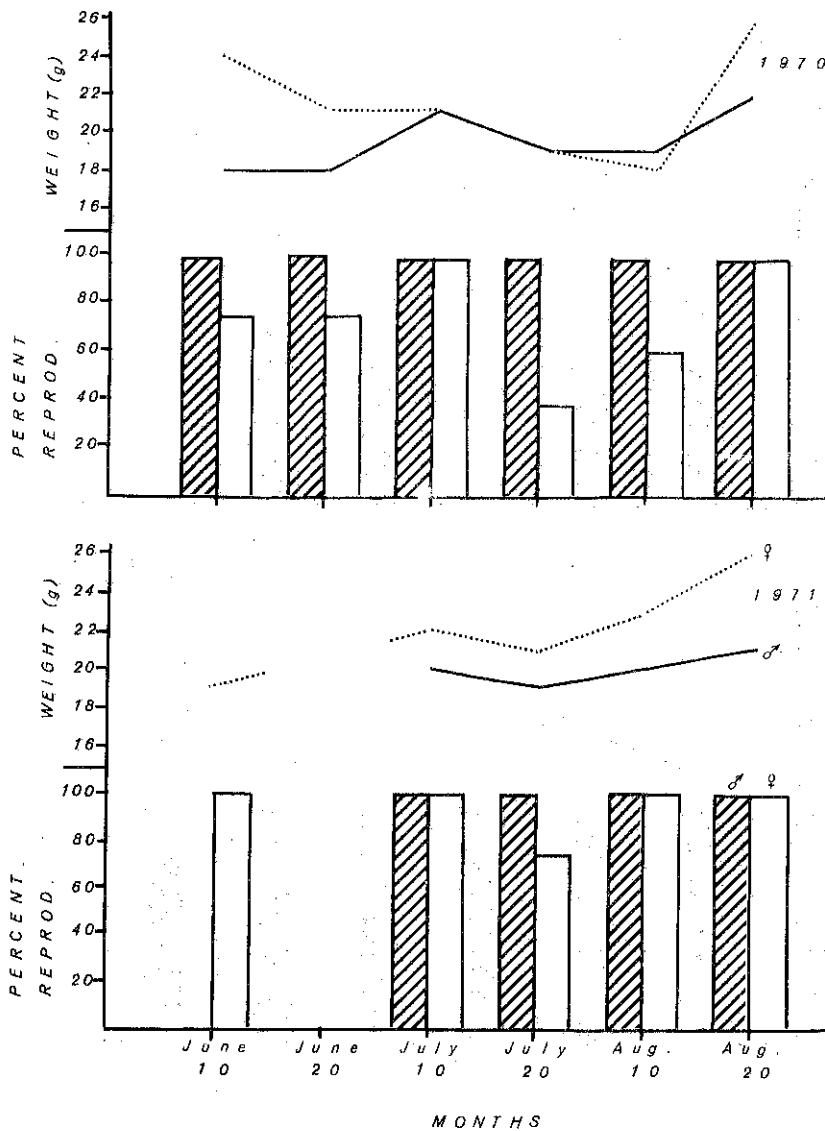


Figure 17. Summary of comparative weight fluctuations and fecundity of adult male and female *Peromyscus eremicus*. Graph represents the six summer trapping periods of both years. Gaps in weight lines indicate lack of specimens. (DSCODES A3UBE21, BE22)

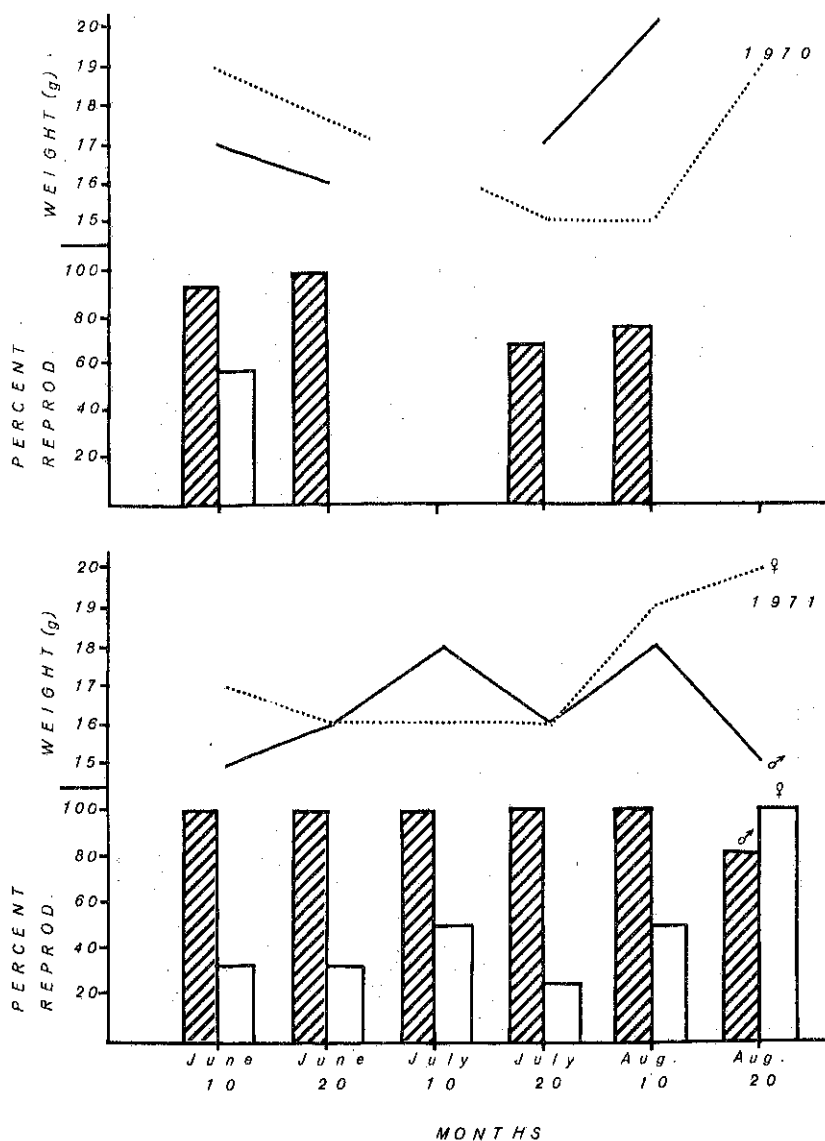


Figure 18. Summary of comparative weight fluctuations and fecundity of adult male and female *Perognathus penicillatus*. Graph represents the six summer trapping periods of both years. Gaps in weight lines indicate lack of specimens. (DSCODES A3UBE21, BE22)

REPRODUCTIVE CYCLES
(DSCODE BE21 BE22)Dipodomys merriami

Male reproductive cycle: Males had a longer reproductive season than did females and a higher, or equal, percentage of individuals reproductively active in any given trapping period (Table 51 and Fig. 8). Butterworth (1960) found active spermatozoa in *D. merriami* when the testes were longer than 5 mm, regardless of the testes position. Bradley and Mauer (1971), using the 5 mm testes dimensions as a criteria, did not examine for active spermatozoa. Care should be used in determining reproductively active animals, especially from small sample sizes. In this study many males were found to have testes longer than 5 mm with no spermatozoa. Some testes, however, were less than 5 mm in length and contained small-to-moderate amounts of spermatozoa. The last trapping period of August, 1970 revealed the lowest percentage of *D. merriami* having spermatozoa (Fig. 9). Following the summer rains in September, 1970, there was a striking increase in reproductive activity. Ninety-two percent of the adult kangaroo rats were reproductively active, an increase of 72% over the previous trapping period.

Lengths and shapes of the bacula varied according to age classification and reproductive condition (Fig. 19). Bacula of juvenile kangaroo rats (N=8) averaged 6.79 mm in length. The bacula of juveniles appeared thicker proximally in proportion to length and had greater flexion than those of other age categories. Subadults (N=63) had bacula averaging 8.49 mm and a less prominent curvature than juveniles. The bacula of 774 adults averaged 11.30 mm in length. The shaft of the adult bacula was relatively straight with a slight distal hook. The proximal end was rounded and more massive. Often when adult animals were in breeding condition, a hardened cartilagenous-like extension attached to and protruded from the distal tip. The function of this penial extension is not known but is assumed to facilitate copulation. The presence of this extension appeared to be correlated with those adult animals having large amounts of spermatozoa. Bacula from animals with large amounts of spermatozoa (N=356) averaged .20 mm longer than bacula from males with moderate amounts of spermatozoa and averaged 1.75 mm longer than adult males with no spermatozoa present (Table 32).

Measurements of various reproductive organs (Figs. 19 and 21) demonstrated size fluctuations that correlated with amounts of spermatozoa observed. Testicular dimensions (Fig. 20), caudal epididymides lengths (Fig. 21) and seminal vesicle lengths (Fig. 22) diminished as spermatozoa content declined. Males were considered reproductively active if spermatozoa were observed in the caudal epididymides. It was only during the autumn and winter of the second year, however, that the majority of males had copious amounts of spermatozoa.

2.3.2.7.-78

Table 51. Summary of the reproductive cycles of *Dipodomys merriami* based on 727 females (669 adults, 58 young) from June 1970 through May 1972—
DSCODE A3UBE22

Month	Estrus	% Reproductive		% Non-reproductive	
		Pregnant	Lactating	Adult	Young
1970					
Jun 10	1.75	54.39	14.04	10.53	19.30
Jun 20	0	55.56	11.11	33.33	0
Jul 10	0	40.00	10.00	30.00	20.00
Jul 20	0	9.09	18.18	50.00	22.73
Aug 10	0	14.29	0	71.42	14.29
Aug 20	0	20.00	0	80.00	0
Sep	4.17	37.50	20.83	29.17	8.33
Oct	0	4.17	16.67	74.99	4.17
Nov	0	0	0	96.97	3.03
Dec	0	0	0	93.75	6.25
1971					
Jan	0	0	0	100.00	0
Feb	0	17.78	0	80.00	2.22
Mar	5.88	0	0	94.12	0
Apr	0	13.33	3.33	83.34	0
May	5.77	17.31	11.54	57.69	7.69
Jun 10	0	6.67	26.67	66.66	0
Jun 20	3.23	3.23	16.13	64.50	12.91
Jul 10	0	10.00	0	85.00	5.00
Jul 20	3.57	25.00	10.71	53.58	7.14
Aug 10	34.36	45.45	0	20.19	0
Aug 20	10.34	79.31	6.90	0	3.45
Sep	0	46.15	38.46	15.39	0
Oct	0	50.00	25.00	0	25.00
Nov	0	46.15	30.77	7.70	15.38
Dec	4.76	9.52	52.38	19.05	14.29
1972					
Jan	10.00	50.00	5.00	20.00	15.00
Feb	0	55.17	20.69	20.69	3.45
Mar	0	73.33	10.00	3.33	13.33
Apr	0	40.00	20.00	20.00	20.00
May	7.69	38.47	26.92	15.39	11.54

Male fecundity in the second year contrasted with that of the first year. Virtually every trapping period of the second year yielded almost 100% of the adult male kangaroo rats in reproductive prime. Only during December, 1971 and January, 1972 were a small portion of the adult male kangaroo rats non-fecund.

Female reproductive cycle: During the first year there were two distinct peaks of reproduction for *D. merriami* (Fig. 23) which apparently is typical for kangaroo rats from southern Arizona (Reynolds, 1960) (Table 52). These two reproductive periods

correspond to the bimodal rainfall patterns typical of the lower Sonoran desert. Only during three months, November, December and January of the first year, were no females in reproductive condition recorded.

The second year was remarkably different from the first. There was a lull in reproduction in *D. merriami* during the early summer months (Fig.23) when reproductive activity of females dropped to 20%. Following this decline, however, reproduction accelerated with 100% of the adult population reproducing during August and October of 1971. Throughout August, 1971 and June, 1972 reproductive activity in *D. merriami* did not fall below the 50% level.

Table 52. Reported reproductive periods for *Dipodomys merriami*

Peaks	Months	Author
Two seasonal peaks	May and September	Reynolds (1960)
Generally two peaks	Early spring and Autumn	Van De Graaff
One peak	March, April and May	Chew and Butterworth (1964)
One peak	March and April	Bradley and Mauer (1971)
One peak	Early spring	Butterworth (1960)
One peak	Late spring	Hall (1946)
One peak	March, April and May	Alcorn (1941)

The duration of estrus condition in *D. merriami* is not known, but for *D. ordii* it is five to six days (Day et al., 1956). When a female is in estrus, the horns and body of the uterus are highly vascularized. Females in estrus had a body weight of 37.30 g; an average of 3.04 g heavier than non-fecund adult females. Increased body weight has an apparent bearing on readiness to mate (Chew, 1958). Females apparently develop a vaginal plug shortly after copulation that is shaped similar to those described for *Dipodomys deserti* by Butterworth (1961).

The body of the developing foetus could not be measured by rump-crown lengths until it was approximately 11.90 mm. Embryos near parturition had rump-crown lengths of approximately 20.30 mm. Gestation in *D. merriami* ranges between 17 to 23 days (Chew, 1958).

As in voles (Fitch, 1957) and other rodents, *D. merriami* has three pair of mammae -- one pair pectoral and the other two abdominal. Of the female kangaroo rats observed lactating, few showed evidence of utilizing the pectoral mammae. This same situation was mentioned in prairie voles by Jameson (1947) and Fitch (1957). In females that

2.3.2.7.-80

had not yet produced young, the teats were small and obscured in the fur. During lactation the teats became prominent, averaging 2.68 mm in length (range 2.20 mm to 2.95 mm). The fur around the teats was often matted down, further exposing the mammae. Subcutaneous mammary tissue was often difficult to detect even in those kangaroo rats that were obviously lactating. This inconspicuous mammary tissue might be correlated to the milk with low-water content of kangaroo rats by Kooyman (1963).

Ovarian dimensions in *D. merriami* are a reliable and sensitive indicator of reproductive activity (Table 53). The smooth, pinkish, turgid ovaries of juveniles had the smallest dimensions. Subadults had larger ovaries with a darker coloration. Ovaries of females in estrus averaged 0.40 mm longer and 0.5 mm wider than those of non-reproductive adults. The ovarian dimensions remained consistent from estrus through pregnancy, regressing slightly during lactation. Average ovary length and average ovary width of postpartum females with placental scars was 2.2 ± 0.3 and 1.4 ± 0.4 respectively. Although corpora lutea of pregnancy were observed, no data concerning their appearance or duration were recorded.

The horns of the uteri of juvenile kangaroo rats were pale pink, translucent, and slightly thicker than in subadults. Uteri of females in estrus were swollen and often a deep red color from the presence of increased vascularization (Table 54). Implantation generally occurred midway down the horn of the uterus from the ovary. Generally an embryo developed in either horn with one or three implantations occasionally occurring. In multiple foetal development the embryos were never in only one horn.

There were only five instances of embryo resorption out of 193 pregnancies. All five resorptions occurred in multiple pregnancies, involved one embryo, and occurred in summer.

Placental scars are large and black immediately postpartum and are located on the medial side of the horn of the uterus. The duration of the scar is not known in *D. merriami* but is assumed to be approximately one year following parturation. The older the placental scar, the more difficult it is to detect as it becomes both lighter and smaller with age. Each trapping period had a high percentage of adults with placental scars; the fewest occurring in the last half of July, 1970 when 12% had scars. The high incidence of placental scars suggests a good carry-over of individuals each year, concurring with the findings of Chew and Butterworth (1964).

Table 53. Ovarian dimensions (mm) of 2,240 adult females representing the six species of desert rodents studied at the Silverbell Biome site *

Species	Non-reproductive	Estrus	Pregnant	Lactating
<i>Dipodomys merriami</i>	length width	2.5±0.4(20)1.9-3.2 1.8±0.5(20)1.1-2.5	2.5±0.4(193)1.3-4.0 1.8±0.3(193)0.9-2.5	2.4±0.3(87)1.5-3.3 1.6±0.3(87)1.0-2.7
<i>Perognathus amplus</i>	length width	1.9±0.2(17)1.6-2.2 1.4±0.2(17)1.2-1.9	1.7±0.3(32)1.3-2.7 1.3±0.3(32)0.8-2.0	1.7±0.4(17)1.2-2.5 1.2±0.4(17)0.7-2.2
<i>Perognathus baileyi</i>	length width	2.5±0.3(4)2.2-2.8 1.7±0.2(4)1.6-2.0	2.6±0.4(16)1.7-3.2 2.0±0.4(16)1.3-2.8	2.2±0.4(9)1.6-2.7 1.5±0.3(9)1.0-1.9
<i>Peromyscus eremicus</i>	length width	2.2±0.2(2)2.0-2.3 1.6±0.2(2)1.5-1.7	2.3±0.7(72)1.0-4.0 1.8±0.5(72)1.0-2.7	2.2±0.6(25)1.5-3.9 1.7±0.4(25)1.0-2.6
<i>Perognathus intermedius</i>	length width	1.9±0.2(16)1.6-2.3 1.3±0.2(16)1.0-1.6	2.0±0.4(82)1.1-3.0 1.5±0.3(82)0.8-2.2	1.8±0.3(45)1.2-2.5 1.3±0.4(45)0.6-2.8
<i>Perognathus penicillatus</i>	length width	1.9±0.2(16)1.6-2.3 1.3±0.2(16)1.0-1.6	2.1±0.3(8)1.6-2.5 1.6±0.4(8)1.1-2.4	2.2±0.4(8)1.8-2.9 1.6±0.4(8)1.1-2.5

* The mean number is given, followed by the standard deviation, the size of the sample (in parentheses), and the range (DSCODE A3UBE22).

Table 54. Measurements (mm) of the length and width of the ovaries and the uteri of adult female *Dipodomys merriami*-----DSCODE A3UBE22

Month	No.	Length		Ovary		Width		Uterus	
		Mean	S.D.	No.	Mean	S.D.	No.	Mean	S.D.
1970									
Jun 10	46	2.2	0.2	46	1.5	0.2	46	2.3	0.6
Jun 20	9	2.4	0.2	9	1.4	0.2	9	2.1	1.0
Jul 10	8	2.4	0.3	8	1.6	0.2	8	2.2	0.5
Jul 20	17	2.3	0.3	17	1.6	0.2	17	2.2	0.4
Aug 10	12	2.2	0.4	12	1.5	0.3	12	2.0	0.4
Aug 20	10	2.4	0.3	10	1.8	0.3	10	2.4	0.5
Sep	22	2.2	0.3	22	1.4	0.4	22	1.7	0.4
Oct	46	2.1	0.3	46	1.2	0.2	46	1.6	0.3
Nov	32	1.9	0.3	32	1.1	0.2	32	1.8	0.4
Dec	30	1.9	0.3	20	1.1	0.3	30	1.7	0.3
1971									
Jan	29	2.0	0.3	29	1.0	0.2	29	1.5	0.4
Feb	44	2.2	0.3	44	1.4	0.3	44	2.1	0.7
Mar	17	2.1	0.3	17	1.3	0.2	17	1.8	0.3
Apr	30	2.0	0.2	30	1.3	0.3	30	1.9	0.5
May	48	2.4	0.3	48	1.7	0.3	48	2.3	0.7
Jun 10	15	2.5	0.3	15	1.7	0.2	15	1.7	0.2
Jun 20	27	2.4	0.2	27	1.7	0.2	27	2.1	0.4
Jul 10	19	2.5	0.3	19	1.8	0.2	19	2.1	0.3
Jul 20	26	2.5	0.3	26	1.8	0.3	26	2.6	0.7
Aug 10	11	2.7	0.3	11	2.1	0.3	11	2.6	0.3
Aug 20	28	2.8	0.3	28	2.1	0.2	28	3.0	0.8
Sep	13	2.6	0.3	13	1.9	0.3	13	2.6	0.4
Oct	3	2.9	0.2	3	2.0	0.3	3	2.3	0.1
Nov	11	2.4	0.3	11	1.7	0.2	11	2.4	0.7
Dec	18	2.3	0.4	18	1.7	0.2	18	2.5	0.6
1972									
Jan	17	2.4	0.3	17	1.6	0.2	17	2.6	0.3
Feb	28	2.2	0.3	28	1.6	0.3	28	2.5	0.6
Mar	26	2.7	0.4	26	1.9	0.4	26	3.1	0.7
Apr	4	2.6	0.1	4	2.1	0.1	4	3.4	0.6
May	23	2.6	0.3	23	1.8	0.2	23	2.8	0.6
Total	669	2.3	0.4	669	1.5	0.4	669	2.2	0.7

D. merriami kangaroo rats may breed before reaching adult weight, especially if optimum environmental conditions prevail. Reynolds (1960) found several pregnant females in the fall which were about 70% of their mature weight. In this study, immature females were also found breeding, especially in autumn and when ideal conditions existed (i.e., presence of green annuals and continued rainfall). Young animals clearly breed within the year of their birth.

In southern Arizona, *D. merriami* is seasonally polyestrous. There were many instances of postpartum estrus in lactating females or females that were pregnant and also lactating. Reynolds (1960), Lidicker (1960), Chew and Butterworth (1964), and Bradley and Mauer (1971) have all found indications that female *D. merriami* are polyestrous throughout their range.

Litter sizes in *D. merriami* vary in different areas of its geographic range (Table 55). Seemingly, litter sizes are largest in localities where there are shortened breeding seasons. Litter sizes from pregnant females in the Silverbell study area averaged 2.03 (Table 55). Placental scars from females gave evidence of litter sizes of 2.00.

Table 55. Reported litter size in *Dipodomys merriami*

Litter size	Sample	Author	Location
2.02	133	Reynolds (1960)	Santa Rita Experimental Station, Pima Co., Arizona
2.03	193	Van De Graaff	Silverbell Biome Site, Pima Co., Arizona
2.10	9	Doran (1952)	San Bernardino Co., California
2.30	4	Eisenberg (1963)	Kern Co., California
2.60	163	Bradley and Mauer (1971)	Las Vegas, Nevada
2.67	127	Lidicker (1960)	Southwest Deserts (over entire range)
3.00	72	Hall (1946)	Nevada
3.10	32	Alcorn (1941)	Churchill Co., Nevada

Compared to other heteromyids, *D. merriami* seems to have lengthened their reproductive period with repeated litters and reduced their litter size (Eisenberg, 1963).

The reproductive performance of *D. merriami* in the first year contrasted with that of the second in the following ways: 1) There were two distinct peaks in the reproductive pattern; 2) activity intensities were lower as indicated by trapping percentages and 3) average body weights were lower. During the first year less greenery was available and was ingested and there was less rainfall.

Perognathus amplus

Male reproductive cycle: Males had a longer reproductive season than did females and a higher percentage of reproductive males were recorded. In *P. amplus* distinctive reproductive peaks were observed; the first year differing from that of the second.

2.3.2.7.-84

Reproduction in the first year for *P. amplus* terminated by August, 1970. During the first half of June 1970, 87% of the adult males were reproductively active (Fig. 11). There was a rapid decline in fertile males from mid-June through July and by August no reproductive adult males were trapped. Following the late summer rains, a few of the adult males (5% in September and 18% in October) became reproductive although no females were found to be reproductive. Those male *P. amplus* trapped immediately prior to winter (November) inactivity had once again become reproductively dormant. Upon emergence from inactivity (April), the number of males that were fertile rapidly increased to 89% by May. Females did not show a corresponding increase in percent reproduction (Fig. 10), so apparently conditions necessary for reproduction did not occur.

The reproduction in the second year was strikingly different from that of the first. Whereas the males showed limited signs of reproduction during the summer months of the first year (Fig. 11) 100% of the adult males trapped from mid-June through August of the second year were reproductively active. The second summer was cooler and moister than the summer of the first year. With the onset of autumn and winter, the adult males responded as they did the first year with a gradual tapering off of reproductive activity prior to their winter's inactivity. *Perognathus amplus* did not remain dormant so long the second year, however, and virtually all of the adult males captured on the surface from January through May, 1972 were fertile.

Lengths of the various reproductive organs in adult male *P. amplus* were good indicators of reproductive activity (Figs. 24 and 25). Testicular dimensions, lengths of the caudal epididymis and seminal vesicles reflected the presence of spermatozoa and hence seasonal fertility.

In *P. amplus* a distinct correlation occurs between the size and shape of the bacula and age and presence of spermatozoa in the caudal epididymides (Fig. 19 and Table 36). The bacula of 15 juveniles averaged 4.85 mm in length; the bacula of 130 subadult males averaged 5.24 mm; those of 555 adult males averaged 6.63 mm. The shaft of the bacula of juveniles was straight with a sharp, terminal distal hook. The bacula of subadults also were characterized by straight shafts, but the distal hooks were not so prominent. The bacula of adults were more robust proximally and the shaft had more curvature. The distal portion, however, was similar to that of subadults. Bacula from 192 animals with large amounts of spermatozoa averaged 7.52 mm in length. This was 164 mm longer than bacula from 34 males with small amounts of spermatozoa present. Non-reproductive adult males had bacula that averaged only 5.74 mm which was 1.78 mm shorter than animals with large amounts of spermatozoa.

Female reproductive cycle: During the spring of the first year there was only one peak in reproduction in *P. amplus* (Fig. 26 and Table 56). One pregnant female was trapped during the last half of July, 1970, however, after the culmination of the main reproductive period. Rainfall was low the winter and spring of the first year and although some males became fertile in the spring, no reproductive females were trapped until the last half of August 1971.

Table 56. Summary of the reproductive cycles of *Perognathus amplus* based on 710 females (530 adults, 180 young) from June, 1970 through May, 1972
DSCODE A3UBE22

Month	Estrus	% Reproductive		% Non-reproductive	
		Pregnant	Lactating	Adult	Young
1970					
Jun 10	0	12.43	4.32	18.92	64.33
Jun 20	4.76	0	4.76	47.62	42.86
Jul 10	0	0	0	72.22	27.78
Jul 20	0	4.76	0	66.97	28.57
Aug 10	0	0	0	91.18	8.82
Aug 20	0	0	0	77.78	22.22
Sep	0	0	0	90.00	10.00
Oct	0	0	0	100.00	0
Nov	0	0	0	100.00	0
Dec	--	--	--	--	--
1971					
Jan	--	--	--	--	--
Feb	--	--	--	--	--
Mar	--	--	--	--	--
Apr	0	0	0	100.00	0
May	0	0	0	77.78	22.22
Jun 10	0	0	2.08	91.67	6.25
Jun 20	0	0	0	97.56	2.44
Jul 10	0	0	2.50	92.50	5.00
Jul 20	0	0	0	93.33	6.67
Aug 10	0	0	0	100.00	0
Aug 20	15.63	18.75	6.25	49.99	9.38
Sep	0	0	14.29	85.70	0
Oct	0	0	16.67	50.00	33.33
Nov	0	0	0	77.78	22.22
Dec	0	0	0	100.00	0
1972					
Jan	--	--	--	--	--
Feb	0	0	0	100.00	0
Mar	45.00	5.00	0	50.00	0
Apr	0	0	0	100.00	0
May	33.33	16.67	16.67	0	33.33

Reproduction patterns in the second year differed from those of the first year; whereas a spring peak in reproduction was apparent during 1970, reproduction in 1971

2.3.2.7.-86

came only after ample summer rains and the appearance of large amounts of green vegetation. Reproduction continued from the last half of August 1971 through September and October and then abruptly terminated with the onset of cold weather. In the spring of the second year reproduction again resumed in *P. amplus* following an abundant production of winter annuals.

Of 710 females examined, only 17 were in estrus. The low number of females trapped that were in estrus may be due to the relatively brief time of reproductive activity (Fig. 26). The duration of estrus for *P. amplus* has not been established but is probably not more than a few days; nor is the gestation period known for *P. amplus*.

Females in estrus had a significantly higher body weight (11.64 g) over adult, non-reproductive females (9.55 g). Conditions conducive for increased body weights (i.e., green vegetation) may also be a prerequisite for initiating estrus in females. Although vaginal plugs were not observed in *P. amplus*, presumably they do occur as they have been observed in other species of *Perognathus*.

Unlike *D. merriami*, the ovarian measurements of *P. amplus* could not be used as an indicator of reproductive activity because they did not seasonally change in size (Table 57). The condition of the ovaries did change with the production of ova, but no observations of these data were tabulated. The width of the uterus and the condition of placental scars were reliable indicators of reproductive activity in *P. amplus*.

The horns of the uteri in juvenile *P. amplus* resembled translucent threads and had a mean width of 0.52 mm. The uterine horns of subadults had a mean width of 0.63 mm and were no longer translucent but rather had a pale pinkish-white coloration. The uterine horns of non-fecund adult females were more pinkish in coloration and averaged 0.82 mm in width. Uterine horns of females in estrus became highly vascularized, had a deep red coloration, and were enlarged to a width of 1.67 mm.

The mean widths of the uterine horns of 126 pregnant females (1.26 mm) and of 17 lactating females (1.40 mm) were not as great as those females in estrus.

No cases of reabsorption of embryos in *P. amplus* were observed, suggesting that reproduction only occurred in prime females during optimal environmental conditions.

Table 57. Measurements (mm) of the length and width of the ovaries and the uteri of adult female *Perognathus amplus*—DSCODE A3UBE22

Month	No.	Ovary			Uterus				
		Length		Width					
		Mean	S.D.	No.	Mean	S.D.	No.	Mean	S.D.
1970									
Jun 10	66	1.5	0.3	66	1.0	0.2	66	1.9	0.4
Jun 20	12	1.7	0.4	12	1.2	0.3	12	1.4	0.3
Jul 10	26	1.4	0.2	26	1.0	0.2	26	1.1	0.3
Jul 20	15	1.5	0.2	15	1.0	0.1	15	1.3	0.3
Aug 10	62	1.4	0.2	62	0.9	0.1	62	1.1	0.2
Aug 20	14	1.4	0.2	14	0.9	0.1	14	1.2	0.1
Sep	36	1.3	0.2	36	0.8	0.1	36	0.8	0.2
Oct	7	1.4	0.2	7	0.9	0.2	7	0.9	0.2
Nov	1	0.9	0	1	0.9	0	1	1.0	0
Dec	0	--	--	0	--	--	0	--	--
1971									
Jan	0	--	--	0	--	--	0	--	--
Feb	0	--	--	0	--	--	0	--	--
Mar	0	--	--	0	--	--	0	--	--
Apr	9	1.5	0.2	9	1.0	0.2	9	1.1	0.2
May	7	1.7	0.1	7	1.3	0.1	7	1.2	0.2
Jun 10	45	1.8	0.2	45	1.3	0.1	45	1.3	0.1
Jun 20	40	1.7	0.2	40	1.3	0.2	40	1.3	0.2
Jul 10	38	1.7	0.2	38	1.2	0.2	38	1.3	0.3
Jul 20	42	1.3	0.2	42	0.9	0.2	42	0.9	0.2
Aug 10	23	1.9	0.2	23	1.5	0.1	23	1.4	0.3
Aug 20	29	1.9	0.3	29	1.5	0.2	29	1.5	0.3
Sep	7	1.6	0.1	7	1.1	0.1	7	1.5	0.3
Oct	8	1.7	0.2	8	1.4	0.3	8	1.5	0.2
Nov	7	1.5	0.2	7	1.1	0.2	7	1.0	0.1
Dec	1	1.2	0	1	0.8	0	1	1.1	0
1972									
Jan	0	--	--	0	--	--	0	--	--
Feb	1	1.9	0	1	1.3	0	1	1.0	0
Mar	20	1.9	0.8	20	1.4	0.2	20	1.7	0.3
Apr	10	2.0	0.3	10	1.5	0.3	10	1.7	0.3
May	4	1.9	0.3	4	1.6	0.2	4	1.6	0.3
Total	530	1.6	0.3	530	1.1	0.3	530	1.3	0.4

Placental scars were recorded in 195 females and averaged 4.15 per female (Table 58). There were only two instances of pregnant females having recent placental scars, both occurring in September 1971. *Perognathus amplus* usually has one litter per season, but some individuals were observed to be polyestrous.

Table 58. Breeding Characteristics of adult female *Perognathus amplus*---DSCODE A3UBE22

Month	Sample Size No.	No.	%	Gravid		No.	%	Postpartum	
				Weight Mean±S.D.	Embryos Mean±S.D.			Weight Mean±S.D.	Placental Scars Mean±S.D.
1970									
Jun 10	66	23	35	13.4±1.3	4.3±0.5	22	33	12.7±1.4	4.2±0.5
Jun 20	12	0	0			5	42	13.5±1.3	4.2±0.5
Jul 10	26	0	0			4	15	11.0±1.6	4.3±0.5
Jul 20	15	1	7	10.6	3.0	4	27	10.6±1.3	4.0±0.8
Aug 10	62	0	0			12	19	10.8±0.8	4.1±0.5
Aug 20	14	0	0			4	29	11.3±2.1	4.0
Sep	36	0	0			9	25	11.6±1.6	4.9±1.1
Oct	7	0	0			2	29	9.4±1.4	5.0
Nov	1	0	0			1	100	10.9	4.0
Dec									
1971									
Jan									
Feb									
Mar									
Apr	9	0	0			2	22	8.9±1.1	4.5±0.7
May	7	0	0			3	43	9.3±0.8	4.3±0.6
Jun 10	45	0	0			12	27	9.7±1.1	4.2±0.6
Jun 20	40	0	0			17	43	9.9±1.1	3.9±0.9
Jul 10	38	0	0			17	45	10.8±1.2	3.9±0.8
Jul 20	42	0	0			14	33	11.5±1.3	4.3±0.9
Aug 10	23	0	0			9	39	12.6±2.1	4.2±0.7
Aug 20	29	6	21	12.7±1.9	4.0±0.6	8	28	11.5±1.3	4.0±0.5
Sep	7	0	0			4	57	13.1±2.2	4.3±0.5
Oct	8	0	0			3	38	15.3±3.5	4.3±0.6
Nov	7	0	0			0	0		
Dec	1	0	0			0	0		
1972									
Jan									
Feb	1	0	0			0	0		
Mar	20	1	5	13.2	5.0	5	25	12.0±1.6	3.8±0.5
Apr	10	0	0			5	50	12.4±1.5	3.8±0.5
May	4	1	25	11.2	3.0	0	0		
Total	530	32	6	13.1±1.5	4.2±0.6	162	31	11.4±1.8	4.2±0.7

Perognathus baileyi

Male reproductive cycle: Males had a longer breeding period than the females and a larger percentage of males than females were reproductive during the reproductive period. These periods of greatest sexual activity were concurrent with new vegetative growth; Reynolds and Haskell (1949) found a similar pattern in southern Arizona.

Data gathered during the first year indicated a breeding period in late spring (as shown by young animals and postpartum females). All of the adult males trapped in June 1970 were fertile. During the continued aridity and hot weather in July, fertility in males rapidly declined. A second breeding peak occurred in August, following summer rains. From this reproductive peak, percentages of fecund males gradually declined through the remainder of the autumn (Fig. 13). Most males were fecund from February through May even though no reproductive females were observed during that same period.

In the second year, in contrast to the first, nearly all of the adult males examined were fertile. Only during December of 1971 were some adult males taken that were not reproductively active.

Bacula from *P. baileyi* were examined for changes associated with age and with reproductive status (Fig. 19). Bacula of four juveniles averaged 8.10 mm in length; they were poorly ossified, and had a straight shaft with only a slight distal hook. Bacula from 30 subadults averaged 8.66 mm in length. Although they were only slightly longer than those of juveniles, they were thicker and had a distinct angle on the tip. The bacula of adults were characterized by their long, thin shape with only a slight hook at the end. Bacula of *P. baileyi* differ markedly from the bacula of the other heteromyids studied.

As in the other heteromyids examined, males with large numbers of spermatozoa had long bacula. The bacula of non-breeding adults averaged 9.26 mm in length as compared to 10.29 mm in individuals with small amounts of spermatozoa, 11.05 mm in adults with moderate amounts, and 11.11 mm in individuals with large amounts. Certainly there is not a regression in the size of the bacula after culmination of breeding, but apparently selective forces favor longer bacula in males that are sexually mature.

Other male reproductive organs also show a linear size increase with age and fecundity. The mean length of testes in juveniles was 4.23 mm; in subadults it was 4.27 mm; in reproductive adults with small amounts of spermatozoa, the length of testes averaged 5.30 mm; and in males having large amounts of spermatozoa, the length of testes averaged 7.08 mm.

There was a definite seasonal pattern of change in testicular size (Fig. 27). The testes in *P. baileyi* decreased in size during late summer and early autumn of both years, but in the second year the testes of adult males were consistently larger than they were in the first year. A similar pattern was apparent with the seminal vesicles and caudal epididymis (Fig. 28).

2.3.2.7.-90

Female reproductive cycle: Reproduction in *P. baileyi* from southern Arizona varies with weather patterns. Reynolds and Haskell (1949) reported a peak in reproductive activity in the late spring for *P. baileyi*, with reproduction diminishing through June and July, but gaining impetus again in August following summer rains. Reproduction in the first year of our study showed a similar trend, with reproduction being most intense in the late spring, diminishing during the hottest and driest portion of the summer, and then a few females becoming active again following summer rains (Fig. 29).

Reproduction in the second year was delayed until late summer (July and August), presumably due to scarcity of rain and the resulting delay in the germination of annual vegetation. By spring of the second year (March, April and May, 1972), females were again reproductive. Considering the normal pattern of rainfall, reproduction in late spring for *P. baileyi* is probably the usual pattern.

The samples included few females in reproductive condition; of those examined, only four were in estrus, 16 were pregnant, and nine were lactating (Table 59). These 29 breeding females represented 12.13% of the female population and 13.74% of the adult female population. The small percentage of *P. baileyi* females in reproductive condition suggests low population turnovers and long individual life spans.

Although few reproductive females were examined, changes in the sizes of reproductive organs were noted. One juvenile was found to have a width of the uterine horn of 0.95 mm with other features of the reproductive tract typical of heteromyids (as described for *P. intermedius*). The uterine horn of 27 subadults averaged 0.87 mm in width. Females in estrus had an average uterine horn width of 1.96 mm. This is over a full mm wider than non-reproductive adults. Sixteen pregnant females had a mean uterine horn width of 2.45 mm and nine lactating females, 1.83 mm. Changes in the dimensions of the ovaries for various stages of reproductive females were not so drastic as changes in the uterine horns (Table 60).

The mean number of placental scars in females was only slightly higher than the mean number of embryos in pregnant females (3.57 vs. 3.50) (Table 61). One subadult female was observed with two recent placental scars, indicating breeding in some subadults. There was no evidence that *P. baileyi* was seasonally polyestrus.

Table 59. Summary of the reproductive cycles of *Perognathus baileyi* based on 239 females (211 adults, 28 young) from June 1970 through May, 1972
DSCODE A3UBE22

Month	Estrus	% Reproductive		% Non-reproductive	
		Pregnant	Lactating	Adult	Young
1970					
Jun 10	0	36.37	0	36.36	27.27
Jun 20	0	9.09	22.73	45.45	22.73
Jul 10	0	0	0	50.00	50.00
Jul 20	0	0	5.26	68.42	26.32
Aug 10	0	0	0	66.67	33.33
Aug 20	0	0	0	66.67	33.33
Sep	2.50	0	0	90.00	7.50
Oct	0	0	0	100.00	0
Nov	0	0	0	93.75	6.25
Dec	0	0	0	100.00	0
1971					
Jan	0	0	0	100.00	0
Feb	0	0	0	100.00	0
Mar	--	--	--	--	--
Apr	0	0	0	100.00	0
May	0	0	0	100.00	0
Jun 10	0	0	0	100.00	0
Jun 20	--	--	--	--	--
Jul 10	20.00	10.00	0	60.00	10.00
Jul 20	0	25.00	50.00	25.00	0
Aug 10	0	28.00	0	57.71	14.29
Aug 20	33.33	33.33	0	33.34	0
Sep	0	0	0	100.00	0
Oct	0	0	0	100.00	0
Nov	0	0	0	77.78	22.22
Dec		0	0	100.00	0
1972					
Jan	--	--	--	--	--
Feb	0	0	0	100.00	0
Mar	0	66.67	0	33.33	0
Apr	--	--	--	--	--
May	0	33.33	33.33	0	33.34

2.3.2.7.-92

Table 60. Measurements (mm) of the length and width of the ovaries and the uteri of adult female *Perognathus baileyi*—DSCODE A3UBE22

Month	No.	Ovary		No.	Uterus		No.	Mean	S.D.
		Length	Width		Length	Width			
		Mean	S.D.		Mean	S.D.		Mean	S.D.
1970									
Jun 10	8	2.1	0.5	8	1.5	0.4	8	2.0	0.9
Jun 20	17	2.1	0.3	17	1.5	0.2	17	2.1	0.5
Jul 10	1	2.2	0	1	1.6	0	1	1.6	0
Jul 20	14	1.9	0.4	14	1.4	0.3	14	1.8	0.3
Aug 10	10	2.1	0.2	10	1.3	0.2	10	1.4	0.4
Aug 20	4	2.0	0.3	4	1.2	0.1	4	1.4	0.3
Sep	37	1.8	0.3	37	1.1	0.3	37	1.2	0.3
Oct	29	1.8	0.3	29	1.0	0.2	29	1.3	0.3
Nov	15	1.8	0.2	15	1.0	0.2	15	1.3	0.4
Dec	8	1.7	0.1	8	0.9	0.2	8	1.0	0.3
1971									
Jan	1	1.7	0	1	1.0	0	1	1.3	0
Feb	1	2.0	0	1	1.4	0	1	2.7	0
Mar	0	--	--	0	--	--	0	--	--
Apr	2	2.0	0.2	2	1.1	0.1	2	1.6	0.1
May	5	2.3	0.3	5	1.8	0.3	5	1.7	0.4
Jun 10	6	2.1	0.1	6	1.6	0.1	6	1.5	0.3
Jun 20	0	--	--	0	--	--	0	--	--
Jul 10	9	2.4	0.2	9	1.8	0.2	9	1.9	0.4
Jul 20	4	2.3	0.5	4	1.6	0.4	4	2.0	0.3
Aug 10	6	2.6	0.3	6	2.3	0.3	6	2.4	0.9
Aug 20	3	2.7	0.5	3	1.9	0.2	3	2.4	0.4
Sep	5	2.2	0.2	5	1.6	0.2	5	2.1	0.7
Oct	6	2.3	0.2	6	1.6	0.2	6	1.6	0.2
Nov	0	--	--	0	--	--	0	--	--
Dec	4	1.8	0.4	4	1.4	0.3	4	1.5	0.5
1972									
Jan	0	--	--	0	--	--	0	--	--
Feb	8	2.2	0.5	8	1.6	0.4	8	1.7	0.4
Mar	6	2.6	0.4	6	1.9	0.4	6	2.6	0.9
Apr	0	--	--	0	--	--	0	--	--
May	2	2.8	0.1	2	2.1	0.3	2	2.3	0.1
Total	211	2.0	0.4	211	1.3	0.4	211	1.6	0.6

Table 61. Breeding characteristics of adult female *Perognathus baileyi*---DSCODE A3UBE22

Month	Sample Size No.	No.	%	Gravid		Embryos Mean S.D.	No.	%	Postpartum		Placental Scars	
				Weight Mean S.D.					Weight Mean S.D.		Mean S.D.	
1970												
Jun 10	8	4	50	28.8±2.5		3.8±0.5	4	50	27.5±1.6		3.8±0.5	
Jun 20	17	2	12	24.9±5.5		2.5±0.7	9	53	25.4±3.1		3.3±0.7	
Jul 10	1	0	0				1	100	30.0		2.0	
Jul 20	14	0	0				10	71	25.9±2.9		3.3±0.8	
Aug 10	10	0	0				5	50	23.8±4.0		2.8±0.8	
Aug 20	4	0	0				1	25	29.0		3.0	
Sep	37	0	0				15	41	27.5±3.5		4.2±0.7	
Oct	29	0	0				17	59	24.6±2.5		4.2±1.4	
Nov	15	0	0				6	40	23.2±2.5		3.5±0.6	
Dec	8	0	0				2	25	25.5±3.5		3.0	
1971												
Jan	1	0	0				1	100	20.4		4.0	
Feb	1	0	0				0	0				
Mar												
Apr	2	0	0				2	100	22.2±0.6		4.0	
May	5	0	0				2	40	26.5±0.7		3.5±0.7	
Jun 10	6	0	0				3	50	21.9±3.3		2.3±1.2	
Jun 20												
Jul 10	9	1	11	22.4		3.0	3	33	22.9±2.0		3.0±1.0	
Jul 20	4	1	25	28.8		3.0	1	25	28.2		4.0	
Aug 10	6	2	33	29.1±2.2		4.0	3	50	24.2±1.7		4.0±1.0	
Aug 20	3	1	33	30.5		5.0	0	0				
Sep	5	0	0				5	100	24.4±4.4		2.8±0.5	
Oct	6	0	0				2	33	26.7±3.0		3.0	
Nov												
Dec	4	0	0				0	0				
1972												
Jan												
Feb	8	0	0				2	25	23.9±1.8		3.5±0.7	
Mar	6	4	67	30.0±4.0		3.0	2	33	27.9±5.4		3.0	
Apr												
May	2	1	50	25.9		5.0	0	0				
Total	211	16	8	28.4±3.5		3.5±0.8	96	46	25.4±3.3		3.6±1.0	

Perognathus intermedius

Male reproductive cycle: As in the other heteromyids, *P. intermedius* males had a greater percentage that were fertile and a larger period of reproduction than did the females (Figs. 14 and 15).

All of the adult males taken in June, 1970 were reproductive but throughout the remainder of this summer there was a gradual decline in the percentage of males with

spermatozoa in the caudal epididymis and only 10% of the males taken in August were reproductively active. With the occurrence of late summer rains (Fig. 15), however, more males became reproductively active. By November, 1970, immediately prior to the dormant period of *P. intermedius*, one of four animals taken was reproductive. *Perognathus intermedius* was not trapped during the coldest winter months (December, January and February), but upon emergence in March, 1971, 38% of eight adult males taken had spermatozoa in their caudal epididymis. The percentage of males considered reproductively active increased each month throughout the spring and by May, 1971, all of the adult males were potentially reproductive.

Reproduction in the second year was unlike that of the first; whereas during the first year the number of reproductive males had a linear decline during the summer, during the second summer there was a sharp rebound in the number of fertile males following intense summer rains. The majority of adult males in the population were fertile from June, 1971 through October, 1971 (Fig. 15). Although *P. intermedius* did not completely suspend surface activity during the second year, the number of fertile males during the coldest winter months (November, December and January) markedly declined. With the warmer spring weather from February through May, 1972, all of the adult males were in reproductive condition. This was also in contrast to the spring of the first year and was perhaps in response to the increased rainfall and available food during the second year.

Changes in the length and shape of the bacula occurred in male *P. intermedius* as animals matured (Table 41). The bacula of juvenile animals averaged 7.79 mm in length, with shafts having a gradual curvature, terminating distally in sharp hooks. The bacula of subadults had a mean length of 8.80 mm with the shaft generally straight and the distal hook not so prominent as in the juveniles (Fig. 19).

The bacula of adults were more robust proximally than those of subadults and the shaft had more flexure with a more pronounced hook on the distal tip. The overall contour was similar regardless of the breeding condition of the male, but the lengths were considerably different. There was positive correlation between the length of the bacula and the amount of spermatozoa observed in the caudal epididymis. A cartilaginous-like penial extension, as described for *Dipodomys merriami*, was also present in some of the male *P. intermedius* that had large amounts of spermatozoa in their reproductive organs. Bacula from animals with large amounts of spermatozoa averaged 12.18 mm, whereas those with moderate amounts of spermatozoa averaged 11.91 mm. Likewise, adult males with small amounts of spermatozoa had an average bacula length of 11.59 mm as compared to adult males with no spermatozoa that had bacula lengths of 10.04 mm.

The mean lengths of the fleshy reproductive organs (testes, seminal vesicles and caudal epididymes) increased in size during periods of reproduction; measurements of these organs are useful indicators of reproductive peaks. These organs were small during the winter months and larger from February through July (Figs. 30 and 31). It is interesting to note that the period in which the males were fertile exceeded by several months the fertile period in the females. This presumably insures fertilization of the recipient female.

Female reproductive cycle: Reproduction during the first year was confined to a succinct late spring and early summer period. During the first trapping period (June 10, 1970), 71% of the females were fertile, indicating a peak of reproduction in late spring (Fig. 32). Reproduction gradually tapered off during the remainder of the summer and had ended by the last half of August. No fertile females were taken again until May, 1971, at which time only 9% of the females trapped were reproductive.

The temporal pattern of reproduction in the second year for *P. intermedius*, as in the other heteromyids studied, was very different than that of the first year (Table 62 and Fig. 32). There was not a clear peak in reproduction in late spring as there was the previous year. Following heavy summer rains, however, reproductive activity increased, with the peak of 86% of the adult female population being reproductive the last half of August, 1971. By this same period in 1970 reproduction had ended for the year. The entire population of *P. intermedius* did not suspend surface activity during the second winter as it had the first, but even while maintaining surface activity, no fertile females were taken from October through February. Apparently conditions were once again favorable for reproduction in spring 1972, as in March over half of the females were in reproductive condition.

Sixteen females (2.49%) from a total of 642 examined were determined to be in estrus (Table 63). The duration of estrus is not known for *P. intermedius*. Females in estrus had an increase in body weight to a mean of 12.27 g over 159 non-reproductive adult females whose mean body weight was 11.59 g. Vaginal plugs were not observed in *P. intermedius* but were presumed to occur as they are present in other heteromyid species (Wilken and Ostwald, 1968).

Because of their underdeveloped state, embryos were measured *in vitro* until they obtained a rump-crown length of approximately 12.05 mm. Embryos near parturition had rump-crown lengths of approximately 14.00 mm and apparently were born in a more precocial state than were fetuses of *Dipodomys merriami* (Van De Graaff, 1973). The gestation period in *P. intermedius* was determined by Svihla (1932) to be approximately 21 days.

Table 62 Breeding characteristics of adult female *Peroganthus intermedius*
DSCODE A3UBE22

Month	Sample Size No.	No.	%	Gravid		No.	%	Postpartum	Placental
				Weight Mean±S.D.	Embryos Mean±S.D.			Weight Mean±S.D.	Scars Mean±S.D.
1970									
Jun 10	49	19	39	14.6±2.1	3.5±0.6	13	27	13.9±2.5	3.7±0.8
Jun 20	38	13	34	14.7±2.5	3.5±0.7	19	50	12.8±1.0	3.5±0.9
Jul 10	17	2	12	15.5±4.9	3.0	13	76	12.5±1.2	3.6±0.7
Jul 20	29	2	7	18.3±0.4	4.0	23	79	12.7±1.4	3.7±0.7
Aug 10	29	1	3	15.4	2.0	19	66	12.3±1.2	3.4±0.7
Aug 20	34	0	0			19	56	12.2±1.1	3.3±0.8
Sep	30	0	0			13	43	14.1±1.8	4.2±0.8
Oct	12	0	0			6	50	11.9±0.8	3.3±1.2
Nov	2	0	0			0	0		
Dec									
1971									
Jan									
Feb									
Mar	3	0	0			2	67	10.0	3.0±1.4
Apr	7	0	0			1	14	10.0	4.0
May	11	0	0			6	55	11.2±0.7	3.0±1.3
Jun 10	18	6	33	12.6±1.3	2.3±0.5	6	33	12.0±1.0	3.5±0.6
Jun 20	42	1	2	14.3	2.0	20	48	11.9±1.1	3.4±0.7
Jul 10	31	3	10	14.7±2.2	2.7±0.6	15	48	11.4±1.3	3.3±0.8
Jul 20	40	1	3	13.6	3.0	18	45	12.3±1.1	3.3±0.8
Aug 10	8	4	50	16.7±2.7	4.0±1.4	2	25	11.2	3.0±1.4
Aug 20	22	14	64	14.2±1.6	3.6±0.7	2	9	12.9±0.9	3.0
Sep	23	1	4	16.8	4.0	14	61	13.0±0.9	3.2±0.7
Oct	14	0	0			8	57	12.6±0.9	3.6±0.9
Nov	16	0	0			8	50	11.9±0.7	3.5±0.5
Dec	10	0	0			3	30	13.8±1.1	3.7±0.6
1972									
Jan	11	0	0			2	18	9.7±1.7	3.0±1.4
Feb	7	0	0			0	0		
Mar	15	5	33	14.9±1.6	3.4±0.6	2	13	14.0±1.7	4.0
Apr	31	8	26	15.7±2.1	2.9±0.8	17	55	13.6±1.3	3.1±0.7
May	11	2	18	15.1±1.9	3.0	7	64	12.5±1.3	2.9±0.9
Total	560	82	15	14.8±2.2	3.3±0.8	258	46	12.7±1.6	3.4±0.8

A slight trend in size fluctuation of the ovary occurred as the females went through a breeding cycle (Table 64). An analysis of the females of various reproductive categories (i.e., estrus, pregnant, lactating, etc.) and age groups (i.e., juvenile, subadult, adult) yields some revealing comparisons (Tables 63 and 64). Young females

had smaller ovaries of light pink coloration. Sixteen females in estrus had ovaries that averaged .26 mm longer and .13 mm wider than non-reproductive adults. The ovarian dimension increased slightly in pregnant females but then the ovarian size stabilized in postpartum females.

Table 63. Summary of the reproductive cycles of *Perognathus intermedius* based on 632 females (560 adults, 72 young) from June, 1970 through May, 1972
DSCODE—A3UBE22

Month	Estrus	% Reproductive		% Non-reproductive	
		Pregnant	Lactating	Adult	Young
1970					
Jun 10	0	31.15	26.23	22.94	19.68
Jun 20	0	22.81	8.77	35.09	33.33
Jul 10	0	6.67	0	49.99	43.34
Jul 20	0	5.88	0	79.41	14.71
Aug 10	0	2.78	0	77.77	19.45
Aug 20	0	0	0	94.44	5.56
Sep	0	0	0	93.75	6.25
Oct	0	0	0	100.00	0
Nov	0	0	0	100.00	0
Dec	--	--	--	--	--
1971					
Jan	--	--	--	--	--
Feb	--	--	--	--	--
Mar	0	0	0	100.00	0
Apr	0	0	0	100.00	0
May	9.09	0	0	90.91	0
Jun 10	0	33.33	11.11	55.56	0
Jun 20	4.76	2.38	4.76	88.10	0
Jul 10	0	7.14	9.52	57.15	26.19
Jul 20	14.29	2.38	7.14	71.43	4.76
Aug 10	0	50.00	0	50.00	0
Aug 20	8.00	56.00	12.00	12.00	12.00
Sep	0	4.17	16.67	74.99	4.17
Oct	0	0	0	87.50	12.50
Nov	0	0	0	94.12	5.88
Dec	0	0	0	100.00	0
1972					
Jan	0	0	0	84.62	15.38
Feb	0	0	0	100.00	0
Mar	20.00	33.33	0	46.67	0
Apr	6.45	25.81	12.90	54.84	0
May	0	18.18	18.18	63.64	0

2.3.2.7.-98

Table 64. Measurements (mm) of the length and width of the ovaries and the uteri of adult female *Perognathus intermedius* ---DSCODE A3UBE22

Month	No.	Ovary		No.	Width		No.	Uterus	
		Length Mean	S.D.		Mean	S.D.		Mean	S.D.
1970									
Jun 10	49	1.6	0.3	49	1.1	0.2	49	1.8	0.5
Jun 20	38	1.7	0.4	38	1.1	0.3	38	1.8	0.5
Jul 10	17	1.7	0.3	17	1.2	0.2	17	1.5	0.3
Jul 20	29	1.6	0.2	29	1.1	0.2	29	1.6	0.5
Aug 10	29	1.5	0.2	29	1.0	0.2	29	1.4	0.4
Aug 20	34	1.5	0.2	34	1.0	0.2	34	1.3	0.3
Sep	30	1.5	0.2	30	0.9	0.2	30	1.0	0.3
Oct	12	1.4	0.2	12	0.9	0.1	12	1.1	0.3
Nov	2	1.2	0.3	2	0.9	0.1	2	0.9	0.1
Dec	0	--	--	0	--	--	0	--	--
1971									
Jan	0	--	--	0	--	--	0	--	--
Feb	0	--	--	0	--	--	0	--	--
Mar	3	1.7	0.4	3	1.0	0	3	1.2	0.3
Apr	7	1.6	0.2	7	1.1	0.1	7	1.3	0.4
May	11	2.0	0.3	11	1.6	0.2	11	1.4	0.2
Jun 10	18	2.0	0.3	18	1.5	0.2	18	1.9	0.5
Jun 20	42	1.8	0.2	42	1.4	0.2	42	1.6	0.4
Jul 10	31	1.9	0.3	31	1.5	0.2	31	1.7	0.5
Jul 20	40	1.6	0.3	40	1.1	0.2	40	1.5	0.4
Aug 10	8	2.2	0.5	8	1.7	0.3	8	2.2	0.6
Aug 20	22	2.3	0.2	22	1.8	0.3	22	2.2	0.4
Sep	23	1.9	0.2	23	1.4	0.2	23	1.8	0.4
Oct	14	1.8	0.2	14	1.3	0.1	14	1.6	0.2
Nov	16	1.6	0.2	16	1.0	0.2	16	1.2	0.3
Dec	10	1.9	0.2	10	1.3	0.2	10	1.4	0.2
1972									
Jan	11	1.6	0.2	11	1.2	0.2	11	1.0	0.2
Feb	7	1.7	0.1	7	1.3	0.1	7	1.1	0.1
Mar	15	2.0	0.3	15	1.4	0.2	15	1.8	0.4
Apr	31	2.0	0.2	31	1.6	0.2	31	2.4	0.6
May	11	2.1	0.2	11	1.5	0.2	11	2.0	0.5
Total	560	1.7	0.3	560	1.2	0.3	560	1.0	0.5

The horns of the uteri are good indicators of reproductive activity. As in other species of *Perognathus* the uterine horns of juveniles were thin ($\bar{x}=0.78$ mm), translucent and a pinkish-white color. Uterine horns of subadults were thicker ($\bar{x}=0.88$ mm) and not so translucent. The uterine horns of non-fecund females averaged 0.95 mm in width and were a definite pinkish color. Females that were in estrus had reddish-colored,

vascularized uterine horns that were enlarged to an average of 1.78 mm. Pregnant females had the widest uterine horns ($\bar{X}=1.87$ mm). The uterine horns of postpartum females in a lactating condition were greatly distended and darkened with no centralized placental scar yet visible.

Perognathus penicillatus

Male reproductive cycle: Fertile males were trapped in each of the summer months from June through September during the first year. The peak in male fecundity during the first summer appeared to be in June, 1970 when over 95% of the males examined were reproductive. From September, 1970 until April, 1971, there were no fertile males trapped.

There was a higher percentage of fertile males in the second year than the first (Fig. 33). During each of the six trapping periods of the second summer (except August, 20), all of the males were found to be fertile. Percentage of fertile males decreased towards the end of August and continued to decline through October, 1971. From November, 1971 through April, 1972, no fertile males were sampled. The increased fertility during the second year was presumably associated with increased rainfall and subsequent vegetation.

Burt (1936) examined the bacula of three specimens of the subspecies of *P. penicillatus* with which we were working. He found the mean length to be 12.58 mm and described the bacula as having a roughly sigmoid curvature when viewed laterally. Bacula of both juveniles and subadults examined in this study lacked the sigmoid appearance that is characteristic of adult males. The bacula of young animals had extensive dorsal curvature, giving it an inverted J-shaped appearance. Three bacula from juveniles averaged 7.65 mm in length and bacula from 14 subadults averaged 9.01 mm.

Of the six species studied, adult *P. penicillatus* had the longest baculum and as in the other heteromyids there was a correlation between fertility and the length of the baculum. Measurements were made on bacula of 90 adult males. Bacula from animals with large amounts of spermatozoa had a mean length of 12.47 mm. This was only a slight increase in length over 17 specimens with moderate amounts of spermatozoa present ($\bar{X}=12.11$ mm). There was an increase, however, in the mean bacula lengths over 13 individuals with small amounts of spermatozoa present ($\bar{X}=11.46$ mm) and over 19 non-fecund adult males ($\bar{X}=10.03$ mm).

Testicular dimensions of *P. penicillatus* differed seasonally. In the first year, the average length of the testes was 6.60 mm during the first trapping period. From this length (6.60 mm), the mean testicular length gradually decreased and just before

the animals went into dormancy, the mean testes length was 3.93 mm. By the time specimens were trapped again following emergence in spring, the mean testicular length was already 6.15 mm. The length of the testes remained high through the second summer and did not appear to atrophy until November, 1971.

Female reproductive cycle: The data showed female *P. penicillatus* to have two reproductive peaks during the first year; there was a late spring and early summer peak that terminated by mid-June and a less intensive peak in September following summer rains (Fig.18). No reproductive females were trapped from October through May of the first year, even though reproductive males were trapped during the same period. Burt and Grossenheider (1964) listed the breeding season for *P. pennicillatus* as April through September.

The breeding season of the second year was longer than that of the first and a greater percentage of the females were reproductive (Fig.18). Reproductive females were continuously trapped from June through October, 1971. Apparently conditions of the second year were very favorable for reproduction in rodents (Table 65).

Vaginal plugs which were obtained from three metestral females (Fig.19) averaged 10.55 mm in length. They were thickest distally and tapered proximally to a bulb-like enlargement that presumably blocked the cervix. Extending into the uterus from the bulb-like enlargement were several short strands of cartilage-like material.

Wilken and Ostwald (1968) have described copulation and associated events in *P. penicillatus*, and state that estrus lasts only a few hours and that the period of gestation is 23 days.

The lengths of the ovary in various age and reproductive categories of females did not reveal any significant changes as the animals matured or the seasons changed. The coloration and texture of the reproductive organs at various ages are similar to those previously described for other *Perognathus* species (Tables 65 and 66).

The mean litter size of eight pregnant females was 3.38 and evidences from placental scars from 34 females indicated mean litter sizes of 3.53. Ten litters from laboratory animals had a mean litter size of 4.9, with a range of three to seven (Wilden and Ostwald, 1968). The greatest number of placental scars or embryos from 42 female *P. penicillatus* in this study was five, suggesting that litters from laboratory animals may be abnormally large due to atypical environmental conditions.

Table 65. Summary of the reproductive cycles of *Perognathus penicillatus* based on 80 females (67 adults, 13 young) from June 1970 through May 1972
DSCODE—A3UBE22

Month	Estrus	% Reproductive		% Non-reproductive	
		Pregnant	Lactating	Adult	Young
1970					
Jun 10	0	28.57	28.57	42.86	0
Jun 20	0	0	0	0	100.00*
Jul 10	--	--	--	--	--
Jul 20	0	0	0	66.67	33.33
Aug 10	0	0	0	100.00	0
Aug 20	0	0	0	100.00	0
Sep	0	9.09	0	81.82	9.09
Oct	0	0	0	100.00	0
Nov	--	--	--	--	--
Dec	--	--	--	--	--
1971					
Jan	0	0	0	100.00	0
Feb	--	--	--	--	--
Mar	--	--	--	--	--
Apr	--	--	--	--	--
May	0	0	0	100.00	0
Jun 10	0	33.33	0	66.67	0
Jun 20	0	11.11	22.22	66.67	0
Jul 10	0	50.00	0	50.00	0
Jul 20	0	0	25.00	75.00	0
Aug 10	0	0	25.00	25.00	50.00
Aug 20	0	0	33.33	0	66.67
Sep	0	11.11	0	66.67	22.22
Oct	0	0	16.67	66.66	16.67
Nov	--	--	--	--	--
Dec	0	0	0	0	100.00*
1972					
Jan	--	--	--	--	--
Feb	--	--	--	--	--
Mar	--	--	--	--	--
Apr	--	--	--	--	--
May	0	0	0	66.67	33.33

*Small sample size

Table 66. Measurements (mm) of the length and width of the ovaries and the uteri of adult female *Perognathus penicillatus*—DSCODE A3UBE22

Month	No.	Length	Ovary	Width	S.D.	No.	Uterus	S.D.	
		Mean	S.D.	No.			Mean		
1970									
Jun 10	7	1.8	0.3	7	1.3	0.3	7	2.3	0.9
Jun 20	0	--	--	0	--	--	0	--	--
Jul 10	0	--	--	0	--	--	0	--	--
Jul 20	2	1.8	0.3	2	1.3	0.1	2	1.5	0.6
Aug 10	3	2.0	0.2	3	1.4	0.1	3	1.8	0.7
Aug 20	1	1.6	0	1	1.0	0	1	1.5	0
Sep	10	1.7	0.3	10	1.1	0.3	10	1.2	0.4
Oct	3	1.8	0.2	3	1.0	0.1	3	1.1	0.1
Nov	0	--	--	0	--	--	0	--	--
Dec	0	--	--	0	--	--	0	--	--
1971									
Jan	1	2.0	0	1	1.1	0	1	1.0	0
Feb	0	--	--	0	--	--	0	--	--
Mar	0	--	--	0	--	--	0	--	--
Apr	0	--	--	0	--	--	0	--	--
May	1	2.1	0	1	1.4	0	1	1.9	0
Jun 10	3	2.0	0.3	3	1.5	0.1	3	2.1	0.4
Jun 20	9	2.0	0.4	9	1.6	0.2	9	2.0	0.2
Jul 10	4	2.1	0.3	4	1.7	0.6	4	2.0	1.0
Jul 20	4	1.5	0.2	4	1.2	0.1	4	1.7	0.4
Aug 10	2	2.1	0	2	1.8	0	2	1.9	0.4
Aug 20	1	2.3	0	1	2.5	0	1	2.3	0
Sep	7	2.0	0.3	7	1.6	0.3	7	2.0	0.4
Oct	5	2.0	0.3	5	1.4	0.2	5	1.7	0.4
Nov	0	--	--	0	--	--	0	--	--
Dec	0	--	--	0	--	--	0	--	--
1972									
Jan	0	--	--	0	--	--	0	--	--
Feb	0	--	--	0	--	--	0	--	--
Mar	0	--	--	0	--	--	0	--	--
Apr	0	--	--	0	--	--	0	--	--
May	4	2.3	0.2	4	1.6	0.2	4	1.9	0.5
Total	67	1.9	0.3	67	1.4	0.4	67	1.8	0.6

Peromyscus eremicus

Male reproductive cycle: In every month in which cactus mice were trapped, the majority of the adult males were fertile (Figs. 16 and 17). During both summers, 100% of all adult males were fertile. Not all of these had scrotal testes; however, they did have small-to-moderate and, in some cases, large amounts of spermatozoa in their caudal epididymes. There were periods during the winter of both years in which there

was decreased fecundity in male *P. eremicus* (Fig. 16). A larger percentage of males were, however, non-fecund during the first year than in the second.

Magidson and Hoffmeister (1965) did a comprehensive study in age variation in the bacula of 182 *P. eremicus* but did not present data correlating bacula measurements with reproductive condition of the male. The above authors divided the bacula into five groups based on tooth development in the specimens from which the bacula were taken. The smallest groups of bacula averaged 6.46 mm in length and the largest group of bacula had a mean length of 9.07 mm.

In this study 279 bacula were examined and categorized into three major divisions; juveniles, subadults and adults. In addition, the adults were further subdivided, based upon the amount of spermatozoa observed or relative fertility. Bacula from juveniles averaged 5.49 mm in length, had a laterally thickened proximal base and a straight, tapering shaft. The mean bacula length of 54 subadults averaged 6.98 mm and was further thickened at the base. The shaft had a slight dorsal curve.

The overall bacula length of 216 males averaged 8.85 mm. The shaft of the bacula had increased flexure (Fig. 19) from that of subadults and had a thicker, more rounded proximal base. There was often a cartilage tip on the terminal knob that occurred more often in fertile males. Thirteen non-fecund adult males had bacula lengths averaging 7.36 mm. As the amount of spermatozoa content increased in the caudal epididymis, so did the length of the bacula. The mean bacula length of 43 animals with small amounts was 8.51 mm, 54 males with moderate amounts averaged 8.89 mm, and 106 males with large amounts had an average bacula length of 9.15 mm.

Just as the bacula increased in length as sexual maturity of the males improved, so did the testes (Fig. 34), seminal vesicles, and caudal epididymis, and measurements of these organs were equally useful guides to reproductive status. The size of the seminal vesicles differ from season to season and are indicative of periods of reproduction (Figure 35). The seminal vesicles atrophied in size during the winter months even though spermatozoa was still found in the caudal epididymis. The caudal epididymis remained fairly consistent in size throughout the two-year study (Fig. 35). Perhaps *P. eremicus* is potentially active during the winter months but they are not actively inseminating. This explanation would agree with the findings of MacMillen (1964).

Female reproductive cycle: A remarkably high (48.77) percentage of all the adult females throughout the two-year study were in breeding condition. There were only four months during the study (January through April, 1972) in which all of the females were non-reproductive (Fig. 16). Females during these same months in the second year were reproductive; the disparity was presumably due to better environmental conditions. *Peromyscus eremicus* eats large quantities of insects and greenery (Reichman, 1973) and these items were more abundant during the second year. An increase in reproduction occurred during the summer of both years (Fig. 17) and a larger percentage of females were breeding in the second summer than in the summer of the first year.

As compared to some of the pocket mice, the cyclic events associated with reproduction is fairly well known for *P. eremicus*. Svihla (1932) reported the gestation period of *P. eremicus* to be 21 days, whereas Davis and Davis (1947) reported individual females had multiple litters at intervals of 28 to 30 days. Postpartum estrus occurs within 24 hr after parturition (Brand and Ryckman, 1968) and lactation is known to extend gestation by two to seven days (Svihla, 1932). Our data, as well as MacMillen's (1964), indicates seasonal polyestrus females are common occurrences in natural populations. On numerous occasions pregnant females were trapped that had recent placental scars and on several occasions some were lactating. Only two of the females trapped were in estrus, indicating that the period of estrus is not so long in *Peromyscus* species as it is in heteromyids.

Because of the continuous breeding patterns in *P. eremicus*, comparing monthly ovarian or uterine measurements were non-revealing as no patterns were established. The size of the ovaries and uterus did increase from juvenile to adult and from non-breeding to breeding. The length of the pinkish-colored ovary for juveniles averaged 1.69 mm and the uterine width averaged 0.81 mm. Forty-four subadults had a mean ovary length of 1.83 mm and a mean uterine width of 1.36 mm. Of the adults, 72 pregnant females had an average ovary length of 2.34 mm and an average uterine width of 2.43 mm. Lactating females had slightly smaller ovary and uterine dimensions, 2.22 mm and 2.26 mm respectively. The ovaries and uterine horns of females in estrus were likewise larger than those of non-reproductive females (Table 67).

Studies by several workers have shown *P. eremicus* to have similar litter sizes. Brand and Ryckman (1968) reported a mean litter size of 2.22 young from 14 females. Svihla (1932) lists a mean litter size of 2.60 based on five litters. Davis and Davis (1947) found the mean number of young in 404 litters to be 2.42 and Lewis (1972) recorded an average of 2.53 per litter in 13 pregnant females examined. In this study, 72 pregnant females and an additional 61 postpartum females with placental scars were examined; both groups showed exactly the same mean data (2.60 ± 0.7) in the number of young per litter.

Table 67. Measurements (mm) of the length and width of the ovaries and the uteri of adult female *Peromyscus eremicus*—DSCODE A3UBE22

Month	No.	Ovary		No.	Uterus		No.	Mean	S.D.
		Length	Width		Length	Width			
		Mean	S.D.		Mean	S.D.			
1970									
Jun 10	12	2.5	0.6	12	1.9	0.6	12	2.8	0.9
Jun 20	8	2.2	0.8	8	1.4	0.4	8	3.0	1.0
Jul 10	3	1.6	0.5	3	1.4	0.3	3	3.9	1.9
Jul 20	8	2.7	0.8	8	1.8	0.4	8	3.1	1.5
Aug 10	5	1.6	0.2	5	1.2	0.1	5	2.5	1.1
Aug 20	1	1.7	0	1	1.4	0	1	5.4	0
Sep	0	--	--	0	--	--	0	--	--
Oct	10	2.7	0.5	10	1.5	0.4	10	1.3	0.3
Nov	11	2.1	0.5	11	1.3	0.4	11	1.4	0.3
Dec	3	1.3	0.4	3	0.9	0.2	3	1.7	0.5
1971									
Jan	2	1.9	1.0	2	1.2	0.3	2	1.7	0.8
Feb	7	2.0	0.3	7	1.2	0.3	7	1.6	0.2
Mar	5	2.0	0.3	5	1.3	0.1	5	1.6	0.4
Apr	2	1.5	0	2	0.9	0	2	1.4	0.4
May	2	2.4	0.1	2	1.9	0.2	2	2.5	0
Jun 10	1	1.8	0	1	1.3	0	1	2.8	0
Jun 20	2	2.2	0.3	2	1.9	0.1	2	3.1	0.2
Jul 10	4	2.9	0.2	4	2.0	0.4	4	3.8	0.3
Jul 20	6	1.9	0.4	6	1.4	0.3	6	2.6	0.8
Aug 10	2	2.1	0.1	2	1.8	0	2	2.6	0.1
Aug 20	1	2.5	0	1	2.1	0	1	4.5	0
Sep	0	--	--	0	--	--	0	--	--
Oct	1	2.1	0	1	1.9	0	1	2.4	0
Nov	14	2.1	0.7	14	1.6	0.5	14	2.5	0.8
Dec	13	2.5	0.4	13	2.1	0.4	13	3.4	1.0
1972									
Jan	24	1.7	0.3	24	1.2	0.3	24	1.8	0.4
Feb	26	1.9	0.4	26	1.5	0.4	26	2.2	0.7
Mar	23	2.3	0.3	23	1.9	0.3	23	2.9	0.8
Apr	8	2.5	0.5	8	2.1	0.4	8	3.1	0.8
May	0	--	--	0	--	--	0	--	--
Total	203	2.1	0.6	203	1.6	0.5	203	2.5	1.0

Subadults becoming reproductive occurs more frequently in *P. eremicus* than in the heteromyids studied. There was only one subadult female observed to have placental scars, but several subadults were found to be pregnant. Likewise, many subadult males were considered fertile.

Peromyscus eremicus is polyestrous, has a continuous breeding season year around, and many of the subadults are fertile. It is surprising, therefore, that the population density was not greater. The high breeding ratio and the low population numbers suggest a short life span and fast population turnover. Indeed, not many pregnant females were observed that had old placental scars. A study to determine longevity and population dynamics in the cactus mouse would be worthwhile.

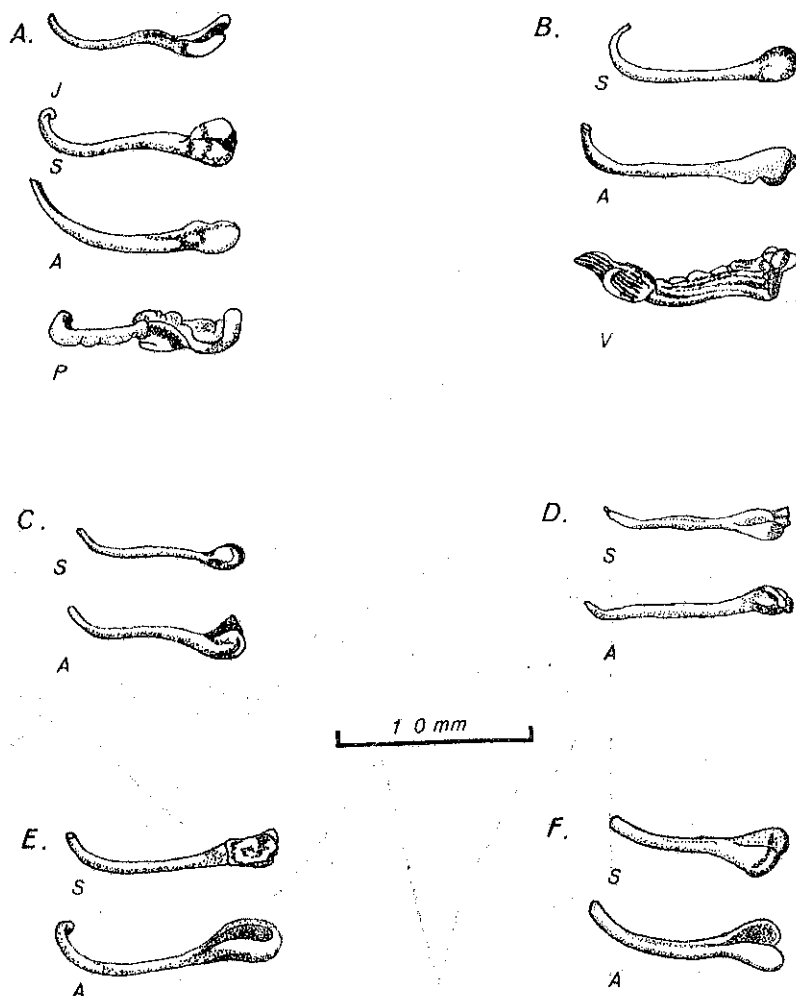


Figure 19. Diagrams of bacula of six species of desert rodents, vaginal plug of *Perognathus penicillatus* (V), and a penial extension of the baculum of *Dipodomys merriami* (P). A. *Dipodomys merriami*; B. *Perognathus penicillatus*; C. *Perognathus amplius*; D. *Perognathus baileyi*; E. *Perognathus intermedius*; F. *Peromyscus eremicus*. Juvenile (J), Subadult (S), and Adult (A). (DSCODES A3UBE21, BE22)

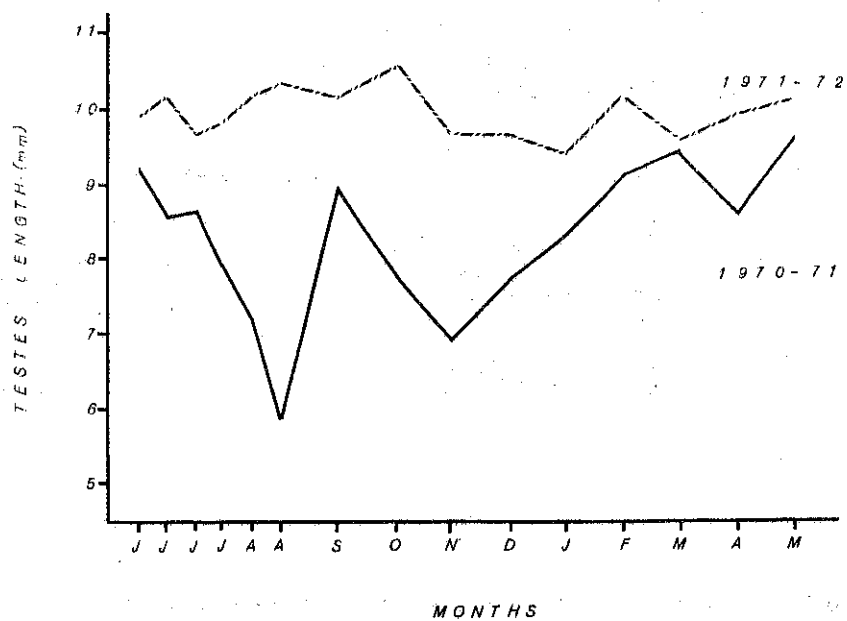


Figure 20. Monthly mean lengths of the testes of 774 *Dipodomys merriami*. Summers were sampled bi-monthly. (DSCODE A30BE21)

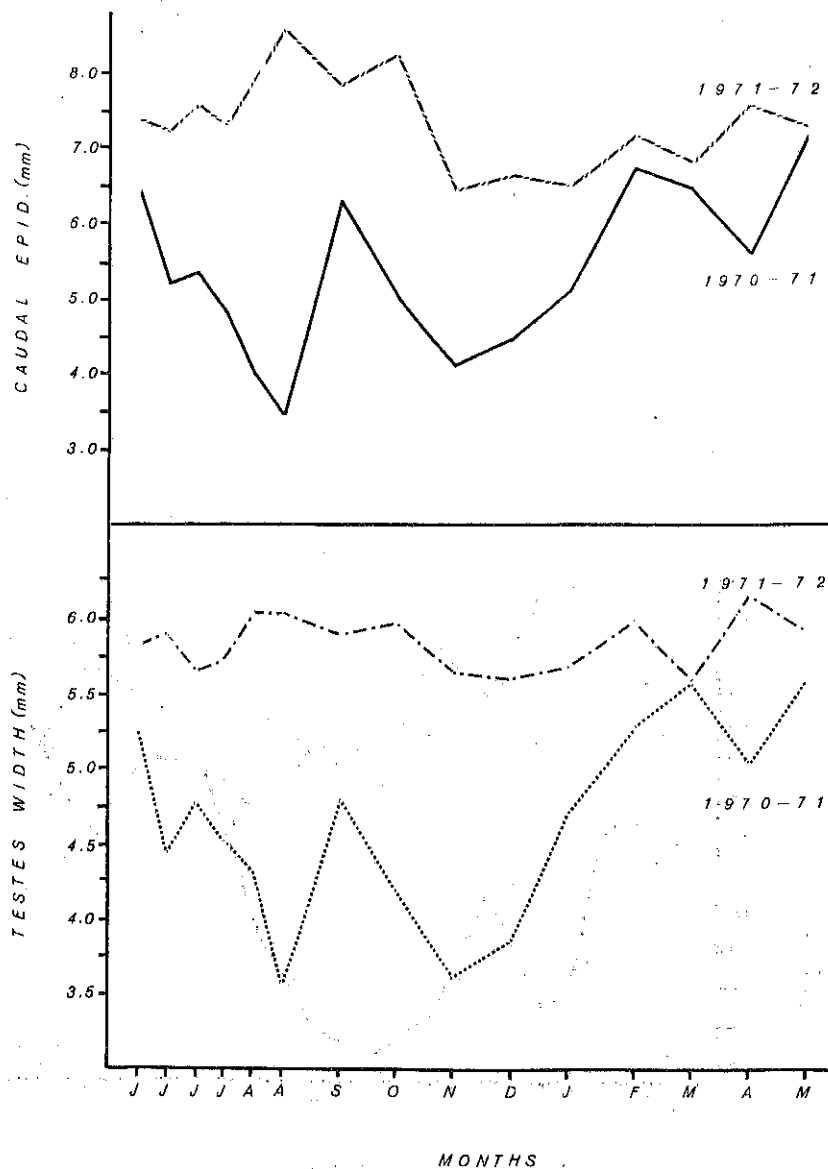


Figure 21. Monthly mean lengths of the caudal epididymides and widths of the testes of 774 adult *Dipodomys merriami*. Summers were sampled bi-monthly. (DSCODE A3UBE21)

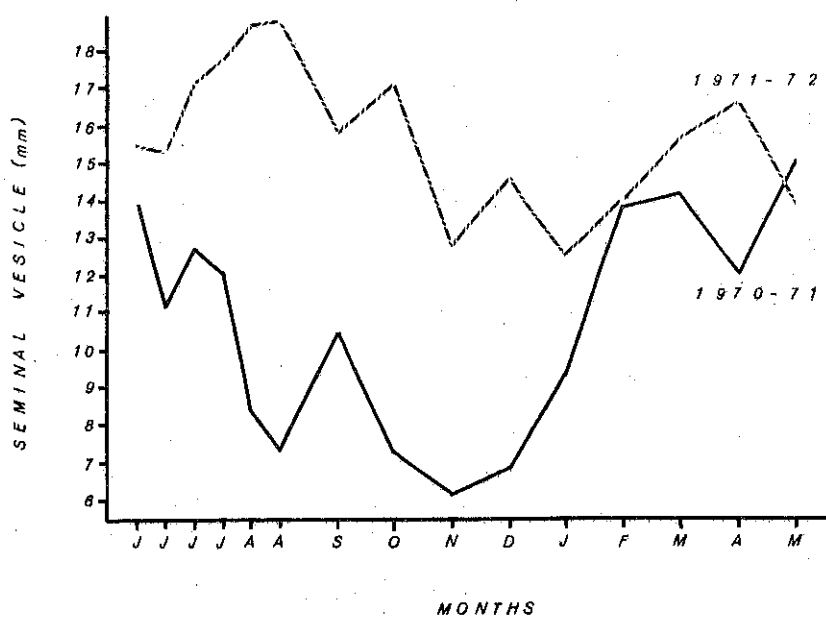


Figure 22. Monthly mean lengths of the seminal vesicles of 774 adult *Dipodomys merriami*. Summers were sampled bi-monthly. (DSCODE A3UBE21)

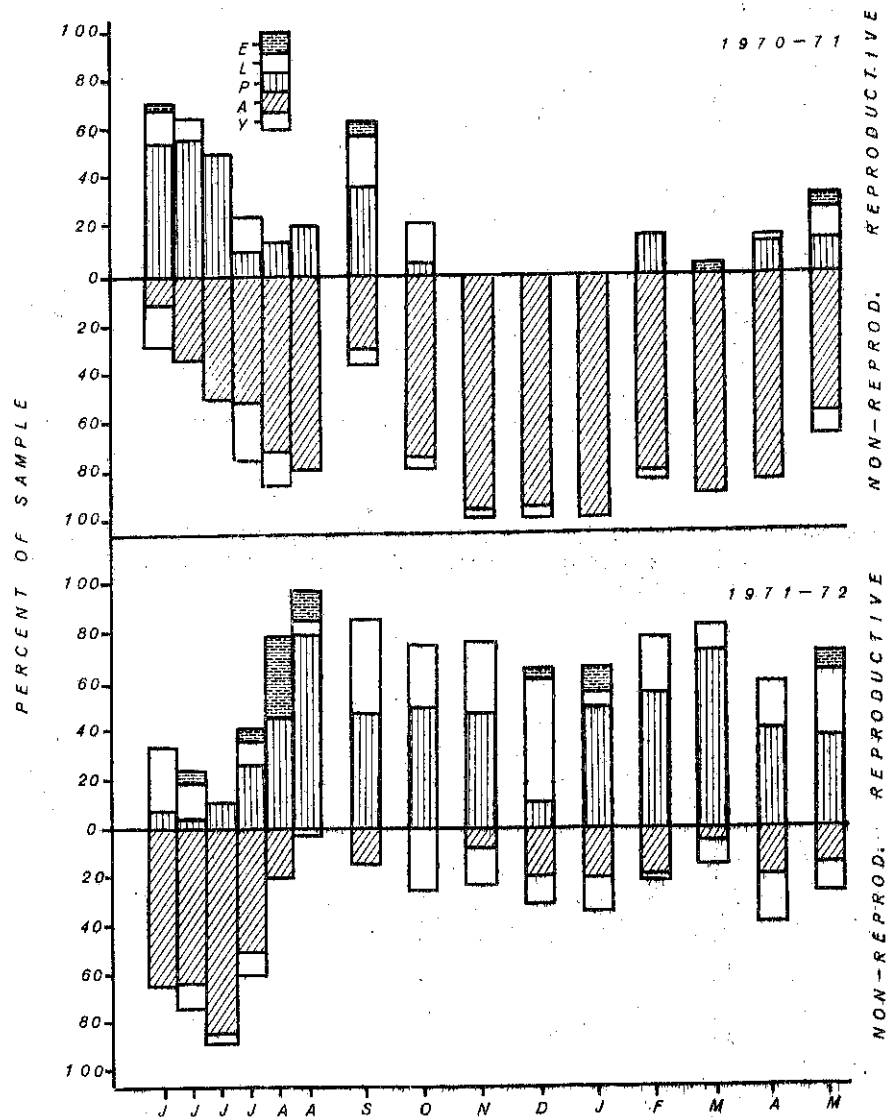


Figure 23. Summary of the reproductive cycles of *Dipodomys merriami* based on 727 females (669 adults, 58 young) trapped from June, 1970 to June, 1972. Reproductive females categorized as estrus (E), lactating (L), or pregnant (P) and non-reproductive females categorized as adults (A) or young (Y). DSCODE A3UBE22)

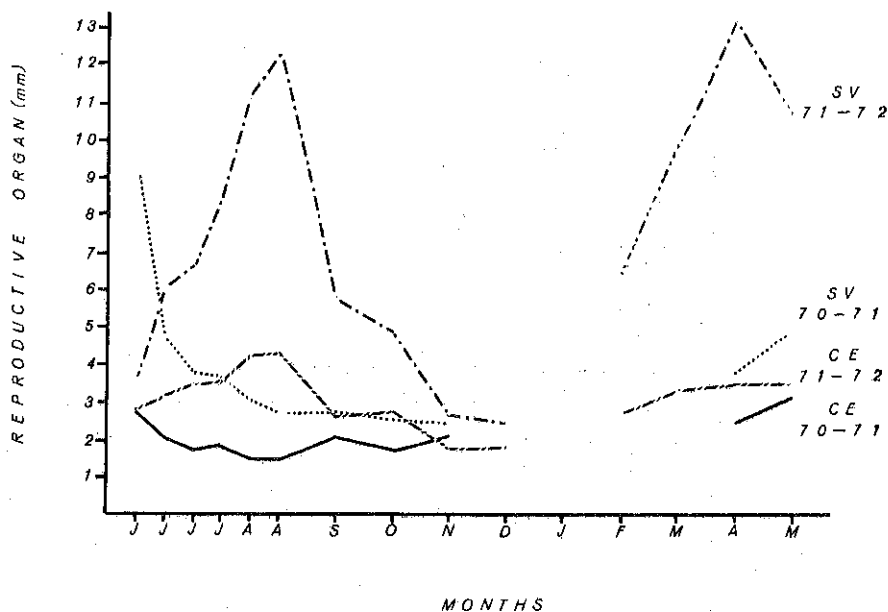


Figure 24. Monthly mean lengths of the caudal epididymides (CE) and seminal vesicles (SV) of 555 adult *Perognathus amplus*. Summers were sampled bi-monthly. (DSCODE A3UBE21)

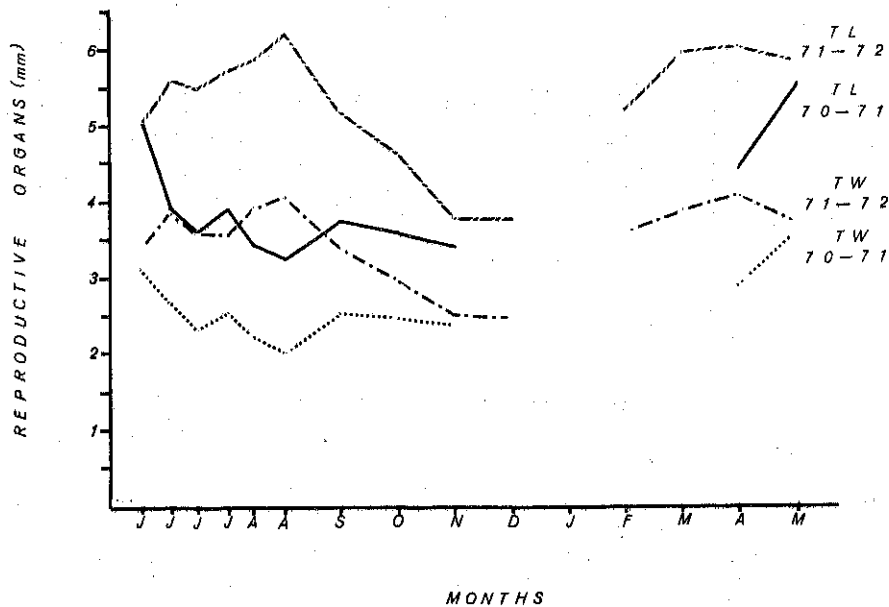


Figure 25. Monthly mean measurements of the testes length (TL) and testes width (TW) of 555 adult *Perognathus amplus*. Summers were sampled bi-monthly. (DSCODE A3UBE21)

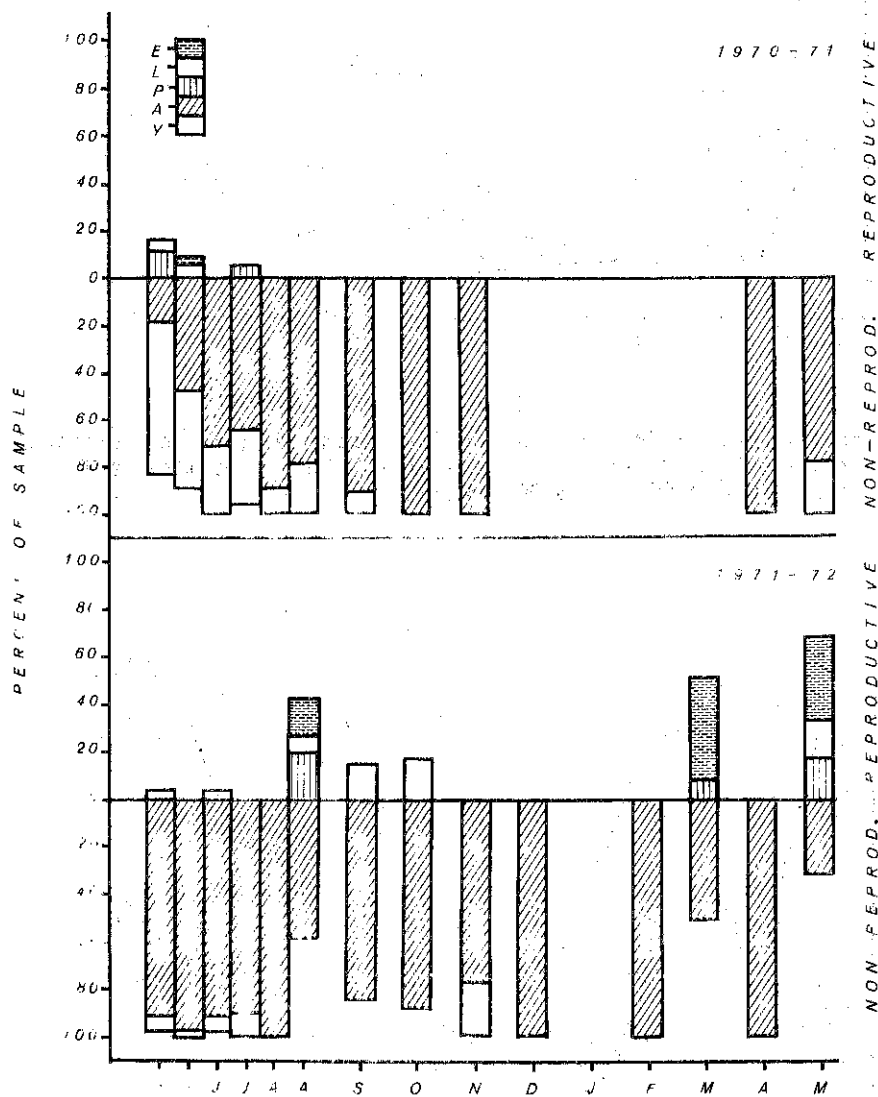


Figure 26. Summary of the reproductive cycles of *Perognathus amplus* based on 710 females (530 adults, 180 young) trapped from June, 1970 to June, 1972. Reproductive females categorized as estrus (E), lactating (L), or pregnant (P) and non-reproductive females categorized as adults (A) or young (Y). (DSCODE A3UBE22)

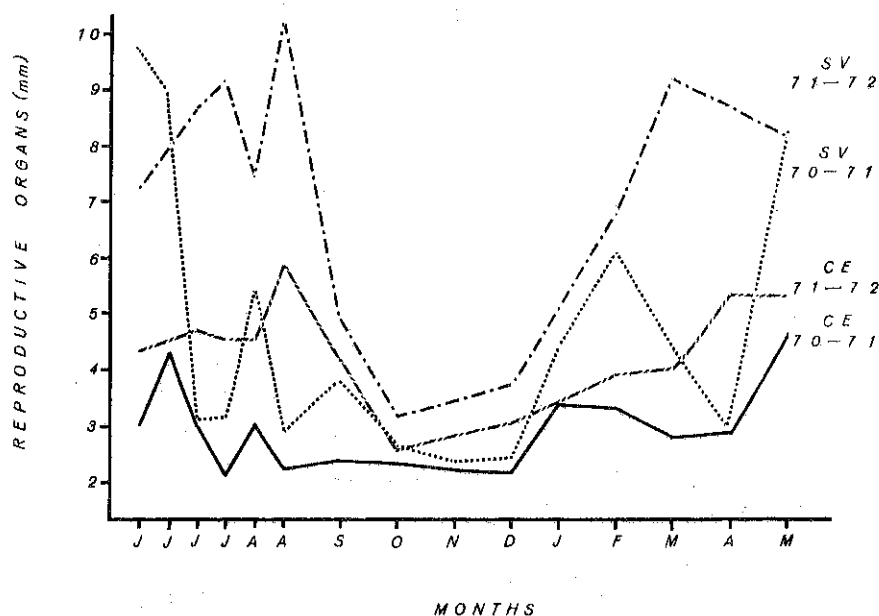


Figure 27. Monthly mean lengths of the caudal epididymides (CE) and seminal vesicles (SV) of 165 adult *Perognathus baileyi*. Summers were sampled bi-monthly. (DSCODE A3UBE21)

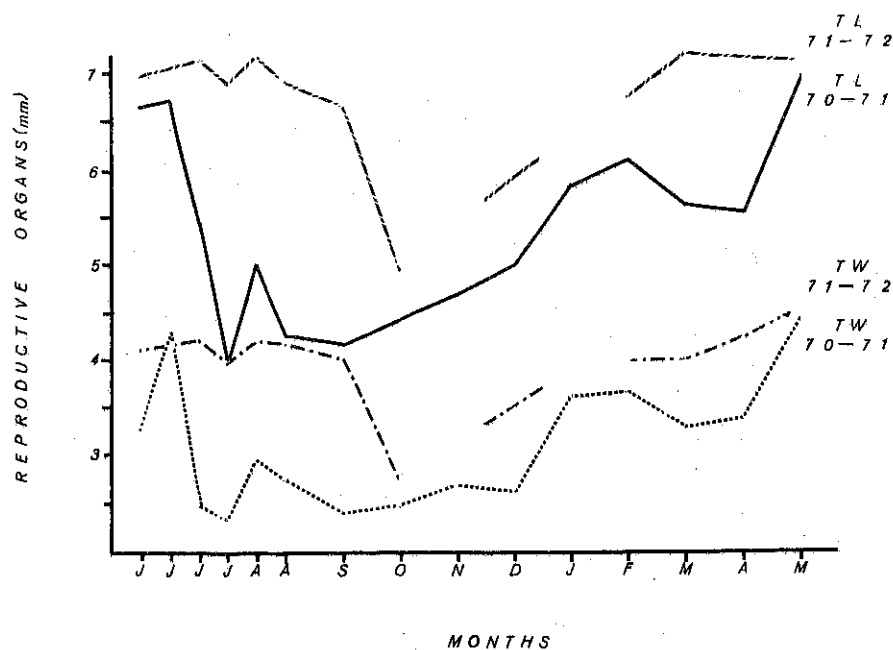


Figure 28. Monthly mean measurements of the testes length (TL) and testes width (TW) of 165 adult *Perognathus baileyi*. Summers were sampled bi-monthly. (DSCODE A3UBE21)

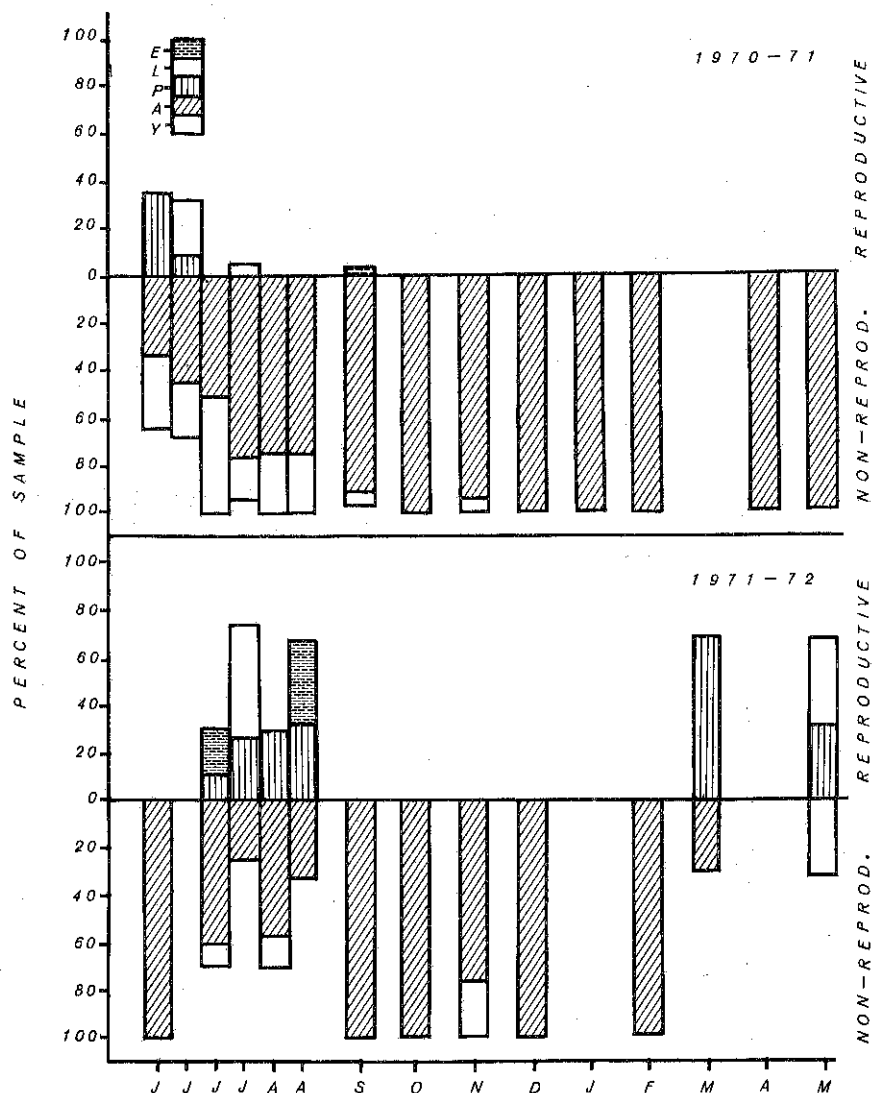


Figure 29. Summary of the reproductive cycles of *Perognathus baileyi* based on 239 females (211 adults, 28 young) trapped from June, 1970 to June, 1972. Reproductive females categorized as estrus (E), lactating (L), or pregnant (P) and non-reproductive females categorized as adults (A) or young (Y). (DSCODE A3UBE22)

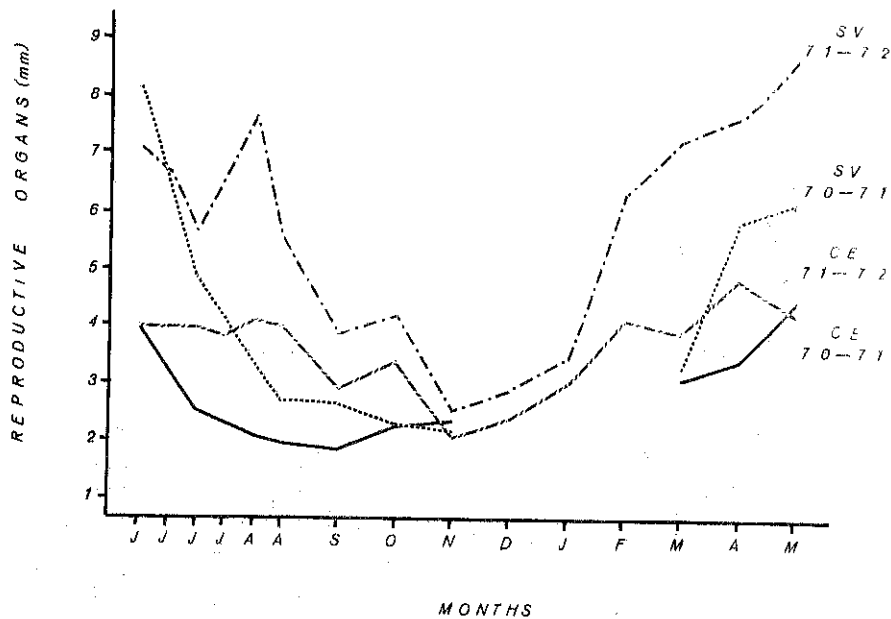


Figure 30. Monthly mean lengths of the caudal epididymides (CE) and seminal vesicles (SV) of 479 adult *Perognathus intermedius*. Summers were sampled bi-monthly. (DSCODE A3UBE21)

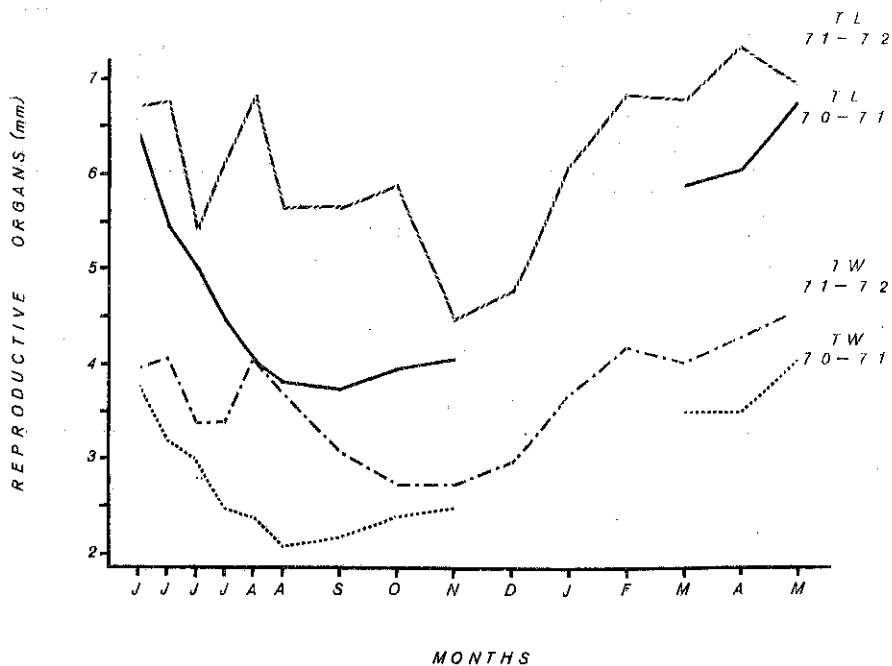


Figure 31. Monthly mean measurements of the testes length (TL) and testes width (TW) of 479 adult *Perognathus intermedius*. Summers were sampled bi-monthly (DSCODE A3UBE21).

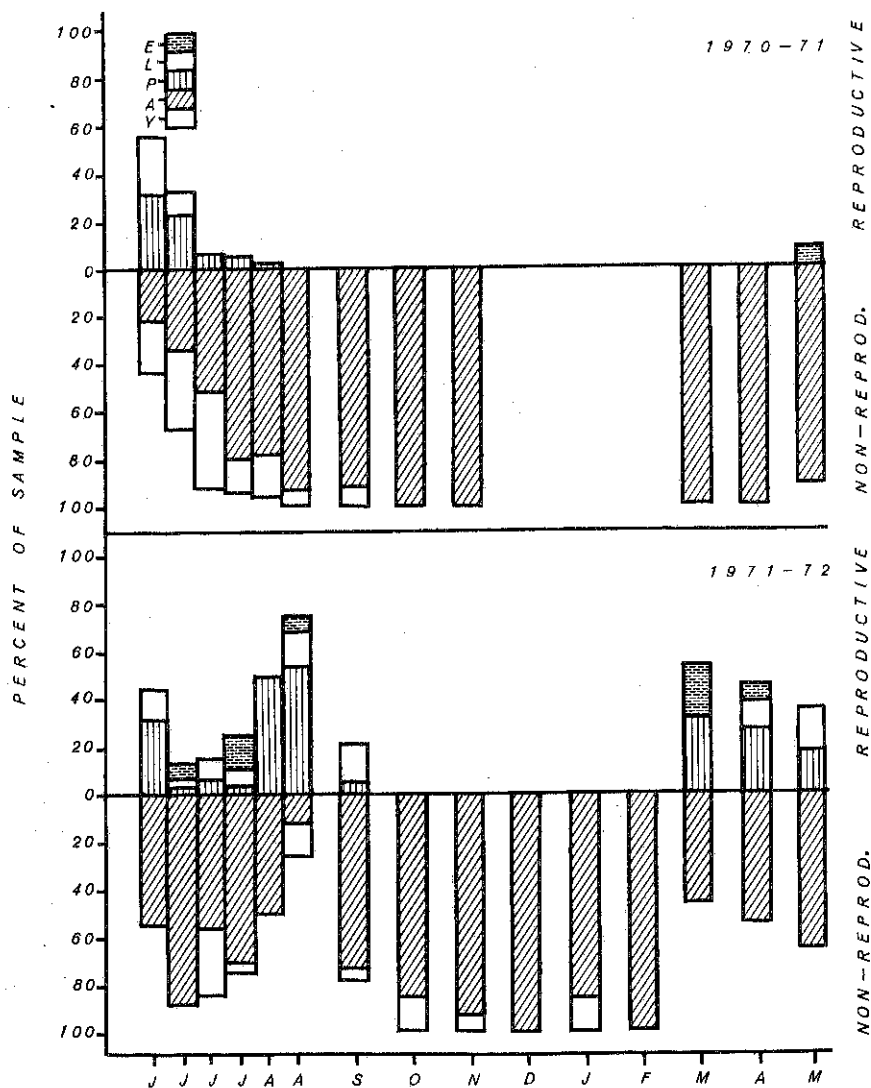


Figure 32. Summary of the reproductive cycles of *Perognathus intermedius* based on 642 females (560 adults, 82 young) trapped from June, 1970 to June, 1972. Reproductive females categorized as estrus (E), lactating (L), or pregnant (P) and non-reproductive females categorized as adults (A) or young (Y). (DSCODE A3UBE22)

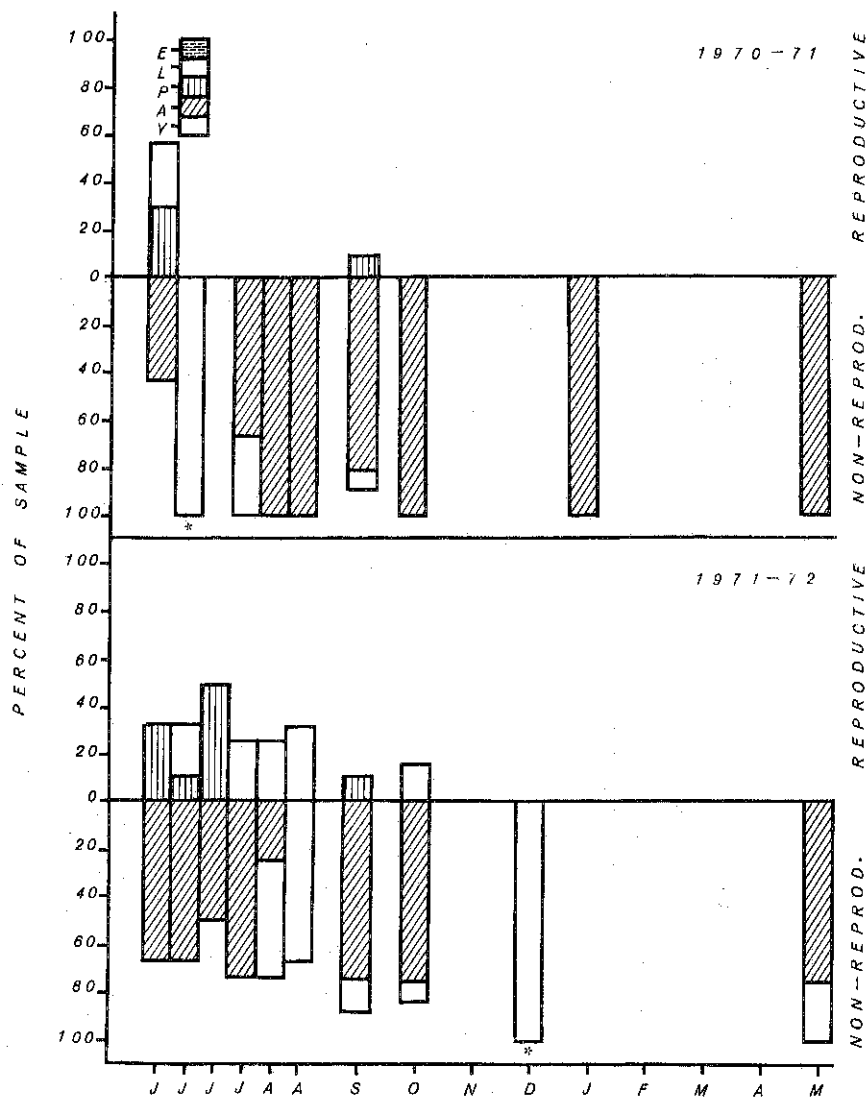


Figure 33. Summary of the reproductive cycles of *Perognathus penicillatus* based on 80 females (67 adults, 13 young) trapped from June, 1970 to June, 1972. Reproductive females categorized as estrus (E), lactating (L), or pregnant (P) and non-reproductive females categorized as adults (A) or young (Y). (DSCODE A3UBE22)
 *Small sample size

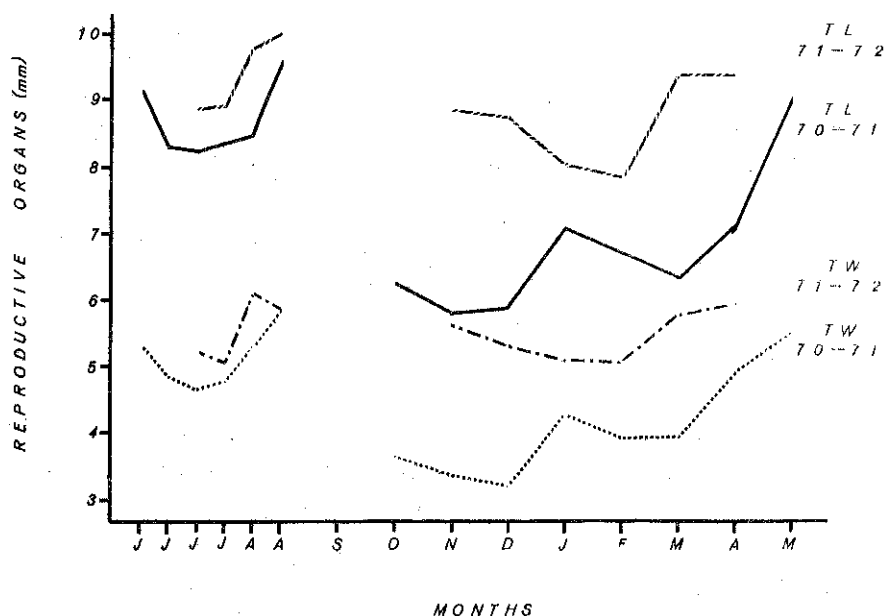


Figure 34. Monthly mean measurements of the testes length (TL) and testes width (TW) of 216 adult *Peromyscus eremicus*. Summers were sampled bi-monthly. (DSCODE A3UBE21)

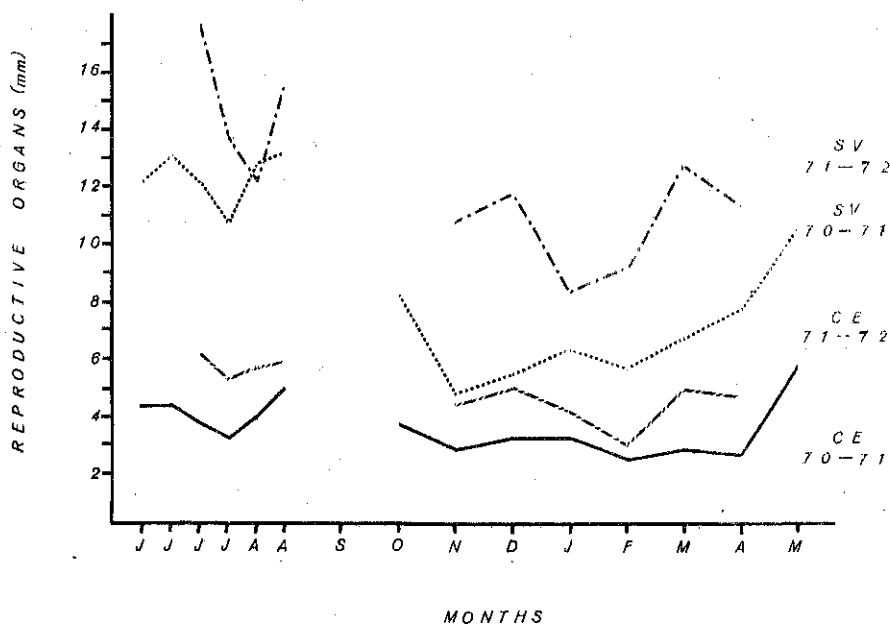


Figure 35. Monthly mean lengths of the caudal epididymides (CE) and seminal vesicles (SV) of 216 adult *Peromyscus eremicus*. Summers were sampled bi-monthly (DSCODE A3UBE21)

Vegetation (DSCODE A3UBE01 A3UBE02, A3UBE03)

The unique geographic position of the Sonoran Desert is demonstrated by two distinct groups of annuals responding to a bi-seasonal rainfall pattern (Shreve, 1951). Bracketed by the Chihuahuan Desert to the east and the Mohave and Great Basin Deserts to the west and north, the Sonoran Desert receives precipitation both winter and summer. In Went's classic desert of Joshua Tree National Monument, two major groups of desert annuals were identified (Juhren et al., 1956). Using both field and lab techniques, Went grouped plants into winter annuals, which included *Festuca octoflora*, *Pectocaryon* spp. and *Plantago insularis*, and summer annuals, which included *Bouteloua aristidoides*, *Boerhaavia intermedia* and *Euphorbia micromera*.

The observations compare favorably with our study area south and east of the monument. Both the kinds of plants and the time that they germinated were reasonably similar. About the only major difference was the observation of *Boerhaavia* by Went. *Boerhaavia* occurred in our study area only in rocky habitats. *Allionia incarnata*, which is in the same family as *Boerhaavia* (Nyctaginaceae) was also observed in the area. These plants are extremely difficult to tell apart in the seedling stage, as is noted by Schiffler (1968) in his phenology study of the Chihuahuan Desert. Mature plants of these species can easily be separated by their distinct seed differences.

Euphorbia spp. and *Allionia-Boerhaavia* were flowering between July and September in the Chihuahuan Desert (Schiffler, 1968). These species apparently flowered earlier and set seed earlier than comparable species in the Sonoran Desert. Approximately 95% of the *Euphorbia* in the Chihuahuan Desert were dead by the middle of September. At our site, maximum density of *Euphorbia* was observed in December of 1970 and in November of 1971. Perhaps a combination of altitude, timing of precipitation, and temperatures accompanying a rainfall could account for distinct differences in growth periods. Went found these factors were extremely critical in the germination of desert annuals in the Mohave Desert (Juren et al., 1956).

Phenological data, considering only one aspect (ripe and dispersing seeds), clearly show a seasonal response. Observations over the entire study area demonstrate that approximately 20% of the herbs were dispersing seeds in June of 1970. Previous winter rains in 1969-1970 must have been substantial because in June of 1971, no herbs were observed with ripe and dispersing seeds. Comparison of observations for the same phenological data after the summer rains was approximately the same. Maximum dispersal occurred in October and November and gradually tapered off during the following months to zero values.

Phenological data is of considerable value in monitoring individual plant species. For example, *Plantago insularis* maintained fairly high densities through the winter

months of both 1971 and 1972. This species remained in the vegetative stage throughout the spring of 1971 without producing any flowers or seeds. In contrast, *Plantago* did flower during the spring of 1972 and produced ripe and dispersing seeds in April and May of 1972. Thus, observation of density alone for both years could lead to some misleading interpretations of plant responses.

It is apparent from this study that the annual plants in the Sonoran Desert have the potential for providing green matter during a large segment of the desert year. During this interval, the plants may remain vegetative (e.g., *Plantago*) or reproduce quickly and put out seeds (e.g., *Bouteloua*). In contrast, seed production for these plants is confined to the period after the summer rains in the Chihuahuan Desert (Schiffler, 1968), or after the winter rains in the Mohave Desert (Beatley, 1969). This distinct "lag" response of annual plants in the Sonoran Desert may be of critical importance to animals depending directly or indirectly on these plants for food.

Unfortunately, the data on the seeds in the soil is not valid for comparing the fluctuating presence of seeds, as the samples were taken in different areas of Avra Valley over the two years of the study. They are, however, most appropriate for comparisons with the diets of the rodents, as they were taken at or near the actual capture sites.

Through the first year of the study, soil samples were secured from random locations on the creosote flats and therefore are comparable only to *Dipodomys merriami* and *Perognathus amplus*. We realized after the first year how important seeds were and began taking samples at the individual rodent capture sites. Table 16 indicates that the seeds available to the sympatric rodents on the flats were very similar. These sympatric rodents are therefore obtaining their seeds from the same basic resource. However, Table 17 indicates that *Perognathus intermedius* and *P. baileyi* on the hills occur in somewhat different habitats in terms of seeds available.

The data presented on the average number of seeds per square meter (Tables 9-14) appear to be much lower than some determinations from other areas. Tevis (1958) presents data on 4.5 billion seeds per hectare.

Diets of rodents (DSCODE A3UVC01)

Because of the predominance of seeds in the diets of the rodents, compared to greenery, the discussion on diets in this section will pertain to seeds. Greenery will be discussed in relation to reproduction in another section. Diet comparisons

will be made between *Dipodomys merriami* and *Perognathus amplus* which are sympatric on the flats, and *Perognathus baileyi* and *P. intermedius*, which are sympatric on the hills. *Peromyscus eremicus* will be discussed separately, as it is not a heteromyid rodent.

Dipodomys merriami: Table 18. Two of the most abundant seed species, *Pectocarya* and *Plantago*, make up a total of 36% of the kangaroo rats diet. Significantly, another major dietary item is insects. For a two year period insects made up 17% of the diets and 62% of the stomach contents contained insects. Comparisons of the two years indicate that the kangaroo rat ate more *Euphorbia* and less *Pectocarya* the second year. Those 13 species making up 1% or more of the diet totaled over 90% of the items ingested.

Dipodomys merriami collected in its cheek pouches more than twice as much *Larrea* and *Plantago* as was in its stomach, perhaps indicating that these seeds are eaten in the burrow. Conversely, insects rarely occurred in the cheek pouches, even though they are an important dietary item.

Perognathus amplus: Table 19. This pocket mouse feeds on two of the most abundant seeds in the soil, *Pectocarya* and *Larrea*. *Erodium* also appears to be an important dietary item. The diet of *P. amplus* was consistent between the two years. Those 10 seed species making up more than 1% of the dietary items totaled over 90%. *Erodium* is found much more frequently in the stomach than in the cheek pouches, as is *Pectocarya*. *Plantago* occurs in the pouches more frequently than in the stomach, and *Larrea* is ingested at the same frequency as it is collected.

D. merriami -- *P. amplus* comparisons: These sympatric rodents ingested many of the same items at similar frequencies. The major trade off of diets appears to be with the kangaroo rat eating many more insects than the pocket mouse, and the pocket mouse eating much more *Larrea*. Perhaps the kangaroo rat is more adept at catching insects than the pocket mouse, and the insects supply the kangaroo rat what *Larrea* provides the pocket mouse.

By comparing frequency figures with usage figures it appears that almost one half of the kangaroo rats used *Larrea* but in no great quantity. By contrast, more kangaroo rats had insects in their diets than any other item. The same is true of *Larrea* in the diet of *P. amplus*.

Perognathus intermedius: Table 20. Several dietary items were of particular importance to *P. intermedius*, including insects, *Larrea*, *Pectocarya*, and various *Opuntia* species. This pocket mouse is the only rodent in the study which uses grass seeds to any extent (*Tridens*, *Festuca*, and *Eriochloa*).

Several of the species in the diet were utilized differently between the two years of the study. *Boerhaavia* increased in consumption considerably the second year, while *Larrea*, *Pectocarya*, and *Festuca* decreased.

As with the other heteromyid species, insects rarely occurred in the cheek pouches, and *Opuntia* was noticeably absent from the pouches while making up a major portion of the diet.

Perognathus baileyi: Table 21. The major dietary items for *P. baileyi* were *Pectocarya* and *Opuntia*. As with its sympatric congener, *Boerhaavia* became important the second year of the study, as did *Opuntia*. The seeds of the grass *Eriochloa* occurred in much greater abundance in the cheek pouches than it did in the diet, as did *Plantago*. Again, insects were only occasionally found in the pouches.

Perognathus intermedius -- *Perognathus baileyi* comparisons: *P. intermedius* utilized almost six times as much grass and twice as many insects as did *P. baileyi*. Conversely, *P. baileyi* used much more *Plantago* and *Pectocarya*. Even though the quantity of these items varies, the usage figures are similar between the two species for the same species of seed. This might indicate that the rodents sample almost all seeds available, but select for major dietary items.

Peromyscus eremicus: Table 22. By far the most important item in the diet of *P. eremicus* is insects. Over 58% of the diet was made up of insects, and almost 95% of the stomachs had insects in them. The important seeds in the diet of *P. eremicus* were *Boerhaavia* and *Opuntia*.

A major point that needs to be made about the diet determinations is that the cheek pouch contents are poor indicators of when an item is eaten and how much is eaten. This is probably responsible for the relatively low figures given in the literature for the occurrence of insects in the diets of heteromyids. It was also found that green vegetation is rarely found in the cheek pouches, even when it is abundant in the stomachs at certain times of the year.

Another point is that there seem to be seeds, such as *Larrea* and *Pectocarya*, which are generally available and used by all rodents in all habitats. Then there are seeds which are abundant and heavily used only in the flats (e.g., *Plantago* and the crucifer), and on the hills (e.g., *Boerhaavia* and *Opuntia*). These items, along with insects, make up the major portions of the diets, with other seeds being less widespread and only seasonally important to the rodents.

The figures for the number of seeds ingested by the species of rodents are probably conservative, even though they intuitively seem high (Table 23). The calculations for the impact do not include those seeds taken and cached, but not ingested. Therefore, impact here means only those seeds ingested, and says nothing about the impact of the rodents which bury caches of seeds and then "forget" them, perhaps lending to the seed's germination.

It is difficult to imagine a kangaroo rat hopping about, gathering 4000 individual seeds in the amount of time available for foraging. This would seem to indicate that the seeds are clumped in distribution so that the rodents can gather several hundred at one stop. Indeed, when there are as many as several hundred seeds in the cheek pouches of an animal, the seeds are primarily (90%) of one species, indicating that the rodents got them from a clumped source. If seeds are dispersed according to some physical parameter such as size or weight, there is every reason to suppose that they are sorted into clumps by wind and/or rain. Another possibility is that the rodents harvest the seeds during those few weeks when the seeds are available on the plants.

It is pertinent to note that *P. intermedius*, which weighs 13 g, eats fewer seeds than *P. amplus*, which weighs 11 g. This can be explained by the fact that *P. intermedius* eats larger seeds than *P. amplus*, and therefore does not have to eat as many.

Diet and reproduction conclusions (DSCODES A3UVC01, A3UBE21, A3UBE22)

From data now analyzed concerning diets and reproduction in desert rodents, certain tentative conclusions seem justified:

1. *Dipodomys merriami* and *Perognathus amplus* share a common seed resource on the flats while *P. baileyi* and *P. intermedius* use somewhat different seed resources on the hills.
2. In most cases, 4 or 5 dietary items make up 60% to 80% of the diets of the rodents.
3. There are some dietary items important to all rodents (*Pectocarya*), some only to those on the flats (*Euphorbia*) or on the hills (*Opuntia*), and some to just one rodent species (*Larrea* to *P. amplus*).
4. Cheek pouch contents are poor indicators of the kind and quantity of items eaten.
5. The population of rodents at the Silverbell site ingest over 15 million seeds a year per hectare.
6. In the five species of heteromyids, the male is, on average, heavier than the female; with *P. eremicus* the reverse is true.
7. The body weight fluctuates seasonally, probably in response to the quality and quantity of food available and environmental stress factors. The animals are heaviest prior to and during a reproductive period.

8. There is a positive correlation within adult males between increased body weight and amount of spermatozoa present in the reproductive organs.
9. There was a correlation between average body weight and surface inactivity for the winter months of the six species studied. *Dipodomys merriami* increased its activity during the winter months whereas the other hereromyids had varying lengths of surface inactivity during winter months.
10. Each of the species were more active during the second year as compared to the first.
11. The males of each species had a longer reproductive season than did females and a higher percentage of reproductive males were recorded.
12. There was a positive correlation between bacula length and both spermatozoa content and age categories. Measurements of testes, caudal epididymes and seminal vesicles demonstrated size fluctuations that correlated with amounts of spermatozoa observed.
13. Both male and female fecundity, for all six species, in the second year greatly contrasted that of the first year.
14. The smaller species have shorter breeding periods and larger litters.

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1972 PROGRESS REPORT

FORAGING ACTIVITY OF THE LEAF-CUTTER ANT, *Acromyrmex versicolor*,
IN RELATION TO SEASON, WEATHER AND COLONY CONDITION

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Research Memorandum, RM 73-28

MAY 1973

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Report Volume 3

Page 2.3.3.1.

A B S T R A C T

This report covers the foraging of 33 marked colonies of *Acromyrmex versicolor* on a 0.36 ha study plot on the Santa Rita Validation Site in 1971. An analysis of the data in Data Set A3UWH04 indicates that peak foraging activity reached well over 300,000 trips per 24-hr day during the most active period on this plot and would run over a million per ha. Plants and parts selected changed through the season, with some that were especially favored gradually being removed entirely. Because of the heavy concentration of foraging in the rainy monsoon period, plants selected then probably are utilized much more heavily than those favored at other seasons.

INTRODUCTION

The leaf-cutter ant, *Acromyrmex (Moellerius) versicolor versicolor* Pergrande, is one of the more prevalent ant species on the Santa Rita Validation Site. It is unique at this location in that it gathers leaves, petals and some other plant material, either removing them from the living plants or gathering them after they have fallen to the ground. This plant material is taken to chambers in the nest and there utilized as the substrate on which a fungus is cultivated. The fungus is then harvested, providing the food for adult and larval ants alike.

The tribe Attini, to which this species belongs, has been extensively studied in tropical America, because some of its members are so diligent in removal of plant material that in some regions conventional agriculture is impossible.

As a first stage in modelling the activity of *A. versicolor* and assessing its impact on the vegetation of the Santa Rita site, the present project undertook to measure foraging activity of the workers and the selection of plant material through the season. A full season of foraging activity is included in the data filed under Data Set A3UWH04. This set of observations should prove useful not only in assessing the relationship of the activity of this ant to weather and other factors, but as a point of departure for similar studies on ants in general. The regular foraging columns of this species have permitted extremely accurate measurement of foraging activity. Such measurement is difficult and therefore less reliable in most other species.

OBJECTIVES

The objectives listed for 1972 were:

1. To measure foraging activity of worker leaf-cutter ants in relation to season and abiotic factors.
2. To record preference for plant species and parts during foraging.
3. To estimate the requirements of the colony in relation to the state of the colony, particularly to the presence of developing larvae.

The last objective was not accomplished. Steven Murray, graduate research assistant, received the M.S. degree in May and left the project. It was not possible to continue the project during the summer months without his help.

The first objectives have been accomplished in a general way, and can certainly be finished when the weather data gaps for the Santa Rita site 1971 record are filled

in by extrapolation from data obtained in surrounding areas. The exact time of observation is included in all of the entries of ant activity.

METHODS

Periodic visits were made to a marked 0.36 ha plot on the Santa Rita undisturbed site, near the weather telemetering tower, from mid-April to early December, 1971. The ant colony entrances on this plot had been marked in 1970, but a few more were discovered in 1971. The site is described fully in Werner and Murray (1972).

The pattern of observation was to make a circuit of the colonies at roughly 2-hr intervals, recording the information indicated below on each circuit. Many of the observation days span the whole period from start to stop of foraging activity, but the time intervals between observations are somewhat irregular. During periods of heavy activity, a circuit of observations might take more than 2 hours by itself.

The data filed under DSCODE A3UWH04 include the following, only part of which have been used in the preparation of this report:

- Columns 1-10. Date and time of observation within 5 min.
- 23-24. Nest No.
- 33. Light conditions at entrance (direct sunlight, shade, moonlight, dark, sun, and shade mosaic).
- 34. Entrance condition (open, closed).
- 35. Activity pattern (guards at entrance; general surface travel around entrance; excavation of soil from nest; foraging, usually in a column; combination of last 2; no workers observed; material from storage or fungus garden being discarded; flight of alates).
- 36-38. Number of individuals in foraging column counted per minute (either leaving or returning).
- 39. Direction of travel (leaving, returning).
- 40. Number of minutes counted.
- 41-42. Length of column from entrance, straight line.
- 43-44. Direction of column, in 10° increments.
- 45-46. Estimate of area foraged in m².
- 47-48. Food (taxonomic code, part, condition of part).

RESULTS

Foraging activity

Foraging in leaf-cutter ants is essentially a year-round activity, but it takes place at a very low rate in the winter. It is readily measured, because it results in columns of relatively slow-moving ants.

An active colony tended to follow a fixed progression in initiating surface activity: a) nest entrance opened, b) workers stationed at entrance, facing out, with some exploration for ± 1 m, and c) full foraging with one to several columns following distinct trails and returning workers carrying material. Cessation of foraging often followed a reverse sequence.

As a general rule there was one foraging entrance and one column per colony. There were rare exceptions of up to three concurrently active entrances, and more commonly a colony foraged in from two to five directions at once.

Foraging trails could be traced by presence of dropped forage; they were not otherwise visible. (Murray, 1972).

Figure 1 summarizes foraging activity actually observed during 1971. The number of foraging trips is based on an average of the number of ants counted per minute on the outward trip over the whole period of foraging and for all of the colonies on the study plot combined, multiplied by the number of minutes spanned by the foraging period. The counts in April and May are probably lower than actual because the emphasis during this period was on determining the starting and stopping of foraging activity, rather than on determining its total span. The numbers obtained from the calculations have been used in preparation of the graph in Figure 4.

Diel pattern of foraging

The diel pattern of foraging is recorded in great detail in Data Set A3UWH04 but some general patterns are indicated here.

Figure 2 provides a summary. The early summer of 1971 was extremely dry with hot days, relatively cool nights, and low relative humidity. During this period foraging was almost strictly nocturnal, as indicated in the June day recorded. It started in late afternoon, near sunset (indicated by the horizontal curve), continued through the night,

diminishing late at night when temperatures had dropped, then had a brief spurt at dawn. Since the lines drawn connect points based on circuits of observation, they tend to extend the period at the beginning and the end of foraging. Actually, foraging may start quite abruptly in a single colony, with a much longer period being required for all colonies to get started. But it stops very abruptly in the early morning, as the soil surface heats.

Foraging continued to be heavily nocturnal during July and August, after the start of the monsoon rains, but started earlier and ceased later after the soil surface was damp. On overcast days it could continue all day, but generally the number of foraging colonies increased sharply in the evening and maintained high activity until after sunrise (Murray, 1972).

As the season progressed in September-December, nocturnal foraging was increasingly depressed, presumably by decreasing night air temperatures. The soil remained moist for much of this period, probably permitting more diurnal activity than would have been possible during a dry year. Low-growing annual and perennial vegetation on this ungrazed plot had become quite luxuriant, providing more shade and probably lowering soil surface temperatures during the day.

Foraging in relation to abiotic factors

In his thesis report, Murray (1972) provides some analysis of foraging in relation to weather factors. He was able to fill in some missing weather data from strip charts produced by other workers in the area, but could not get records for late July and August, the period of maximum foraging activity.

Murray records foraging at air temperatures from 8.5-31.5 C, with 58% of the observations between 18.5-27.5 and 25% between 21.5-24.5 C. The mean value for 397 observations of activity (omitting late July and early August) was 21.78 C, S.D. 5.13.

The influence of moisture in the air was noticeable mostly during early summer. No foraging was observed at a relative humidity of less than 12%. Foraging by more than 50% of the colonies did not occur below 24% relative humidity, and increased foraging followed after summer rainfall when humidity could be assumed to be high. The response to humidity during the spring and early summer dry season was such that daily maximum foraging coincided with daily maximum humidity at sunrise.

Murray (1972) describes the effects of heavy rainfall: An afternoon thunderstorm occurred July 14, 1971, seriously disrupting the foraging pattern of eleven colonies. An observation circuit made about two hours after the rainfall showed these eleven colonies in a random search pattern. At this same time, thirteen other colonies were foraging on trail routes.

2.3.3.1.-6

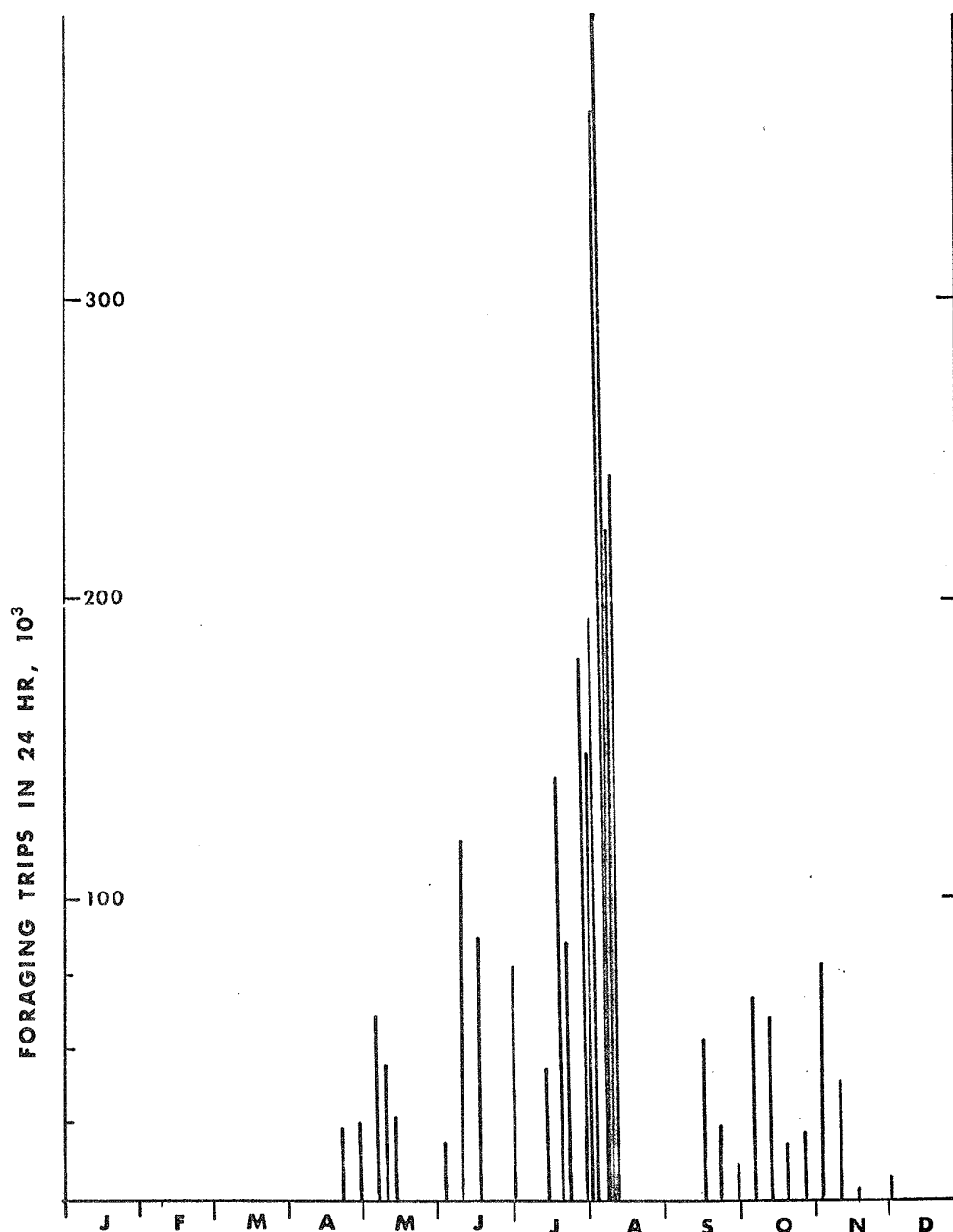


Figure 1. Number of foraging trips per 24-hr observation period, in 1971, of all colonies on the 0.36 ha Santa Rita plot, based on average number of workers counted per minute, going away from nest, multiplied by total number of minutes spanned by foraging period. (DSCODE A3UWH04)

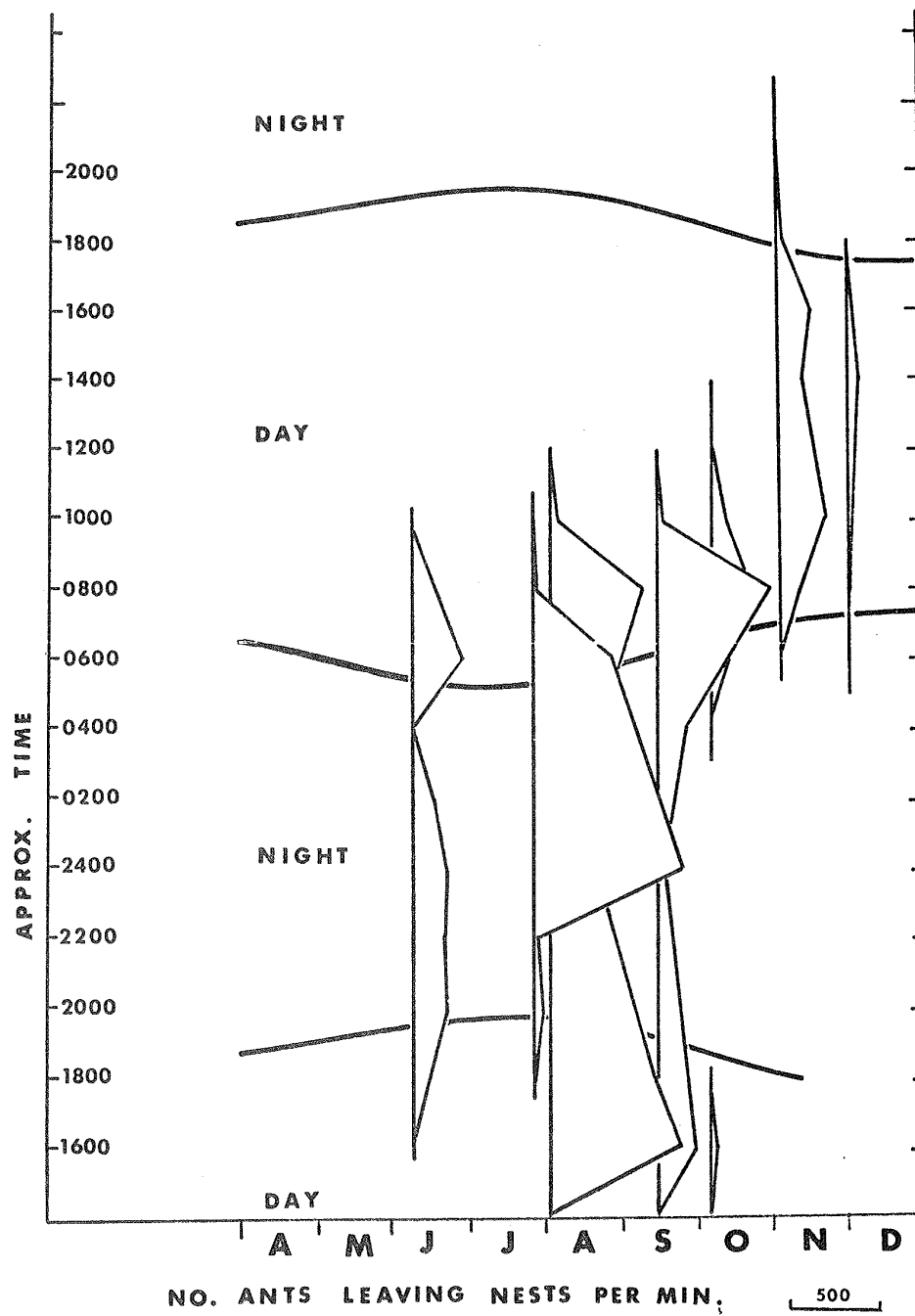


Figure 2. Patterns of foraging on representative days in 1971 of all colonies on the 0.36 ha Santa Rita plot, based on number of workers counted per minute, going away from the nest. Horizontal curves represent approximate time of sunrise and sunset. (DSCODE A3UWH04)

2.3.3.1.-8

Internidal variation in foraging

Individual colonies showed great variability in the extent to which they foraged during periods when surface conditions were favorable. Murray found that the number of times a colony was foraging during the season of observation ranged from 2 to 97, mean 45.06, S.D. 23.47. Several of the colonies were not discovered until late in the season, perhaps because of their small size. Even if these are omitted the range and deviation are extreme.

Plant species and parts foraged

Figure 3 shows the materials foraged during the year, on a month-to-month basis, as derived from records in DSCODE A3UWH04 of actual observations of foraging by a colony. This graph shows only the percent of observations, giving an indication of preference but not of quantity. The plants recorded are:

- Grass -- all species of Gramineae, perennial and annual.
- Mesquite -- *Prosopis juliflora* - Leguminosae Mimosoideae, tree.
- Allionia -- *Allionia incarnata* - Nyctaginaceae, annual.
- Burroweed -- *Haplopappus tenuisectus* - Compositae, perennial shrub
- Opuntia -- *Opuntia* - Cactaceae. 3 spp., *O. phaeacantha* (prickly pear), *O. fulgida* and *O. spinosior* (chollas). *O. phaeacantha* accounted for most records.
- Acacia -- *Acacia greggii* - Leguminosae Mimosoideae, shrub.
- Ephedra -- *Ephedra trifurca* - Ephedraceae, shrub.
- Euphorbia -- *Euphorbia melandenia* - Euphorbiaceae, annual.
- Palo verde -- *Cercidium floridum* - Leguminosae Caesalpinoideae, tree.

In addition a few records were made for *Proboscidea arenaria* (Martyniaceae, root perennial), *Tidestromia lanuginosa* (Amaranthaceae, annual), and *Zinnia pumila* (Compositae, perennial).

A frequently collected item in the fall was grasshopper feces (Insecta, Orthoptera, Acrididae), which seemed to be selected very heavily. Ants were also observed during the summer to favor fecal pellets of *Celerio lineata* (Lepidoptera: Sphingidae), but not during the observations reported.

In Figure 4 an attempt is made to place the foraging in the perspective of how much might be removed from month to month. The potential foraging contacts per day each month were obtained by multiplying the average number of foragers per 24-hr-day, calculated from the numbers on which Figure 1 was based, by the percent of observations during the month indicated in Figure 3. *Ephedra* and *Euphorbia* have been omitted, because they contribute very little, early in the season.

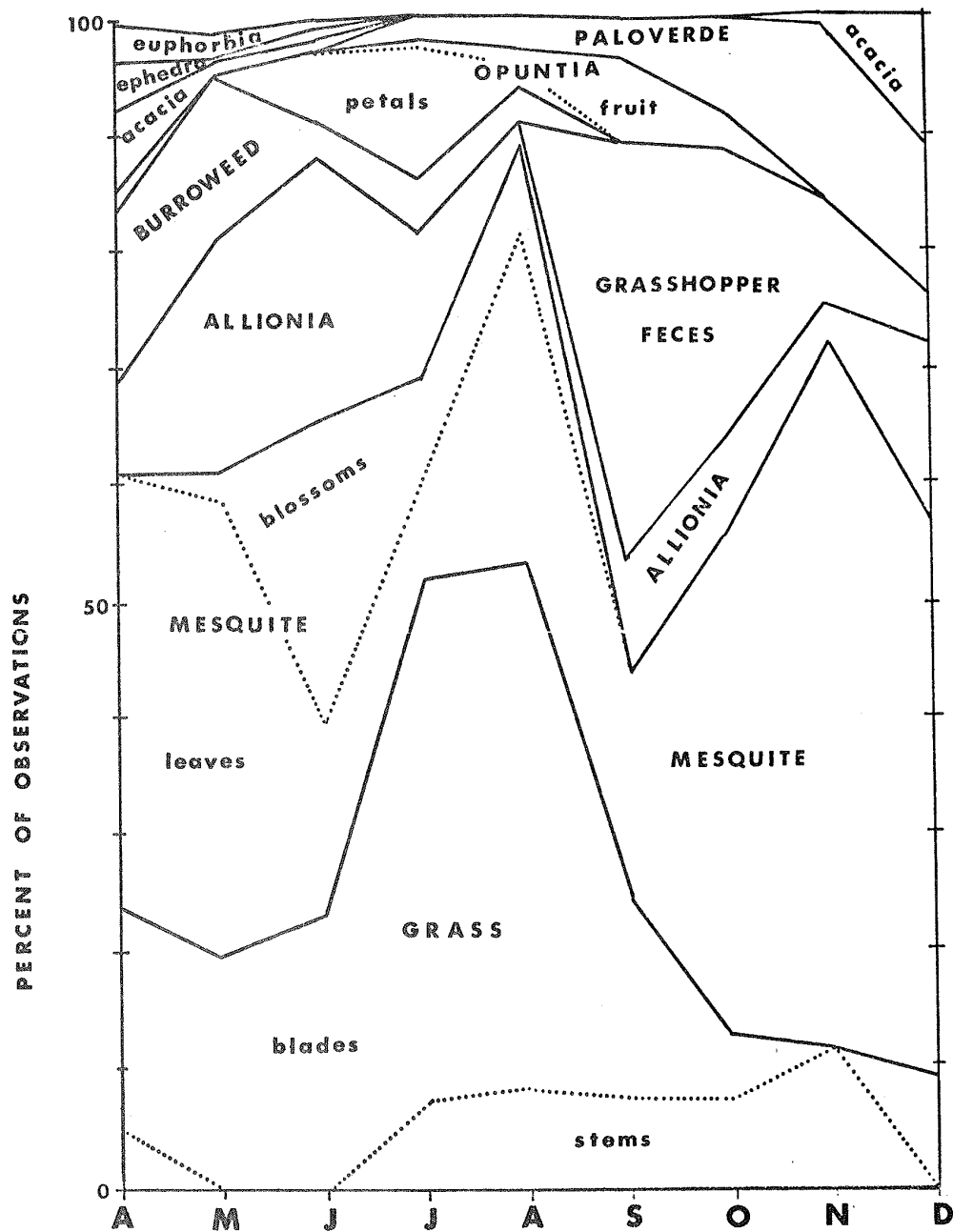


Figure 3. Forage selection of all colonies on the 0.36 ha Santa Rita plot in 1971, based on number of times individual colonies were observed selecting items during the month. (DSCODE A3UWH04)

Acacia = *Acacia greggii*
 Allionia = *Allionia incarnata*
 Burroweed = *Haplopappus tenuisectus*
 Ephedra = *Ephedra trifurca*
 Euphorbia = *Euphorbia melandenia*

Grass = Gramineae
 Grasshopper = Acrididae (several species)
 Mesquite = *Prosopis juliflora*
 Palo verde = *Cercidium floridum*
 Opuntia = *Opuntia phaeacantha* plus some
O. fulgida and *O. spinosior*

2.3.3.1.-10

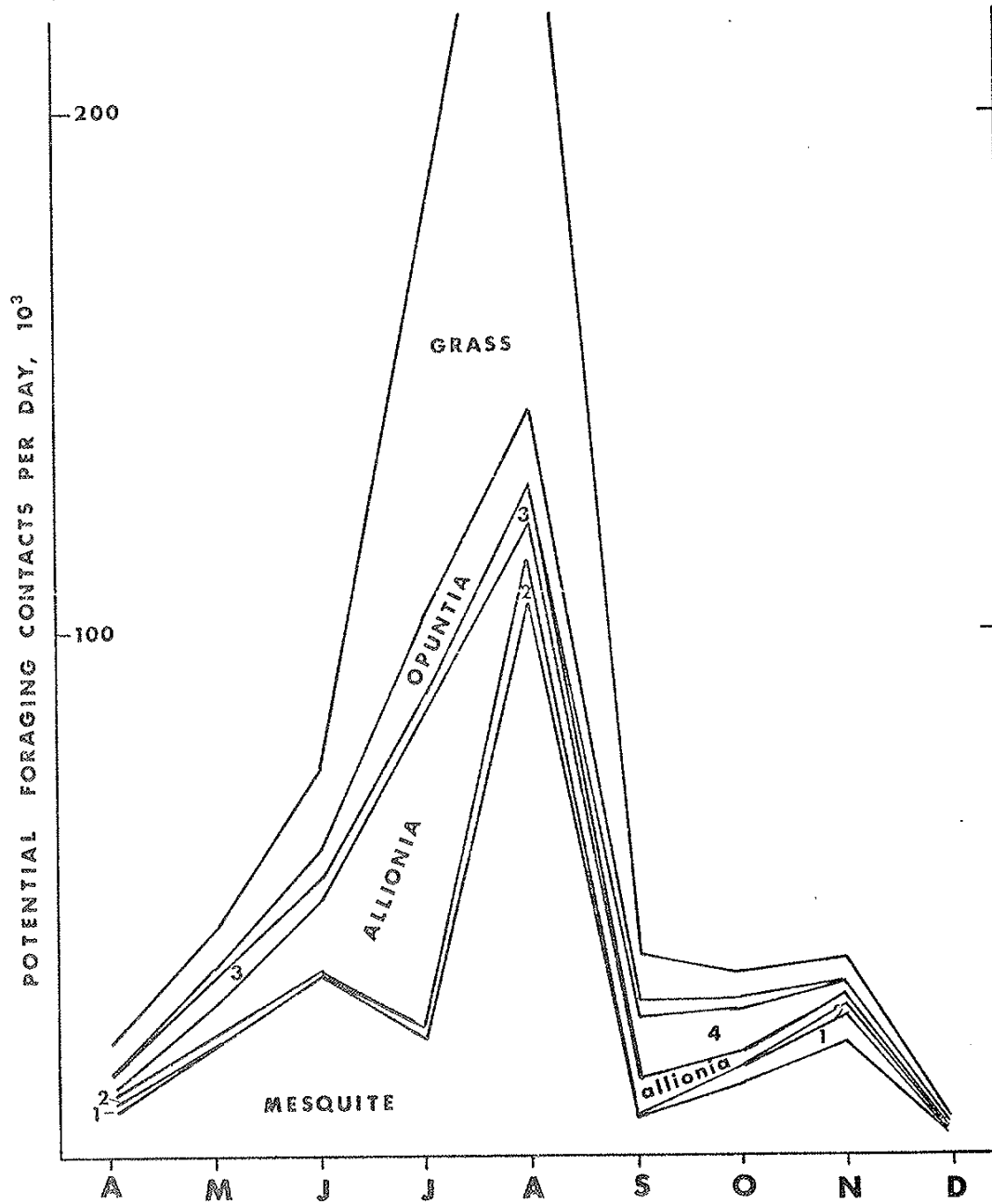


Figure 4. Potential foraging contacts on the 0.36 ha Santa Rita plot in 1971, based on average foraging trips per day during month, from data used for Fig. 1, and percentages shown in Fig. 3. Names as in Fig. 3.

1 = Palo verde
2 = *Acacia*

3 = Burroweed
4 = grasshopper feces

DISCUSSION

Foraging in relation to abiotic factors

While the data reported in the Results section indicate that foraging takes place only within specific extremes of air temperature and relative humidity, a more sophisticated analysis of foraging and weather measurements should show more meaningful correlations.

The environment of the foraging worker is probably most profoundly affected by the soil surface temperature, a parameter that is not measured in standard weather monitoring. During the daytime the largest component of soil surface temperature must be solar input. During cloudless days in the dry season, soil surface temperature rises extremely rapidly soon after dawn, and drops nearly as rapidly, but not to as low a temperature, as sunset approaches. Whether it is the sun's contribution to soil temperature or insolation of the ant itself that limits foraging may be a moot point. But foraging may take place with the sun in a higher position if the soil is moist. Under these conditions, both the soil surface and the air in which the ant moves are probably cooled by evaporation.

If the number of workers involved in the foraging is more or less fixed, as seems likely, the body temperature of the ants largely determines the number of foraging trips possible during a given period, because of its effect on rate of movement.

Moisture may also play an important part in foraging activity, but whether the relative humidity of the air is the direct determinant could be argued. Very low relative humidity of the air is directly associated with low moisture levels in shallow soil. Foraging activity reaches a maximum after a rain. At this time the relative humidity of the air is very high, but so also are soil moisture and probably the relative humidity of the air in chambers near the surface.

Deep-soil temperatures, which change very slowly through the year, undoubtedly have a moderating influence on surface activity. Colonies of this and other ant species excavated in late winter had deep cavities filled with dormant ants, even though there were some active ants in shallow chambers and some on the surface foraging. Leaf-cutter nests extend at least 3 m depth. Even in the driest seasons the air in deep chambers is very moist. Since fungus culture seems to be confined to these deeper levels, temperatures there may be of greater importance to the colony than conditions on the surface.

A model of the surface temperature of bare soil throughout the year would be an extremely valuable tool for developing regressions with foraging activity and thus a

2.3.3.1.-12

description of the total foraging potential of these ants. The dampening effect of rainfall could be incorporated as a fine-tuning of the model.

Foraging in relation to intrinsic biotic factors

The observations reported indicate an extremely great variability in the response of individual colonies to surface conditions favorable to foraging activity. Other observations indicate that individual nests may remain closed for weeks at a time, while other nests are open and the colonies very actively foraging. So a simple modeling of weather factors in the air and soil may not provide an adequate description of the activities of individual colonies, even if it serves well in general.

The availability of and demand for the fungus that is cultivated probably has a direct bearing on the response of a colony to favorable foraging conditions on the surface. Plant parts taken into a nest appear to be stored first in shallow chambers, and sometimes on the nest disc or along foraging trails, apparently until they have dried somewhat. It appears that storage space must be limited. Even so, individual colonies take in very large quantities. When the limit of space is reached, foraging must cease until space is available due to utilization of the plant material previously stored.

Colonies apparently have no eggs, larvae, or alates in them in late winter. Yet, flights of alates occur soon after the start of rains during the monsoon season. Unless there is more going on in the deepest recesses of the nest than we have discovered thus far, all of the alates released from the nest in July or August must have had all of their development prior to that time in the same year. Demand for food must be high during this period.

This probably means that whatever is available and preferred is subjected to unusual pressure. In 1972 there was little variety, due to extreme drought. Because conditions on the surface were so severe, the individual colonies that were foraging during this period probably continued to have a demand for plant material at the time that they were forced to cease foraging by surface conditions.

Selection of materials foraged

Figures 3 and 4 provide a general view of the materials foraged during the year, but not a quantitative estimate. Figure 3 perhaps illustrates more clearly the changing preferences during the season. What is actually taken at any one time probably is the result of an interaction between availability and preference.

Because many of the colonies have their nests under mesquite trees in the minor washes on the plot, and because this tree leafs out early no matter how dry the season,

mesquite probably provides the principal source of plant material throughout the season, even though some other plants may have been selected more frequently at times. Blossoms are selected over leaves during the period that they are available.

Grass is obviously favored, especially the blades but also the green stems if blades are not available. Because the grasses are the most important plants on the plot from a grazing standpoint, this preference should be examined more closely.

Other plant associations result in different choices. Of interest is the frequent choice of *Larrea divaricata* leaves and terminals at the Silverbell Validation Site and elsewhere in the Tucson region. Unfortunately, the study plot at Santa Rita does not contain a plant of this species, although a few are present on the site as a whole.

Insect feces seem to be very highly favored, but would rarely be abundant enough to provide a stable source of forage. Dry bird feces are also taken quickly, but did not appear in the records for 1971. The uric acid and other nitrogenous wastes in this fecal material could be important in the cultivation of the ant's fungi.

ACKNOWLEDGEMENTS

I wish to thank Dr. Charles Romesburg for providing the special printouts of DSCODE A3UWH04 on which the Figures were based, and Steven L. Murray, for his diligence in the field in 1971 and subsequent analysis of data.

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1972 PROGRESS REPORT

DEMOGRAPHY AND BIOENERGETICS OF HERBIVOROUS ANTS IN A DESERT
ECOSYSTEM AS FUNCTIONS OF VEGETATION,
SOIL TYPE AND WEATHER VARIABLES

W. G. Whitford, Project Leader

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Research Memorandum, RM 73-29

MAY 1973

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Report Volume 3

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A B S T R A C T

Soil surface temperature (T_s) and saturation deficit (SD) combinations regulate the foraging activity of harvester ants. *Novomessor cockerelli* which is active nocturnally, was active at T_s 15-45 C with maximum activity at T_s between 20 C and 30 C and SD $<25 \text{ g/m}^3$. *Pogonomyrmex rugosus* was active at T_s 20-55 C and SD $<40 \text{ g/m}^3$ with peak activity at 45 C. *P. desertorum* was active at T_s 25-55 C and SD $<40 \text{ g/m}^3$, with peak activity at 45 C, and *P. californicus* was active at T_s 35-60 C and SD $<45 \text{ g/m}^3$, with peak activity at 45 C. There was nearly complete overlap of foraging territories between colonies of the same species and different species (*P. rugosus* and *N. cockerelli* only). Foraging effort was shown to exhibit a natural log decay function with increasing distance from the nest. Foraging effort also varied as a function of resource concentration. There was considerable overlap in the foraging preferences of the *Pogonomyrmex* species studied. In a year such as 1972 which results in high density annual forb and grass production, harvester ant foraging had a small impact on seed reserves but the seed reserves of selected plant species were significantly affected, e.g., *Eriogonum trichopes* and *Bouteloua barbata*. Regression equations were developed for predicting fruit number and biomass in several species of annual forbs and grasses.

Forager population estimates were highest coincident with maximum forage availability. Comparison with the colony sizes of excavated colonies suggested that all foragers were mobilized at that time, providing a reasonable estimate of total colony size. *P. desertorum* and *N. cockerelli* exhibited clumped distribution and *P. rugosus* colonies were randomly distributed at the Jornada Validation Site.

INTRODUCTION

Studies of ecosystems may be conducted in a number of ways and at varying levels of complexity. In the Desert Biome program, research efforts are being conducted at: 1) the whole system level, with an emphasis on models of the transfer of energy and nutrients through the components of the system, 2) parts of the system with emphasis on answering specific kinds of questions, question oriented models, and 3) synthesis and testing of ecological principles not necessarily utilizing simulation models. This study was designed to provide data for all three approaches, but with emphasis on the data requirements of a harvester ant foraging-seed reserve model produced under the direction of Dr. Kent Bridges and with the assistance of several modellers at Utah State University.

In order to predict the impact of harvester ants on the seed reserves of a given year, several behavioral parameters of harvester ant species involved must be predictable. Of these, factors affecting foraging activity and intensity must be elucidated. The literature provides few studies with information on foraging behavior in harvester ants (Tevis, 1958; Creighton, 1953; Cole, 1934; Eddy, 1970; Lavigne et al., 1971; Willard and Crowell, 1965). Of these studies, the only quantitative data on factors affecting foraging activity deal with *Pogonomyrmex occidentalis* or *P. owyheei* (Willard and Crowell, 1965; Eddy, 1970; Lavigne et al., 1971). None of these studies adequately treat climatic factors other than temperature. Therefore our studies were designed to evaluate the interrelationship between soil surface temperature and the drying power of the air (saturation deficit) as components determining foraging activity in harvester ants.

The preliminary studies demonstrated that while climatic factors were extremely important determinants of foraging activity in harvester ants, other factors probably affected foraging intensity (e.g., relative abundance and pattern of distribution of food items). No reference to papers evaluating the responses of harvester ants to variations in these parameters was found. Consequently field experiments were designed to obtain the data necessary to evaluate these parameters.

Maximum foraging distance, distribution of foraging effort as a function of distance from the nest and interactions between colonies of the same species or different species are parameters which must be measured in order to determine the reliability of uniformly applying the data provided by foraging studies to a large area. In addition, evaluation of these parameters provides data for testing hypotheses concerned with intra- and interspecific competition, niche separation etc., within natural communities. Numerous field experiments were designed to provide these data.

In addition to foraging rates, kinds and frequency of plant parts foraged as a function of availability and production must be ascertained. In desert areas, the composition of the annual plant community changes from year to year. Therefore studies of food habits of species of harvester ants at a point in time would have little predictive value unless accompanied by data on rate of production of fruits and/or seeds of various species. Data on food habits of harvester ants are also somewhat limited (Tevis, 1958; Eddy, 1970; Lavigne et al., 1971; and Willard and Crowell, 1965). Tevis (1958) presented data on material foraged by *Veromessor pergandei* as a function of seed reserves. Eddy (1970) provided data on material foraged by *P. occidentalis* in four areas in Kansas as related to seed production in the area. The other studies cited provided some data of a more qualitative nature. Our studies were designed to provide data on food preference as a function of food availability.

OBJECTIVES

1. To estimate density, biomass and population structure of harvester ants in the Jornada area. Research in 1972 concentrated on obtaining reliable data for forager populations and continued to evaluate techniques for estimating total populations.
2. To measure activity patterns as functions of temperature and season. This was accomplished for four species including saturation deficit as an independent variable.
3. To measure food-consumption rates and species of plant seeds consumed as functions of vegetation phenology, production and season.
4. To measure egestion, assimilation and metabolic rates of harvester ants. [A manuscript dealing with oxygen consumption in two species has been submitted for publication.]

In addition to the objectives stated in the original proposal (1-4) the following were added.

5. To investigate interactions between colonies of the same species and different species to provide insight into spatial relationships.
6. To identify and quantify factors in addition to climate which influence foraging activity.

METHODS

Our studies centered around four sympatric species of harvester ants which are important at the Jornada Validation Site and which are widely distributed in desert areas in the U.S. and Mexico: *Pogonomyrmex rugosus*, *P. desertorum*, *P. californicus* and *Novomessor cockerelli*. Field studies were conducted on an area adjacent to the Jornada Validation Site, 40 km NNE of Las Cruces, Dona Ana Co., N.M. and on an area 11 km east of New Mexico State University, Dona Ana Co., N.M.

Foraging activity (DSCODE A3UEE03)

Foraging activity was studied by placing a wire reference circle over a number of randomly selected nests of harvester ants. The circles were divided in eight equal areas (Fig. 1). Activity was monitored by counting the number of ants returning to the nest per unit time. The portion of reference circle counted depended on the foraging intensity (that portion that could be counted accurately). When fractions of a circle were counted at a single measurement period, several sections were counted. Sections were selected at random to eliminate the bias of a segment over a foraging trail. Foraging activity was calculated by multiplying the number of ants returning by the denominator of the reference circle fraction and dividing by the number of minutes observed. At each observation period we also measured wet and dry bulb air temperatures as close to the soil-air interface as possible with a gun psychrometer or sling psychrometer, and the soil surface temperature by laying the bulb of a mercury thermometer on the soil surface and covering it with a fine layer of sand. Foraging activity was monitored at 2 hr intervals from dawn until dusk once a week or every two weeks, depending on the season. Several all-night activity studies were conducted in mid-summer when it was obvious that some species did not cease foraging at sunset.

Variations in foraging behavior as a function of distance, colony interaction, food availability and distribution (A3UEE10)

The feasibility of using seeds dyed with vegetable dye to determine the relationships between distance and foraging behavior had previously been determined (Whitford and Ettershank, 1971). In 1972, a luxuriant growth of annuals covered the site and, as a consequence, abundance of natural food complicated such studies since the ants preferred natural seeds to the cracked milo we provided. Therefore, we selected three *Pogonomyrmex rugosus* colonies for study and completely cleared an area 15 m in radius around each nest. All vegetation was uprooted and the area swept clean with a broom. This provided us with an area essentially devoid of food in which to conduct our experiments. The experiments performed are outlined below:

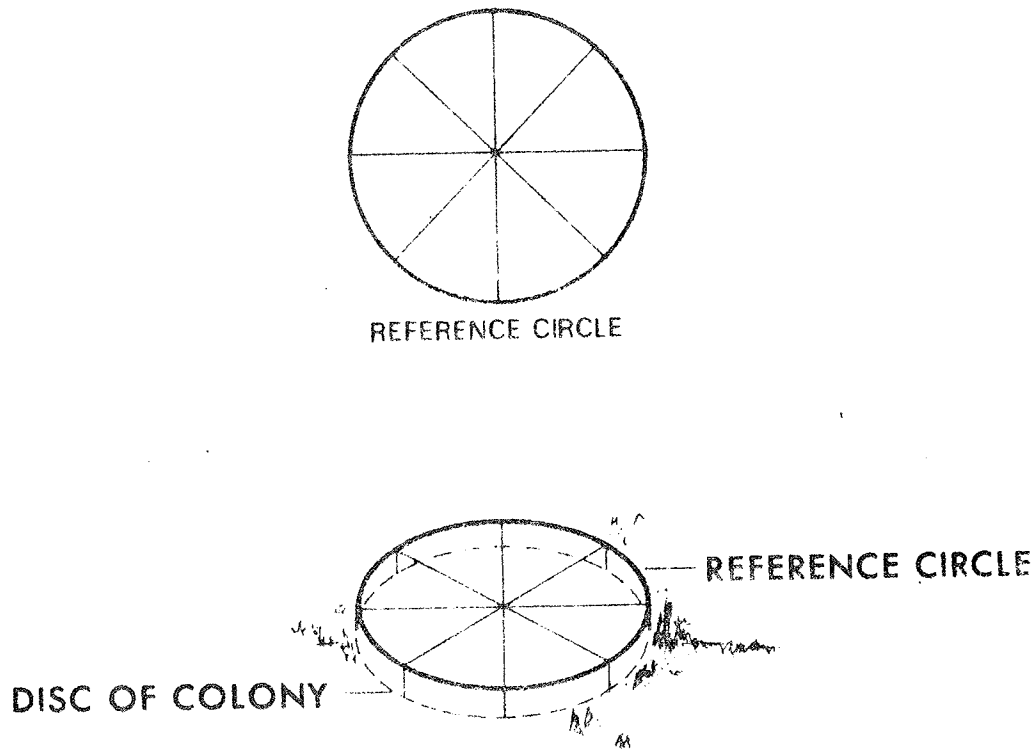


Figure 1. Diagram of the reference circle and relationship to harvester ant colony.

(1) Foraging activity; food concentration constant. Quantities of dyed milo were measured out to provide equal concentrations of food per unit area at varying distances from the reference nest. In some experiments the seeds were distributed in evenly spaced piles and in some as continuous rings (Fig. 2). Observers were stationed at colonies adjacent to the cleared area and at the reference colony to record the number of seeds of the various colors returned to the nest per unit time. Soil surface temperatures and wet and dry bulb air temperatures were recorded at the beginning of each experiment.

(2) Foraging activity; food concentration varied. To evaluate the effect of an uneven distribution of food on foraging intensity, the concentration of seeds at a selected distance was multiplied by a factor five or ten (for example, line 3 in Figure 2 might be increased to 3000 g of blue seeds). The data recorded as in (1).

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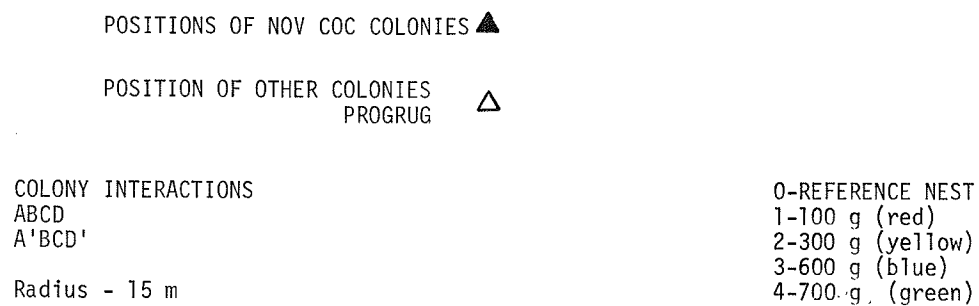


Figure 2. The relationships of harvester ant colonies and distribution of colored seeds in foraging experiments in the cleared areas. See text for details of experiments.

(3) Colony interaction. Interaction of colonies was studied by modifying the experimental design in experiment (1) by providing colored seeds on two sets of arcs out of the entire circle (Fig. 2). For example, the area indicated by A was supplied with arcs of red at 1, yellow at 2, blue at 3, and green at 4 while A¹ was supplied with pink at 1, brown at 2, purple at 3, and natural at 4. Arcs BB¹CC¹DD¹ received no seeds. Data were recorded as in experiment (1). Successive experiments were conducted to evaluate seed removal from areas BB¹, CC¹, and DD¹.

Forage selection: A3UEE11

Data on forage selection by species of harvester ants were obtained by collecting all of the foragers returning to a randomly selected colony over a 5 min period. Aspirators were used to collect returning foragers and their forage. Sampling by this routine was conducted monthly and at different times of the day to insure sampling at peak activity times for the species under consideration. Additional data on materials foraged were obtained during mark-recapture studies. Forage materials carried by ants collected for marking or census were collected from the foragers picked up by aspirators and stored in vials. Reference collections of fruits and seeds were made in order to classify foraged materials. Samples stored in vials were identified using a dissecting microscope and tabulated by sampling date.

Seed production -- annual and perennial forb production (A3UEE13, A3UEE14)

Analysis of food preferences of a species demands that the food preferences be expressed as a function of food availability if food habits are to have any predictive ecological significance. Since harvester ants primarily utilize the fruits of annual and perennial forbs and grasses and occasionally fruits, flowers or seeds of shrubs, a series of vegetation surveys were conducted on the ant study area adjacent to the Jornada Playa Validation Site. Initially a series of 50 m line intercept samples were run to obtain cover estimates of shrubs and perennial grasses at one point in time -- June, 1972.

At monthly intervals, density estimates were obtained of annual and perennial forbs, annual grasses and those perennial grasses such as *Tridens pulchellus* which produced fruits foraged by ants. Density estimates were obtained by the point quarter method. Randomly selected *Pogonomyrmex rugosus* colonies were used as central points. One 50 m line was laid out at a randomly selected angle in each of the four 90° quadrats. Random points within each 5 m interval were used as the center points for the point quarter. The distance to the nearest plant in each quadrat, mean canopy diameter, height, and phenology and species were recorded for each plant. More than 40 points were measured in each sampling period.

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In order to estimate seed (fruit) production and hence availability, it was necessary to calculate seed production from the density and size distribution estimates obtained by monthly point quarter samples. Therefore, as species of forbs or grasses attained maximum fruiting as determined by continuous observation at the study site, individual plants of varying sizes were carefully excavated, bagged and returned to the laboratory, where they were dried at 60 C. Prior to excavation the mean canopy diameter and height of each plant was recorded. The dried plants were separated by parts: seeds and fruits, leaves, stem, and roots, and the weights of the parts determined with a Mettler balance to $\pm .001$ g. Subsamples of reproductive units (seeds and fruits) were counted and weighed. Total number of reproductive units was obtained by relating number to weight.

Forager population estimates (A3UEE15)

Estimates of forager populations were obtained by the Lincoln Index. Foragers were collected with an aspirator as they returned to the nest. The aspirator jar containing the ants was placed in an iced container to immobilize them. Immobilized ants were marked with a dot of airplane dope on the gaster. Colonies had to be censused within 48 hr since ant grooming tends to eliminate these marks (Brian, 1971).

Colony distribution (A3UEE12)

In order to determine the role of harvester ants in an ecosystem, it is necessary to determine if colony density estimates have general applicability (i.e., if colonies are randomly dispersed) or if there is a degree of clumping or evenness in the pattern of distribution. Distribution of colonies and density was determined by the nearest-neighbor method. The distance from random points in the study area to the nearest nest in each quarter was measured (this provided point-quarter distances for density estimates). The distance from each nest to its nearest neighbor of the same species was measured.

RESULTS

Foraging activity (A3UEE03)

Prediction of foraging activity requires the prediction of seasonal initiation and cessation of foraging, as well as foraging intensity during the summer. Weekly observations during March, 1972 showed that while soil surface temperatures reached 37-43 C, harvester ants were not active. By mid-April, 50% of the *Novomessor cockerelli* colonies were active in the middle of the day. Soil temperatures varied from 15-24 C

at 10 cm and between 15-18 C at 50 cm between mid-April and early May. *Pogonomyrmex rugosus* also initiated activity in mid-April. *Pogonomyrmex desertorum* and *P. californicus* did not initiate activity until the last week in May, when soil temperatures were 19-30 C at 10 cm and 19-21 C at 50 cm. Soil temperatures resulting in cessation of foraging activity in the fall were much below the spring temperatures at the initiation of activity. *P. rugosus* and *N. cockerelli* were still foraging in mid-November when soil temperatures at 10 cm ranged between 4-10 C and at 50 cm ranged between 7-10 C. *P. desertorum* and *P. californicus* did not cease activity until early November when soil temperatures were 5-10 C at 10 cm and 8-10 C at 50 cm.

The data on the effects of soil surface temperature and saturation deficit on the foraging activity of the four species of harvester ants are summarized in Figures 3-7. In mid-summer *N. cockerelli* was primarily nocturnal, ceasing foraging activity about two hours after sunrise and beginning again approximately one hr prior to sunset. Peak foraging activity was at soil surface temperatures between 5-25 C and at saturation deficits below 20 g/m³ (Fig. 3).

The foraging patterns of the *Pogonomyrmex* species differed in intensity of foraging effort per unit time and the range of environmental conditions over which they were active (Figs. 4-6). Surprisingly, all three species exhibited peak activity at 45 C (Fig. 7). *P. californicus* was the only species foraging at mid-day. Some *P. californicus* were observed foraging at soil surface temperatures between 60-62 C but no data on foraging rate were obtained under these conditions. In mid-summer, *P. rugosus* exhibited nocturnal foraging but *P. desertorum* and *P. californicus* ceased foraging at sundown. All the *Pogonomyrmex* exhibited some activity at saturation deficits as high as 36 g/m³. However, saturation deficits greater than 27 g/m³ resulted in a larger reduction in foraging rate in *P. desertorum* and *P. rugosus* (Figs. 4 and 5) than in *P. californicus* (Fig. 6).

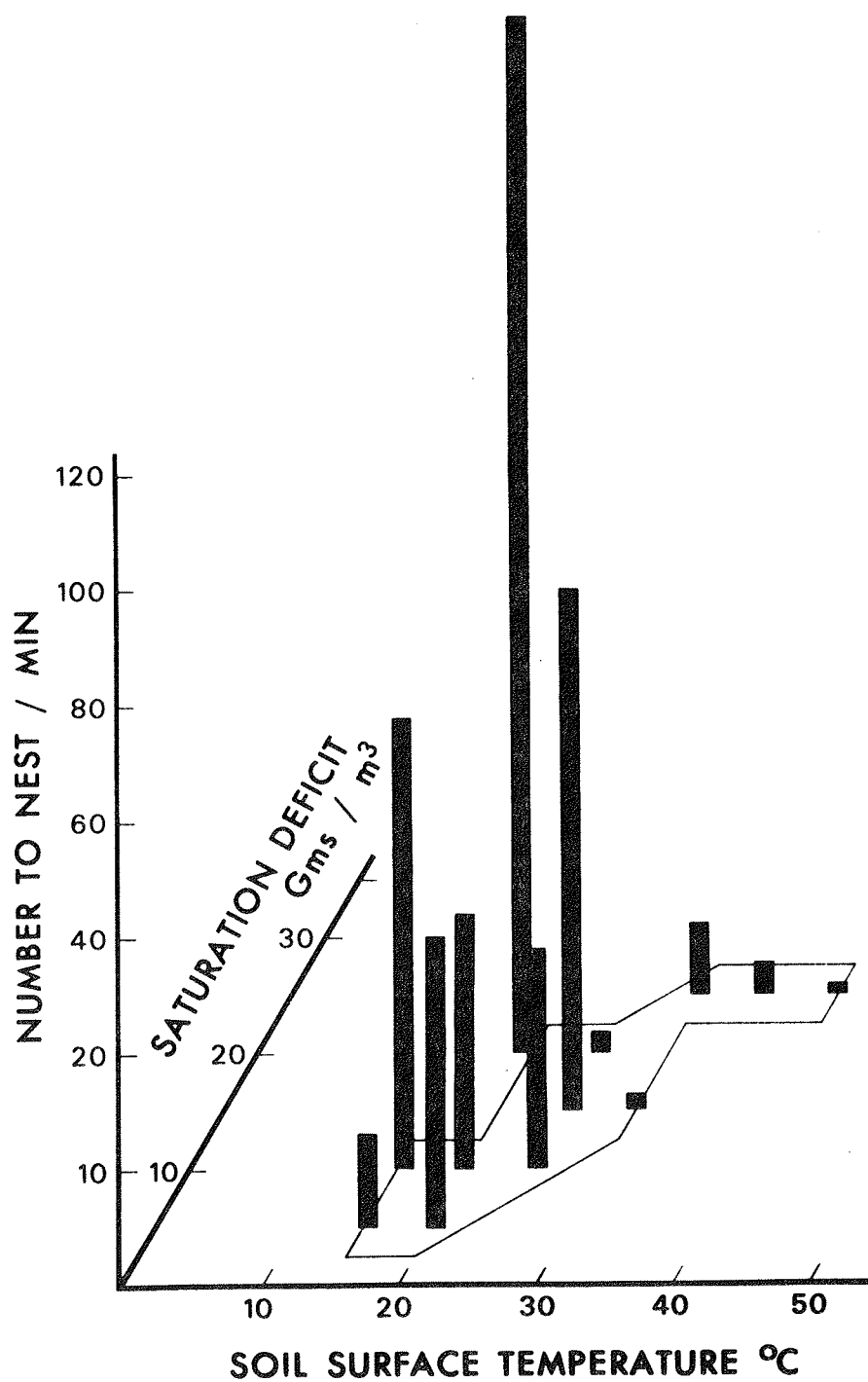


Figure 3. The effect of saturation deficit and soil surface temperature on foraging activity in *Novomessor cockerelli*. The scale for foraging activity on the ordinate applies to the length of the bars.

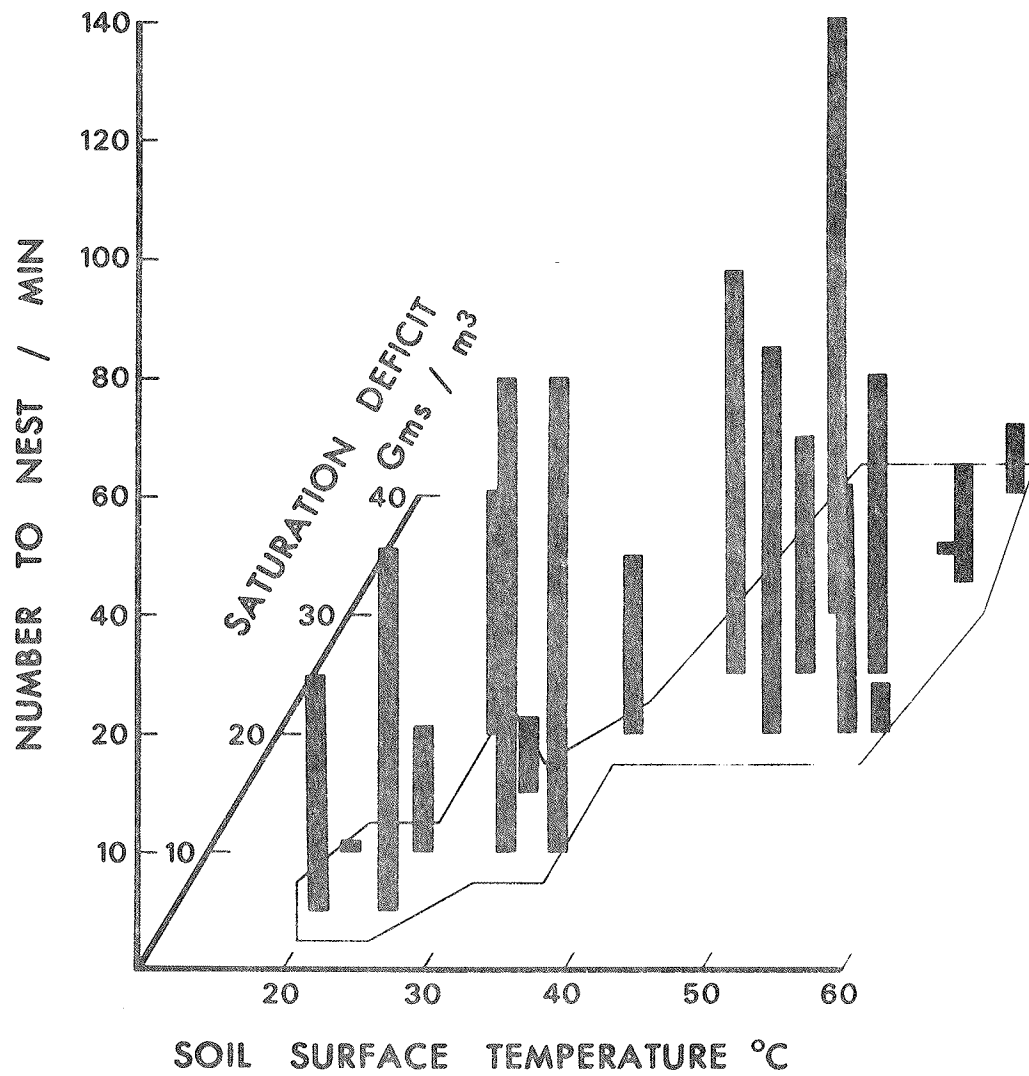


Figure 4. The effect of saturation deficit and soil surface temperature on foraging activity in *Pogonomyrmex rugosus*. Presentation is the same as in Figure 3.

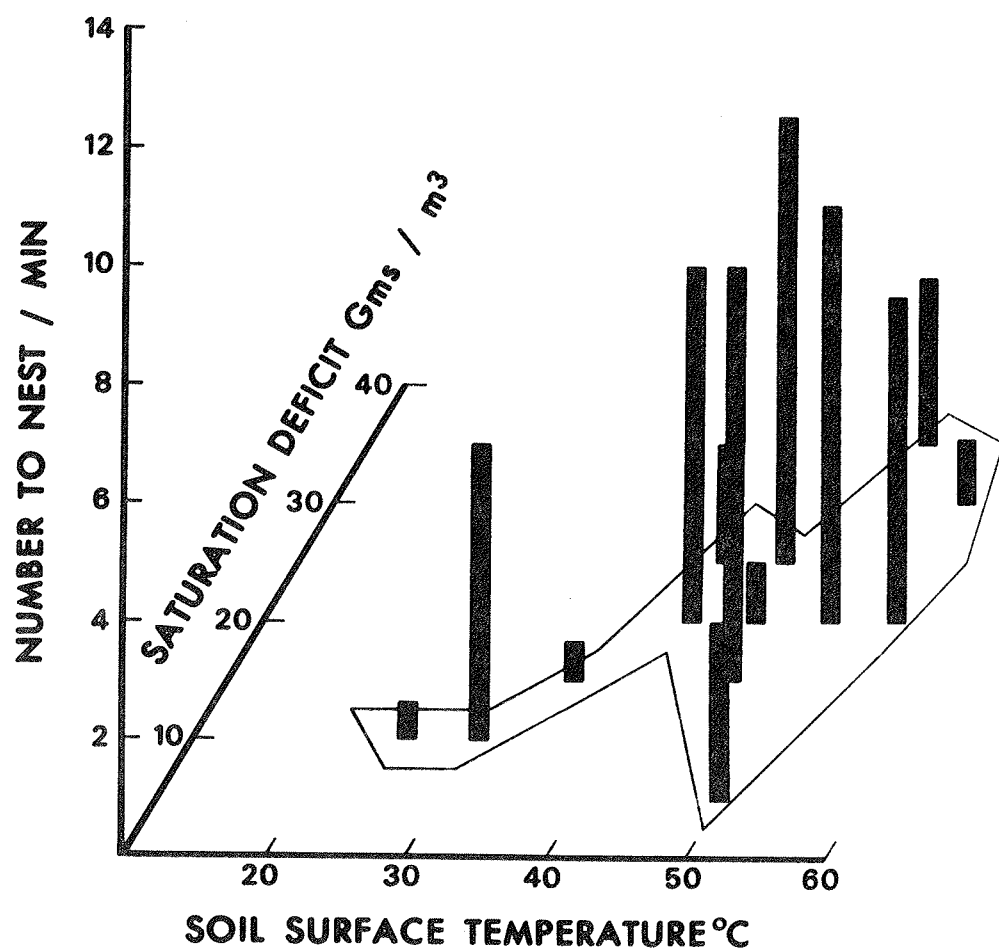


Figure 5. The effect of saturation deficit and soil surface temperature on the foraging activity of *Pogonomyrmex desertorum*. Presentation is the same as in Figure 3.

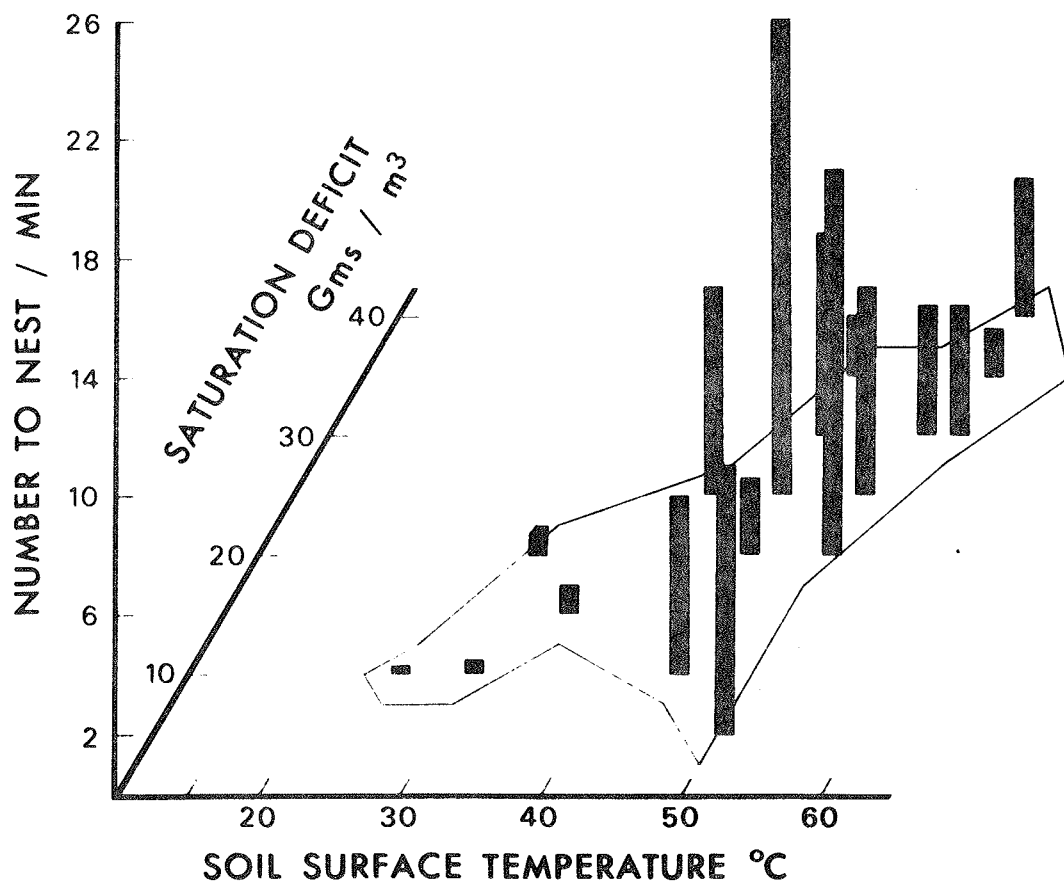


Figure 6. The effect of saturation deficit and soil surface temperature on the foraging activity of *Pogonomyrmex californicus*. Presentation is the same as in Figure 3.

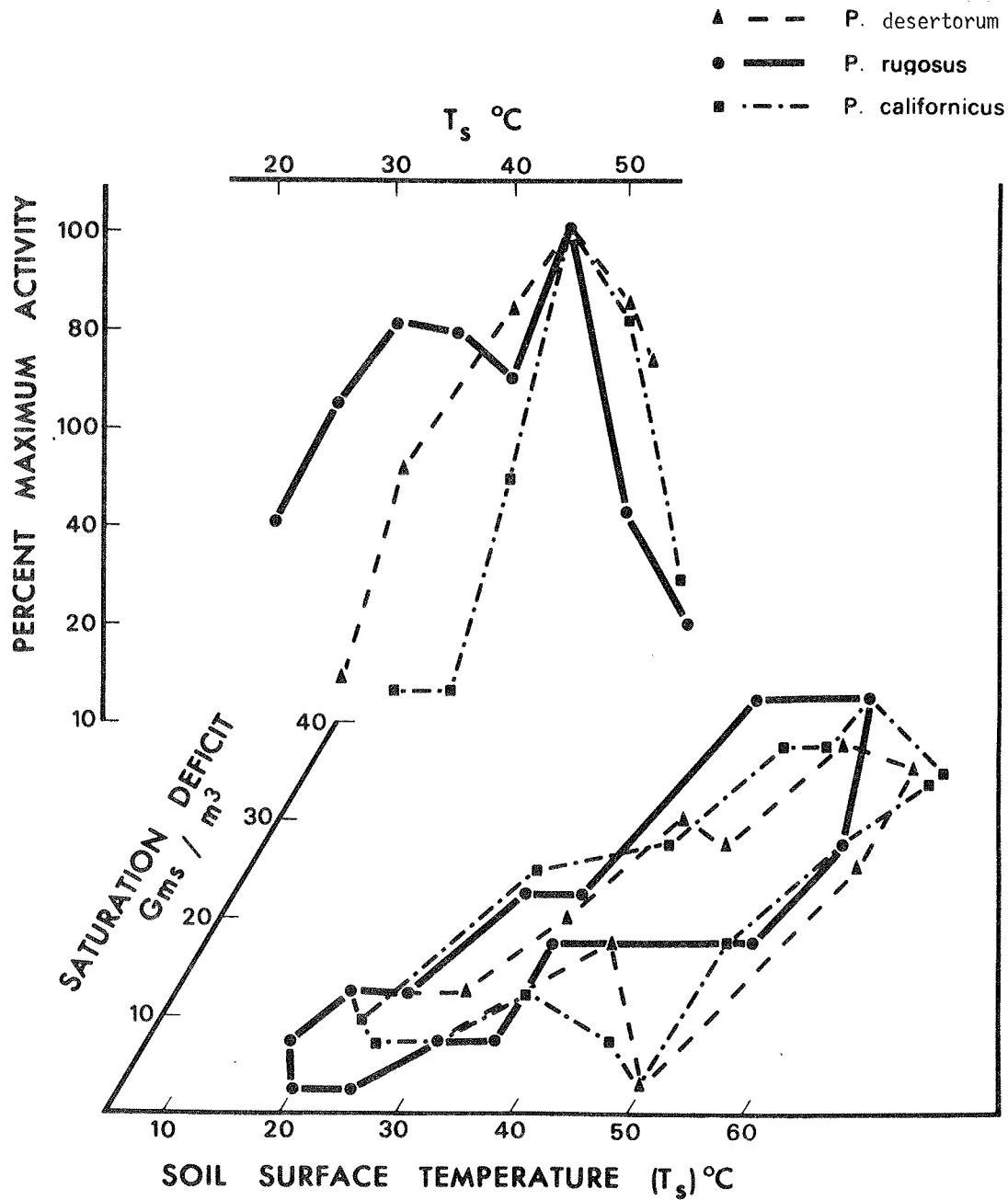


Figure 7. Comparison of effects of saturation deficit (presented as planes of activity) and soil surface temperature (T_s) on foraging activity in *Pogonomyrmex* species.

Foraging intensity, distribution of effort and colony interactions (A3UEE10)

The studies with dyed seeds provided data on the effects of food resource distribution pattern on the distribution of foraging effort and intensity of foraging in the two larger species of harvester ants, *N. cockerelli* and *P. rugosus*. In experiments where the density of food items per unit area was held constant, foraging effort exhibited a log decay with increasing distance from the colony (Fig. 8). Regression analysis of \ln number to the nest per minute on distance from the colony in meters (D) gave an r^2 of 0.71. This relationship is expressed by the equation $\ln \text{Num} = 1.6 + (-.19D)$. The data were adjusted to eliminate variance due to intrinsic differences in levels of foraging activity between colonies.

Under natural conditions, it is unlikely that the distribution of food resources would remain regular. Additional observations on the constant density experiments without grain supplement showed that intense foraging near the colony quickly depleted the "close in" resources which resulted in a more even distribution of foraging effort at varying distances from the colony (Fig. 9). In the vegetation survey, it was noted that annuals, particularly *Eriogonum* spp., tended to be clumped, providing dense clumps of food items for the harvester ants. In order to examine the effect of clumped resources on foraging effort, experiments were conducted in which the ants were provided seeds in widely scattered piles; at a distance from the colony greater than the distance to the piles, we placed a dense ring of seeds (Fig. 10). These experiments demonstrated that high concentrations of food items resulted in greater forager effort at that location than would be predicted on the basis of distance from the colony. However, a solid circle of food items did not result in the cessation of foraging activity at a distance greater than the dense line, because some foragers crossed the dense line and returned with seeds from the less concentrated sources at an even greater distance from the colony.

In 60% of the experiments for which we have baseline data, addition of seed material appeared to stimulate activity (Table 1). In one of the experiments where the intensity of foraging decreased after addition of seeds, the ants were not foraging on the seeds we supplied. Although it is tempting to assume that seed supplementation stimulated an increase in foraging activity, additional experiments designed to evaluate this hypothesis using paired colonies, treated and untreated, are necessary.

Foragers returning to the colony often appeared to have been unsuccessful at finding a suitable food item. In a number of the experiments with colored seeds, the number of successful and unsuccessful returning foragers (28 experiments with *P. rugosus* and 13 experiments with *N. cockerelli*) were tallied. Percent foraging success was

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regressed on soil temperature, saturation deficit and hour of the day, all of which gave $r^2 < 0.1$. The range of percent success was between 0 and 96% with a mean of 48% in *P. rugosus*, and between 15 and 19% with a mean of 59% in *N. cockerelli*. Observations of returning foragers in other parts of the study and in samples of foraged materials support the 50% estimate of foraging success in these two species.

Table 1. The effect of seed addition on foraging activity (Novcoc = *Novomessor cockerelli*, Pogrug = *Pogonomyrmex rugosus*)

Colony and #	Number to nest · min ⁻¹		Number to nest · min ⁻¹	
	Baseline	Δ Time		Δ N. min ⁻¹
Pogrug 60	11.3	25	6.4	-7.3
Pogrug 61	9.3	25	12.6	+3.3
Pogrug 61	12.3	30	12.5	+ .2
Pogrug 60	14.3	30	21.0	+6.7
Pogrug 62	8.3	30	10.7	+2.4
Pogrug 50	32.6	15	18.4	-14.2
Novcoc 50	4.0	15	11.2	+7.2
Pogrug 53	30.0	15	7.4*	-22.6
Novcoc 58	4.0	60	10.8	+6.8
Pogrug 50	32.6	60	15.2	-17.4

* Not foraging on supplied seeds.

The analysis of interaction of colonies involved plotting the number of seeds of different colors returned to the colony in the cleared circle and to the adjacent colonies. The first experiments (Fig. 11) showed there was considerable overlap in foraging territory between colonies of the same species and between *P. rugosus* and *N. cockerelli*. *N. cockerelli* were often observed removing materials from the cleared disc of colonies of *P. rugosus*. The foraging territories of two *P. rugosus* colonies in relation to their associated colonies were mapped (Figs. 12 and 13). The interaction between *P. rugosus* colony 18 and *P. rugosus* 50 was selected for further study since there was considerable overlap in foraging range of these colonies (Figs. 11 and 12) and distortion in the foraging range of *P. rugosus* 50 which might have been caused by interactions with other *P. rugosus* colonies.

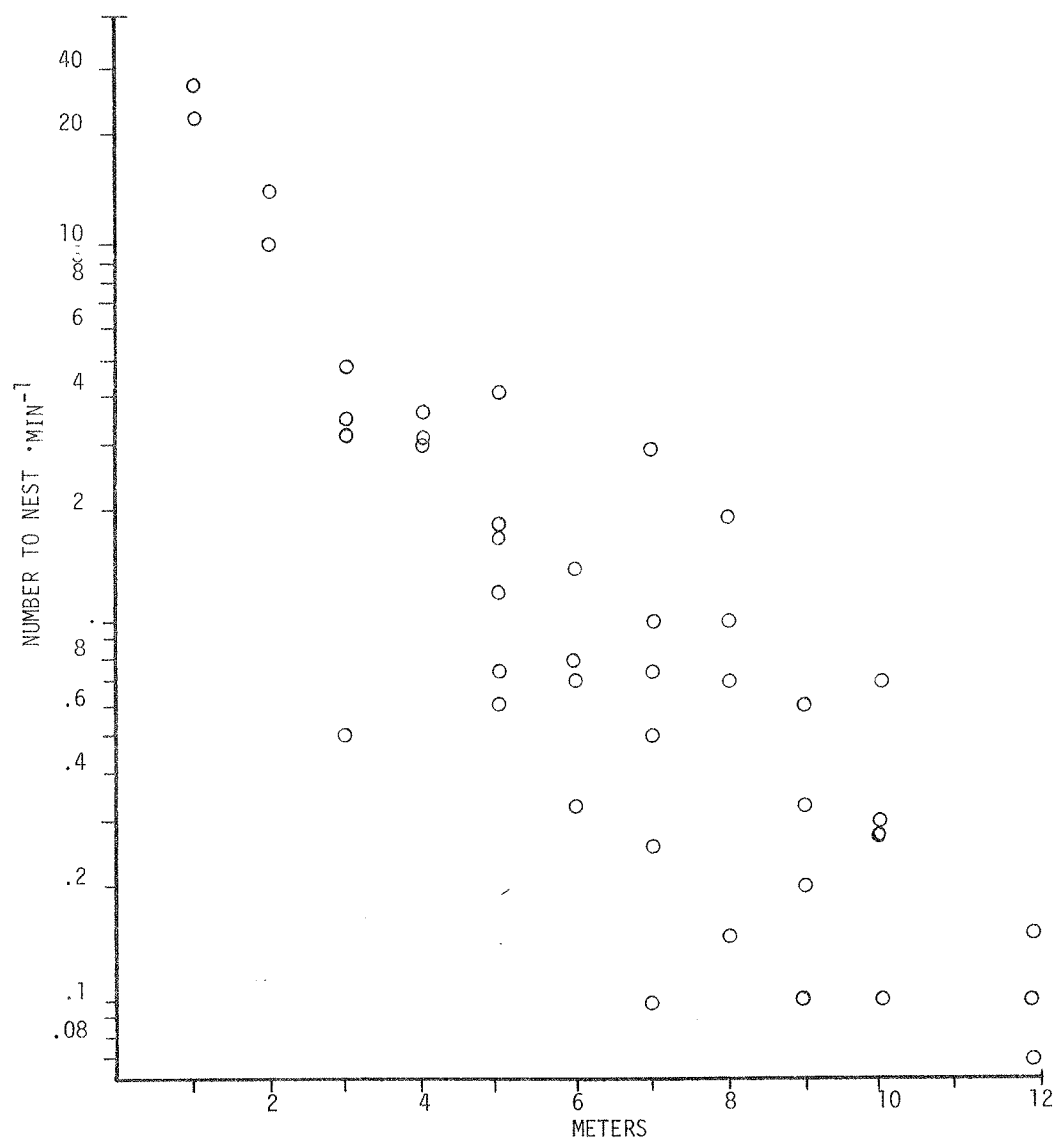


Figure 8. The effect of distance on foraging intensity of *Pogonomyrmex rugosus* and *Novomessor cockerelli* when forage distribution was even.

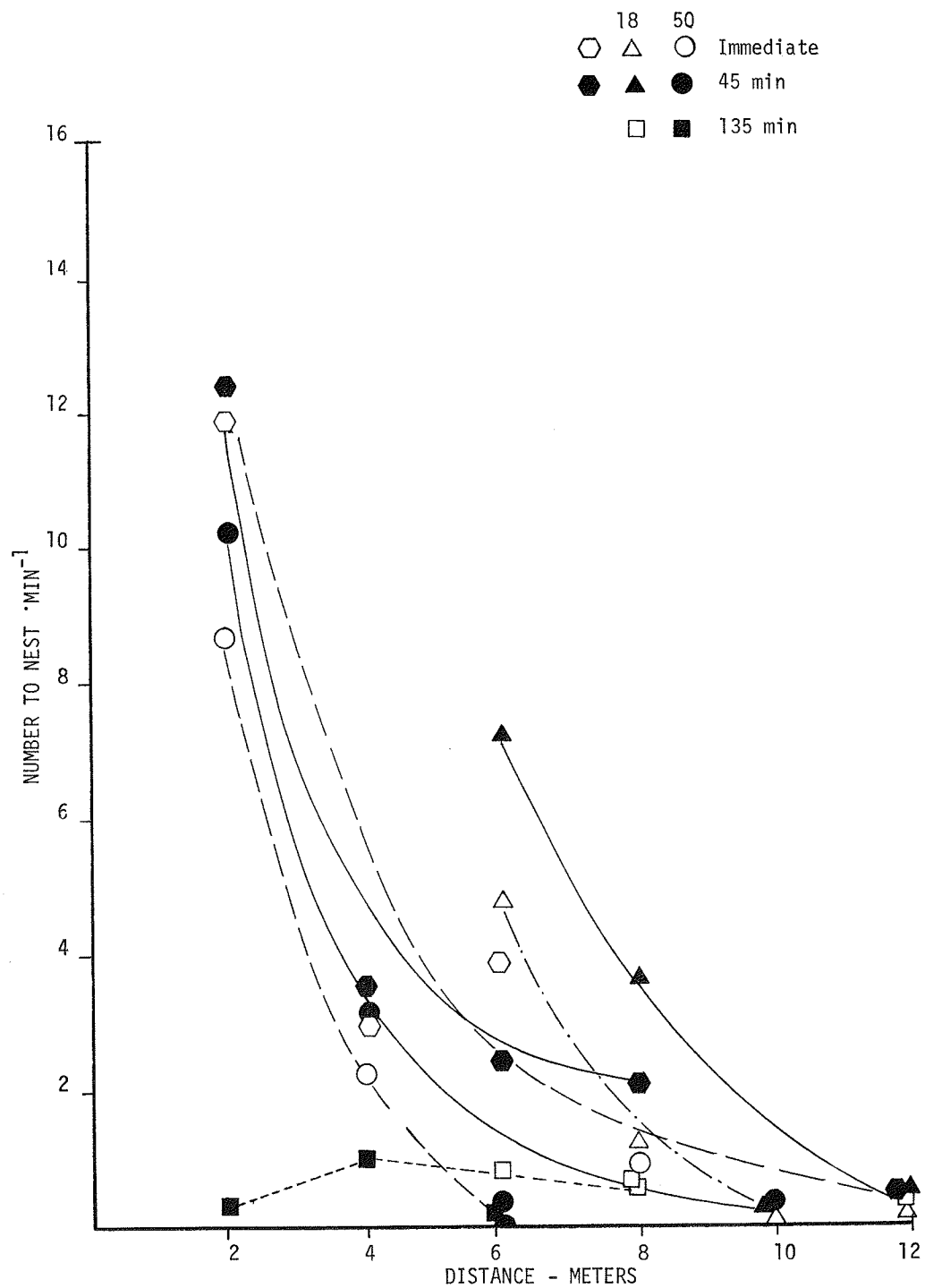


Figure 9. Effect of foraging time and distance on foraging in *Pogonomyrmex rugosus*.

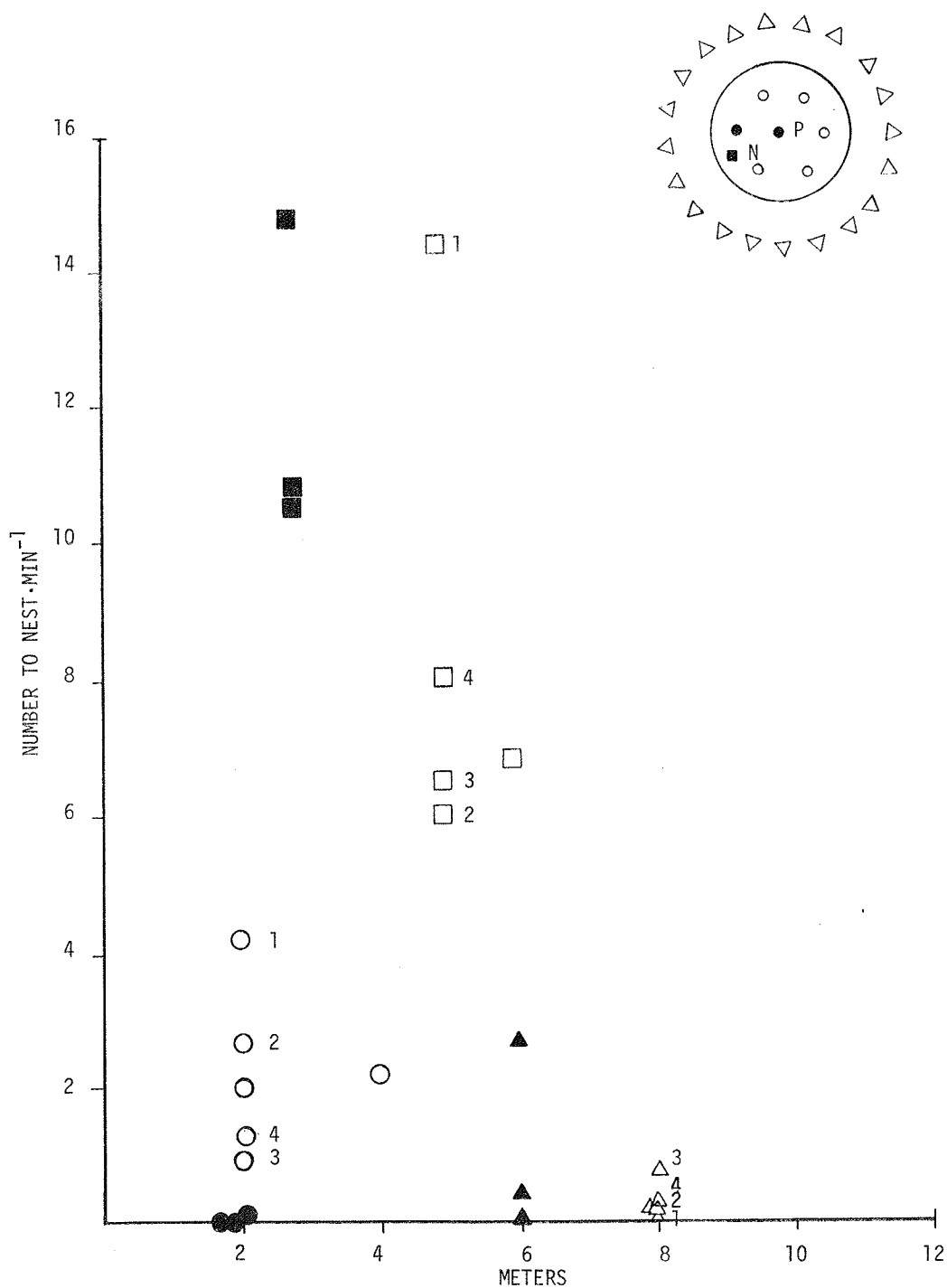


Figure 10. Effect of seed concentration and distance on foraging intensity. The diagram in the upper right shows the distribution of seed piles and ring in the experimental design. The numbers identify points in the same experiment period. Open symbols are *Pogonomyrmex rugosus* and solid symbols are *Novomessor cockerelli*. Squares represent data from dense time and the other symbols represent piles of grain.

2.3.3.2.-20

On 4 October 1972, the experiments were repeated to test the response of *P. rugosus* colony 50 to the removal of *P. rugosus* colony 18, which had been completely excavated by 15 September 1972. These data are summarized in Figure 14. Comparison of Figures 11 and 14 shows that the removal of colony 18 had no effect on the foraging pattern of *P. rugosus* colony 50. In this experiment 45% of the returning foragers were carrying native fruits of *Eriogonum abertianum* and *Tridens pulchellus*. Foragers passed over the cracked milo piles to forage in the native vegetation 15 m away from the colony. No foragers were observed around the colored grain 5 m from *P. rugosus* 50 in the direction of the excavated colony.

Forage selection (A3UEE11) and seed production (A3UEE13 and A3UEE14)

There was considerable overlap in forage selection in the three species of *Pogonomyrmex* studied (Table 2). Seasonal changes in forage preference were related to the phenology of the annuals and their relative densities (Table 3). The fruits of the buckwheats, *Eriogonum abertianum* and *Eriogonum trichopes*, accounted for approximately half of the foraged materials from June through August in these species. *Chenopodium incanum*, which exhibited rapid growth in June and ripened in July, was selected by *P. rugosus* but was of much lower importance to *P. californicus* and *P. desertorum*. The composites, *Bahia* and *Baileya*, which had a high fruit production, were of low importance as forage items. *P. desertorum* foraged heavily on grass seeds when these were available; at the end of the growing season, piles of the feathery fruits of *Tridens pulchellus* and *Bouteloua barbata* ringed the mounds of this species.

Forage selection in *Novomessor cockerelli* is summarized in Table 4. In this species over half of the forage consisted of termites and other insects and miscellaneous plant parts. Forage preferences for fruits were similar to the *Pogonomyrmex* species, with the buckwheats, *Eriogonum* spp., ranking as the most frequent fruits foraged.

The data on the relationship of plant parts and seed numbers to either canopy area or canopy volume estimate for several species of forbs and grasses are summarized in Figures 15-33. The regression equations are provided below: Other data sets are currently being processed and analyzed.

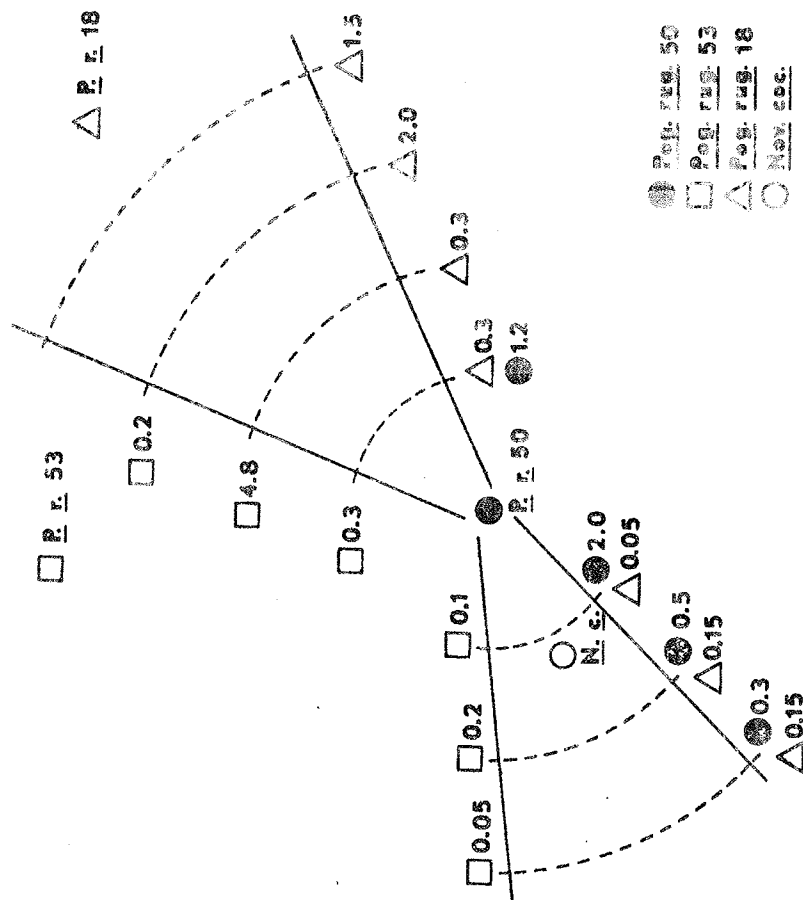
Chenopodium incanum

No. Fruit = $963 + .45 \text{ CV}$	$r^2 = .69$
Biomass = $32.5 + .00036 \text{ CV}$	$r^2 = .44$

Eriogonum abertianum var. *ruberrimum*

Root wt. = $.11 + 3.9\text{E}^{-5} \text{ CV (CA} \times \text{CH} \div 3)$	$r^2 = .78$
Biomass = $3.27 + 7.5\text{E}^{-4} \text{ CV}$	$r^2 = .80$
No. Fruit = $1348 + 6.5\text{E}^{-1} \text{ CV}$	$r^2 = .81$

* E = Exponentiation: eg. $3.\text{E}^{-5} = 3 \times 10^5$



FORAGING PATTERNS

Figure 11. The interaction of foraging activity in colonies of *Pogonomyrmex rugosus* (Pog rug) and *Novomessor cockerelli* (Nov coc). Symbols refer to colonies in the area. Numbers are numbers of seeds/minute to the colony indicated from the area shown.

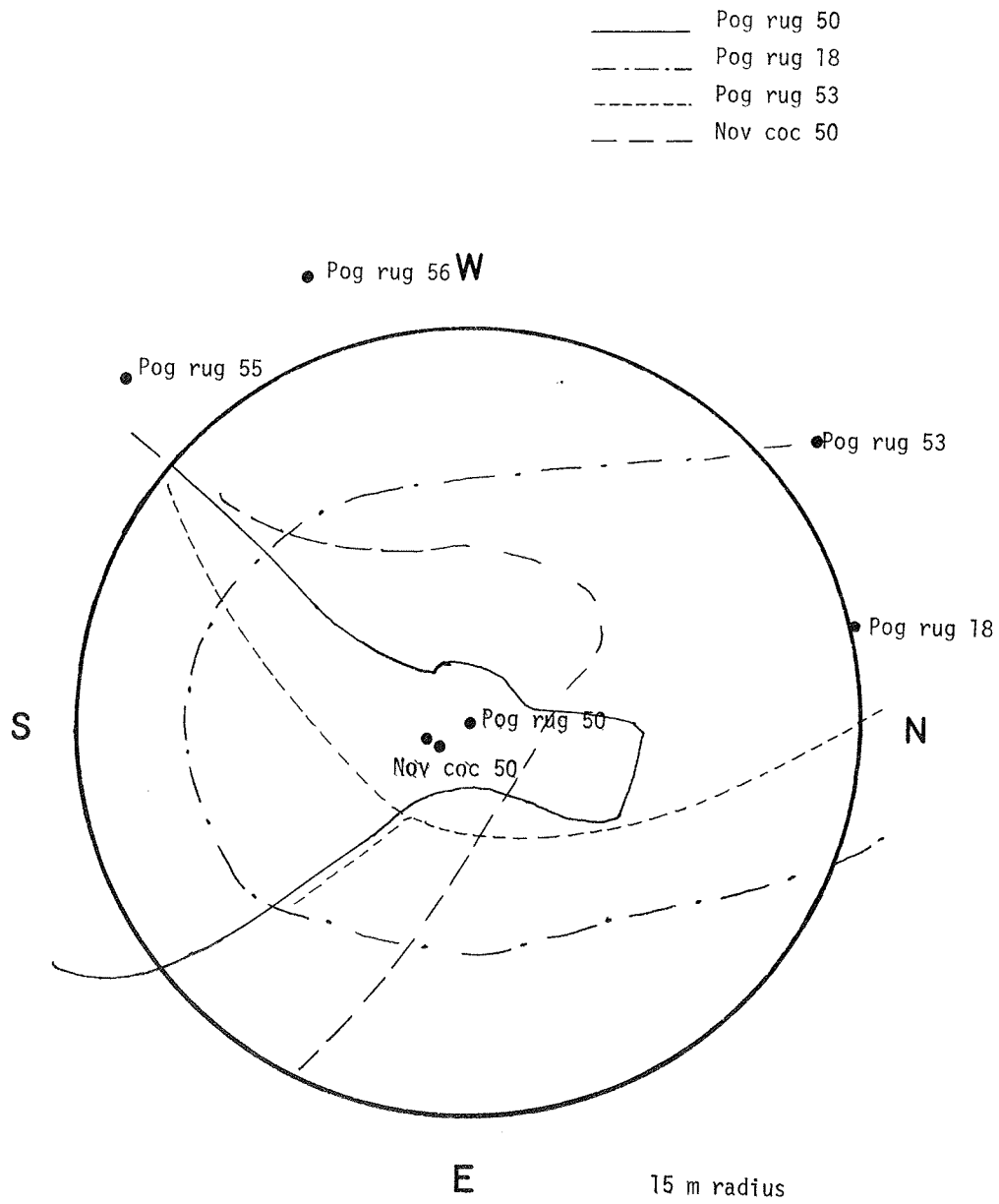


Figure 12. Map of the foraging territories of *Pogonomyrmex rugosus* and *Novomessor cockerelli* as mapped in colored seed experiments, example 1.

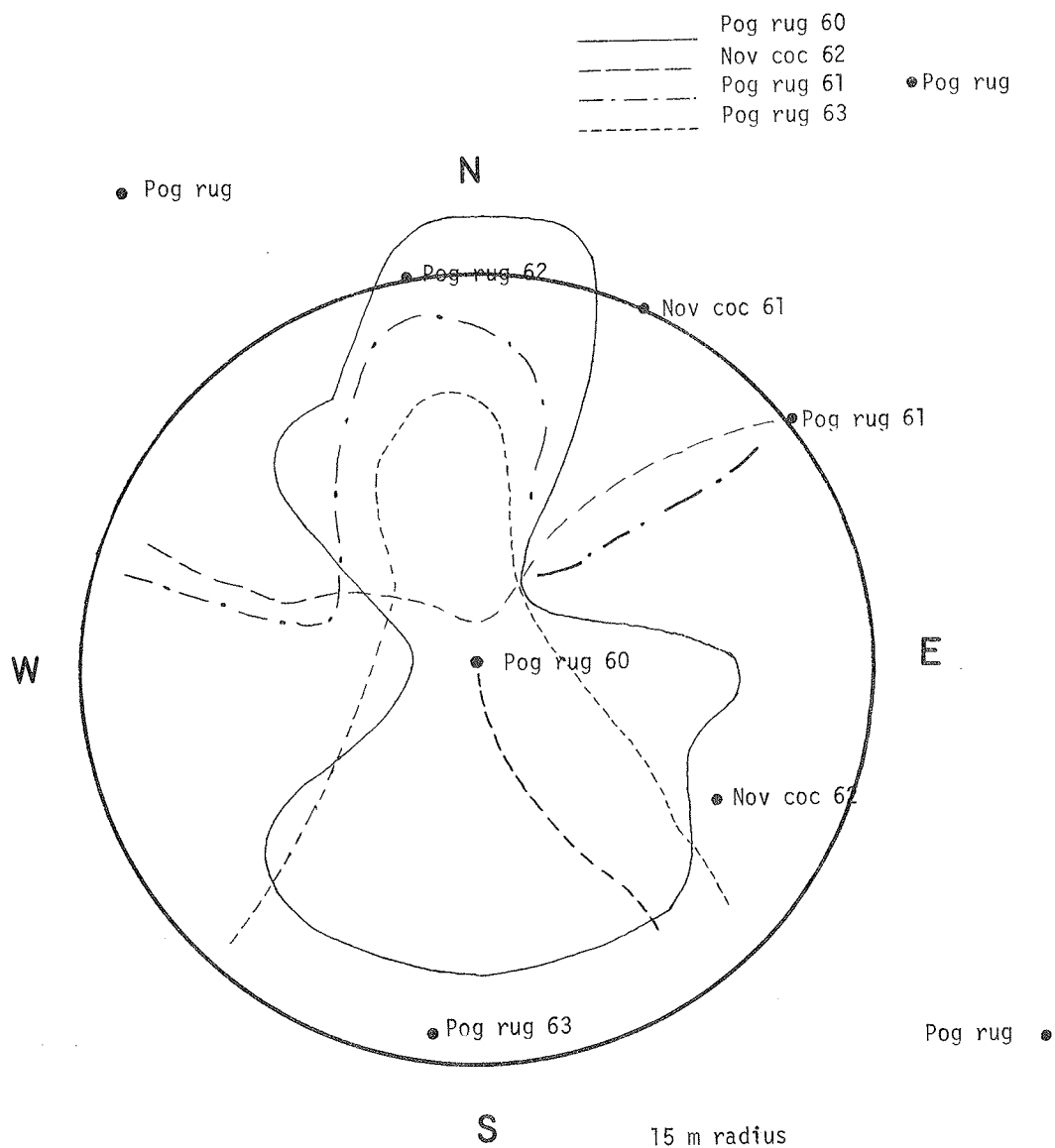


Figure 13. Map of foraging territories of *Pogonomyrmex rugosus* and *Novomessor cockerelli* colonies as mapped in colored seed experiments, example 2.

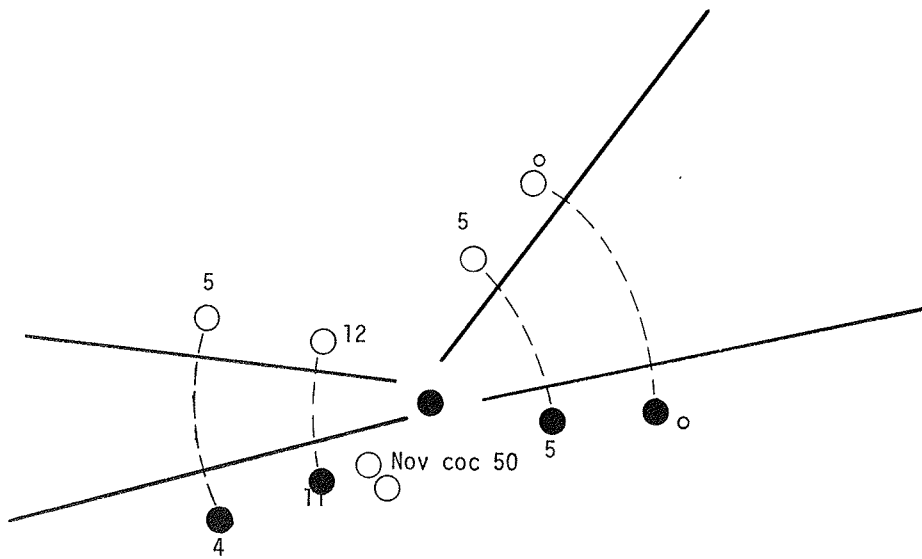


Figure 14. The results of the repeat of the experiment summarized in Figure 11 after the removal of Pog rug 18 by excavation.

Eriogonum abertianum var. *abertianum*

$$\text{Biomass} = 1.8 + 4.64\text{E}^{-3} \text{ CV } (\text{CA} \times \text{CH} \div 3) \quad r^2 = .64$$

$$\text{No. Fruit} = 2388 + 1.8 \text{ CV} \quad r^2 = .13$$

$$\text{Foot wt.} = .21 + 6.3\text{E}^{-4} \text{ CV} \quad r^2 = .31$$

$$\bar{x} \text{ seed number} = 3095$$

Bahia absinthifolia

$$\text{No. Fruit} = 378 + 8.4 \text{ CA} \quad r^2 = .73$$

$$\text{Biomass} = -0.0106 + .011 \text{ CA} \quad r^2 = .84$$

$$\text{Root wt.} = .36 + .00062 \text{ CA} \quad r^2 = .48$$

Baileya multiradiata

$$\text{No. Fruit} = -351 + 3.77 \text{ CA} \quad r^2 = .88$$

$$\text{Root wt.} = .57 + 1.56\text{E}^{-5} \text{ CV } (\text{CH} \times \text{CA} \div 3) \quad r^2 = .41$$

$$\text{Biomass} = 5.32 + 6.5\text{E}^{-4} \text{ CV} \quad r^2 = .87$$

$$\text{Biomass} = -.56 + .0115 \text{ CA} \quad r^2 = .89$$

$$\text{No Fruit} = 1158 + -.04 \text{ CV} \quad r^2 = .19$$

Bouteloua barbata

$$\text{No. Fruit} = .89 + .17 \text{ CV } (\text{CH} \times \text{CA} \div 3) \quad r^2 = .54$$

$$\text{Biomass} = .077 + .0026 \text{ CA} \quad r^2 = .49$$

$$\text{No. Fruit} = .135 + .94 \text{ CA} \quad r^2 = .48$$

Eriogonum trichopes

$$\text{No. Fruit} = 209 + .028 \text{ CV } (\text{CH} \times \text{CA} \div 3) \quad r^2 = .08$$

$$\text{Biomass} = 1.2 + 0.00034 \text{ CV} \quad r^2 = .53$$

$$\text{Stem wt.} = .92 + .0003 \text{ CV} \quad r^2 = .52$$

$$\bar{x} \text{ FFN} = 278/\text{plant}$$

With data on seed production, foraging behavior of species of harvester ants, and density estimates, we were able to estimate the impact of the harvester ant population on the potential seed reserves (Table 5). Harvester ants had the greatest impact on the potential seed reserve of *Eriogonum trichopes*, removing more than 90% of the total estimated production. In contrast, the foraging activities of these species removed only an estimated 8% of the fruit production of *Eriogonum abertianum* var. *abertianum*. *Bouteloua barbata* was also hit hard by foraging, which accounted for approximately 71% of its seed production.

Table 2. Food items foraged by harvester ants of the genus *Pogonomyrmex* at different times during the active foraging season*

	Early June		June		July		August		Sept		October	
	rug	cal	rug	cal	rug	cal	rug	cal	rug	cal	rug	cal
<i>Eriogonum abertianum</i>	14	43	<1	32	55	27	17	27	21	56	11	35
<i>Eriogonum trichopes</i>	3	37	74	59	3	73	19	32	4	5	0	20
<i>Baileya multiradiata</i>			3		3	2	5	10	3		17	20
<i>Euphorbia</i> sp.					6	11	2	<1	21	12	29	12
<i>Chenopodium incanum</i>			1		24	1	29	1		6	9	10
<i>Eriogonum rotundifolium</i>		<1	<1		3	0	<1	5	1	3	4	0
<i>Allionia incarnata</i>							<1		1	1		
<i>Bahia absinthifolia</i>					<1		<1	7	7	<1	<1	
<i>Bahia pedata</i>							<1					
<i>Bouteloua barbata</i>							9		10		57	3
<i>Boerhaavia spicata</i>									2		4	
<i>Cassia bauhinioides</i>							2					
<i>Croton pottsii</i>	<1	<1										
<i>Cryptantha</i> sp.	40	5			<1							
<i>Descurainia pinnata</i>	10											
<i>Kallstroemia parviflora</i>							<1					
<i>Larrea divaricata</i>	8	2						<1				
<i>Muhlenbergia porteri</i>	14								14			
<i>Salsola kali</i>		1			<1		<1	<1	6		12	7
<i>Tridens pulchellus</i>		2	<1	<1			<1	<1	<1	3		
Annual parts	2	2	3	<1	<1	<1	4	1	<1	6	5	5
Plant parts	1	1	12	3	<1		<1	3	2		<1	1
Termites		3	4	<1	<1	5	2	<1		6	<1	1
Other seeds	5							0				

* Species of *Pogonomyrmex* represented as follows: rug - *P. rugosus*, des - *P. desertorum*, cal - *P. californicus*. Foraged items are expressed as percent to total items foraged.

Table 3. Density of annual grasses and forbs on the study area south of the Jornada Playa Validation Site

	June 16			July 25			Aug. 31			Oct. 5		
	PC	REL	DEN	PC	REL	DEN	PC	REL	DEN	PC	REL	DEN
<i>Bahia absinthifolia</i>	1			1	1.3	5,407	2			3		7.4
<i>Baileya multiradiata</i>	1	8.3	8,567	2	6.3	26,201	2	7.0	15,895	3		6.4
<i>Bouteloua aristoides</i>	0			0			3			4	4.4	9,331
<i>Bouteloua barbata</i>	0			1	2.1	8,734	3			4	5.5	11,665
<i>Boerhaavia spicata</i>	1			1	2.5	10,397	3	.5	1,135	0		
<i>Cassia bauhinioides</i>	1			1			3	4.5	15,895	3		
<i>Chenopodium incanum</i>	1	31.2	32,166	3	33.3	137,245	3	28.5	65,853	4	13.2	27,995
<i>Croton pottsii</i>	2	9.3	9,601	2	6.3	26,201	3	4.0	9,083	3		13.8
<i>Eriogonum abertianum</i>	1	7.0	7,201	3	14.7	62,397	3	15.0	34,062	3-4	5.5	24.5
<i>Eriogonum trichopes</i>	2	11.2	11,522	3	6.3	26,201	3	9.5	22,708	4		23.4
<i>Euphorbia</i> spp.	1			1	15.6	66,543	2	18.0	40,875	3	25.3	53,057
<i>Kalistroemia parviflora</i>	1			1	6.3	26,201	0			0		
<i>Tridens pulchellus</i>	1			1	5.5	22,874	1	6.0	13,625	3	13.2	27,995
Total density estimates: forbs and grasses/hectare												
June 16, 1972			103,220									
July 25, 1972			415,893									
August 31, 1972			227,082									
October 5, 1972			212,299									
*			116,500									

PC indicates the phenology code: 1 = green vegetative; 2 = flowering; 3 = flowering and fruiting; 4 = stem cured.

REL indicates relative density in percent and DEN indicates computed densities in numbers per hectare.

Columns and data marked with an asterisk indicate sampling of selected forbs and grasses which appeared to be important to the ants.

Table 4. Forage selection by *Novomessor cockerelli* during the growing season 1972

Forage Item	Percent of Total			
	June	July*	August	Sept.*
<i>Eriogonum abertianum</i>	20	6	29	22
<i>Eriogonum trichopes</i>	6	4	0	2
<i>Eriogonum rotundifolium</i>	6		1	
<i>Baileya multiradiata</i>	1			
<i>Bahia absinthifolia</i>			4	
<i>Allionia incarnata</i>			<1	33
<i>Euphorbia</i> sp.			4	8
<i>Chenopodium incanum</i>			2	
<i>Croton pottsii</i>			4	
Insect and insect parts	29	25	2	
Termites	17	11	47	25
Plant parts	13	52	1	8
Miscellaneous fruits	5		2	
\bar{x} Fruits	38	10	49	65
\bar{x} Animal	46	36	49	25
\bar{x} Plant parts	13	52	2	8

* small sample size collection from one or two colonies only.

	Estimated total number of seeds foraged per month per ant species											
	June			July			August			September		
	P. rug	P. des	P. cal	P. rug	P. des	P. cal	P. rug	P. des	P. cal	*P. rug	P. des	P. cal
	33.6E6	14.5E6	5E6	16.8E6	7.15E6	2.5E5	15.1E6	8.25E6	3E6	15.1E6	6.2E6	2.25E5
	Estimated number of seeds of important forage plant species per month per ant species											
<i>Ericogonum abertianum</i>	7.2E6		8E4	9.2E6	1E6	6.75E4	2.56E6	2.2E6	1.38E5	1.79E6	1.3E6	12.6E4
<i>Ericogonum trichopes</i>	6.2E6	5.4E6	1.4E5	5E5	5.3E6	1.2E5	2.85E6	2.4E6	9.6E4	1.42E6	2.4E5	1.13E4
<i>Chenopodium incanum</i>				4E6	1.4E5	2.75E4	4.4E6	7.4E5	3E3	3.57E6		2.7E4
<i>Baileya multiradiata</i>	2.1E5			5E5	1.4E5		7.5E5	1.4E6	3E4	3.75E5	1.8E5	
<i>Bouteloua barbata</i>							1.35E5			7E4	6.2E5	

Production vs. forage impact.[†]

	Totals											
	PROD	FOR	%	PROD	FOR	%	PROD	FOR	%	PROD	FOR	%
<i>B. abertiianum</i>	2.23E7	7.28E6	32%	1.9E8	1.7E7	8.8%	1.06E8	4.9E6	4.6%	7.1E7	3.2E6	4.5%
<i>E. trichopes</i>	3.2E6	13E6	400% [†]	7.3E6	1.57E6	21%	6.3E6	5.35E6	84%	3.15E6	1.7E6	53%
<i>B. multiradiata</i>				4.96E7	6.4E5	1.2%	20.6E6	17.8E5	8.6%	3.15E6	5.6E6	1.6%
<i>C. inegnum</i>				2.2E8	4.17E6	0.2%	4.1E6	5.14E6	1.3%	7.5E7	4.2E6	.5%
<i>B. barbata</i>							1.8E6	2.09E6	100%	2.1E6	6.9E5	32%

[†] if rather than average production maximum seed production assumed (eg. 70g/plant) for June, the foraging in past on *E. trichopes* is reduced to 20%.

**Fruit production based on plant densities, regressions for fruit number on canopy volume or canopy area, and mean plant volumes or canopy areas for one month indicated. Foraging was calculated on the number of hours per month suitable for foraging for each species x a 50% success factor x the percent of foraged materials by ant species for each plant species represented, x the density per hectare for each species.

[†]PROD = seeds produced, FOR = seeds foraged, % = % total production removed

†PROD = seeds produced, FOR = seeds foraged, % = % total production removed

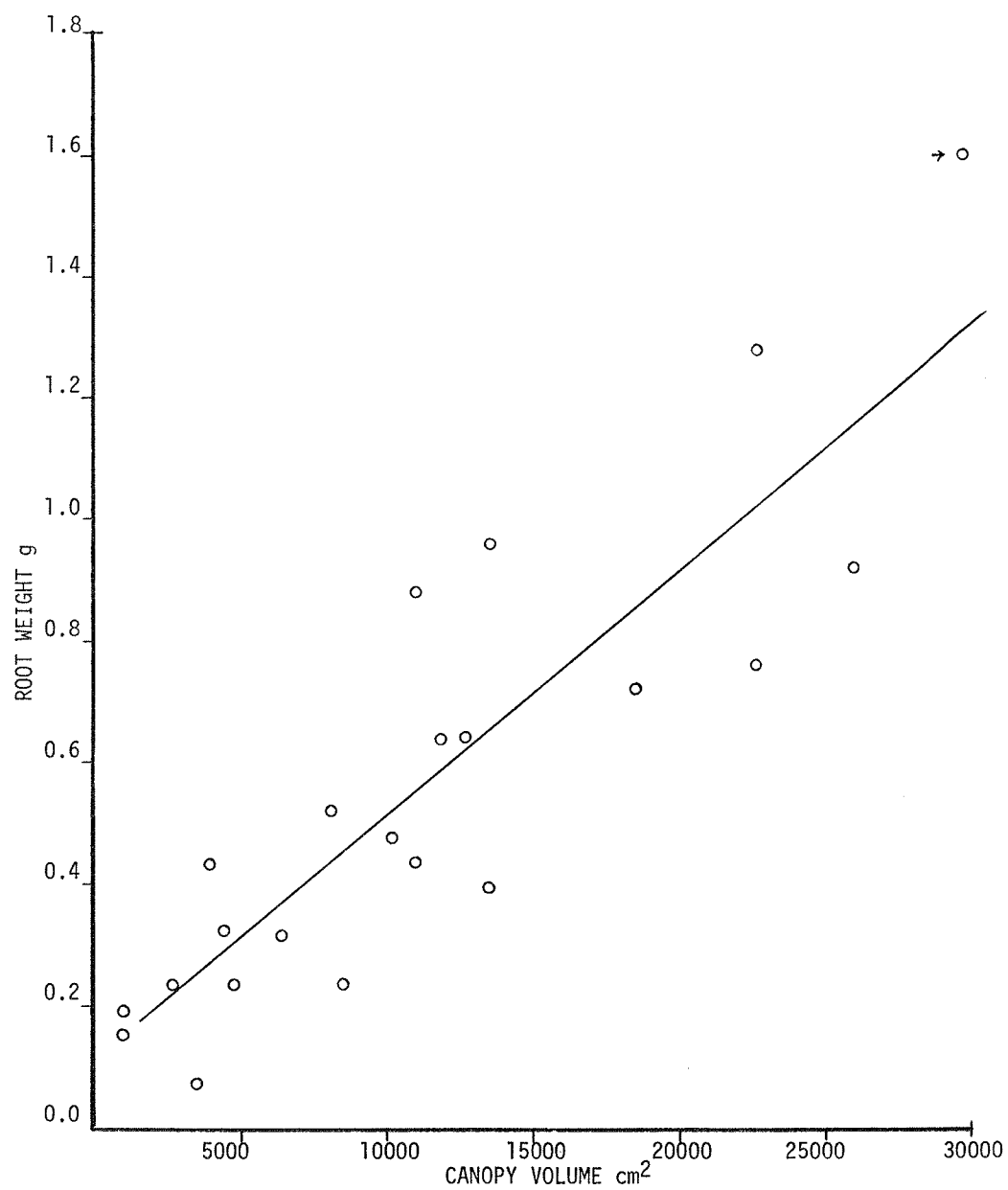


Figure 15. The relationship between root weight and canopy volume in *Eriogonum abertianum* var. *ruberrimum*. (DSCODE A3UEE14)

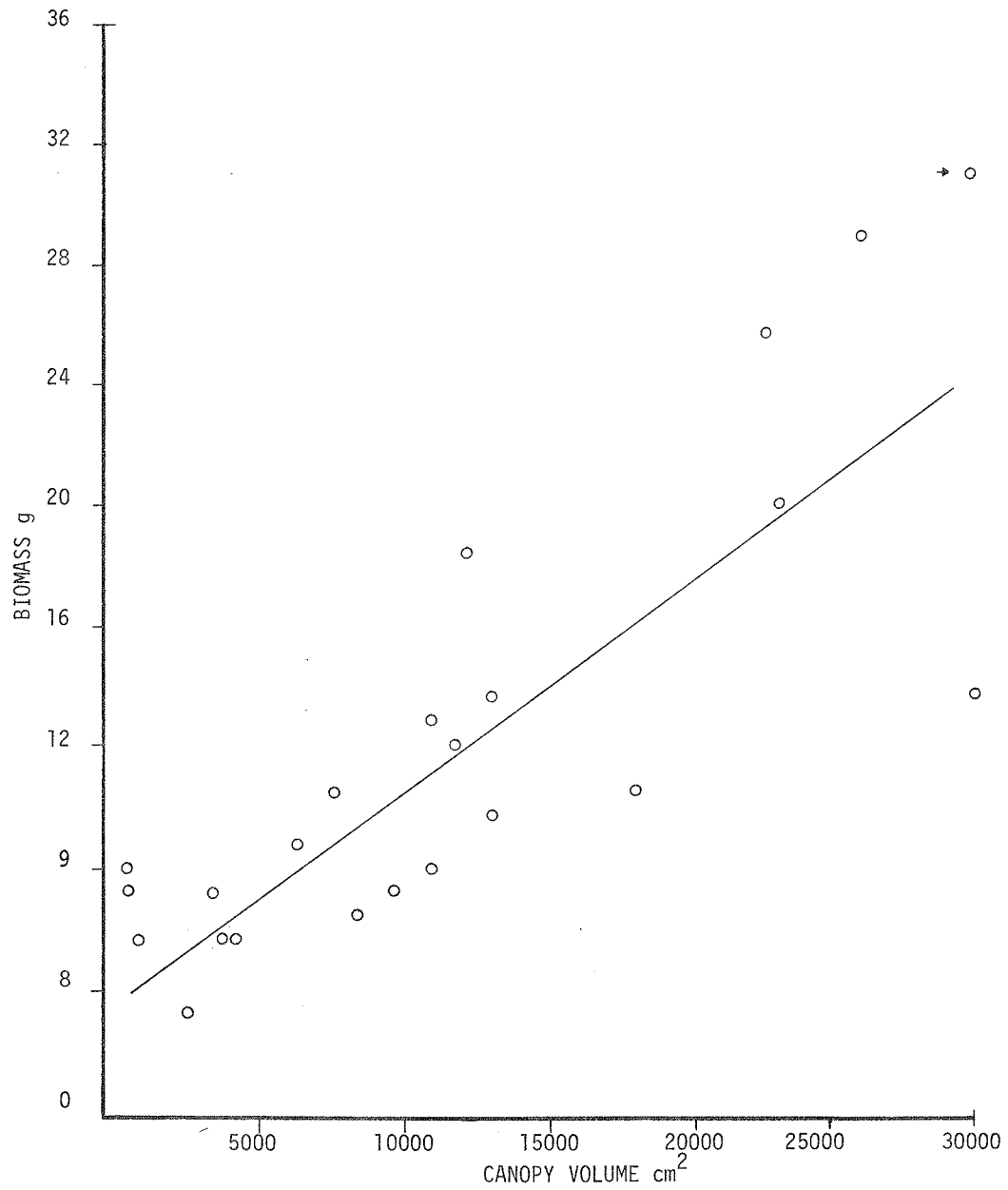


Figure 16. The relationship between total above-ground dry weight biomass and canopy volume in *Eriogonum abertianum* var. *ruberrimum*. (DSCODE A3UEE14)

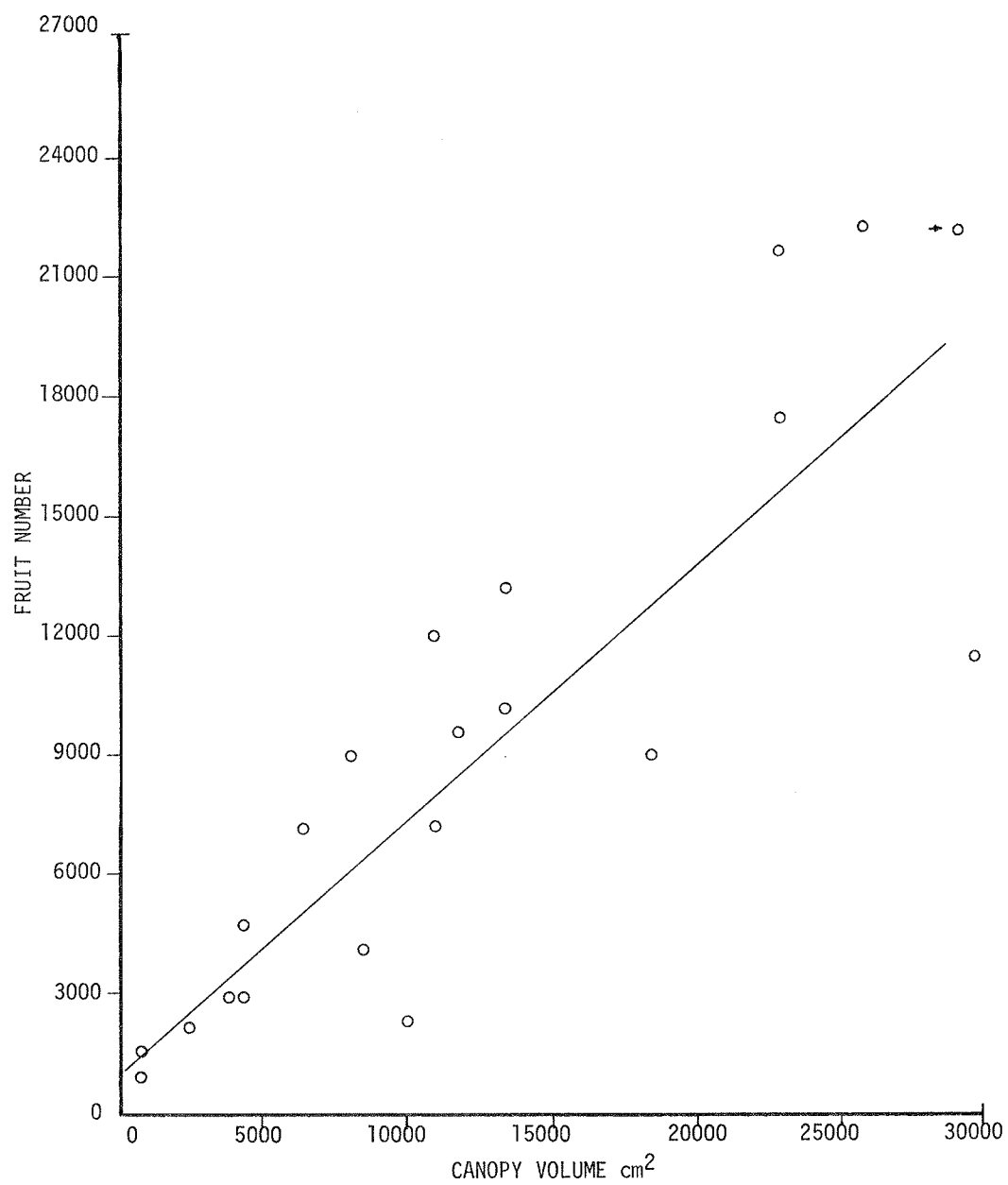


Figure 17. The relationship between fruit number and canopy volume in *Eriogonum abertianum* var. *ruberrimum*. (DSCODE A3UEE14)

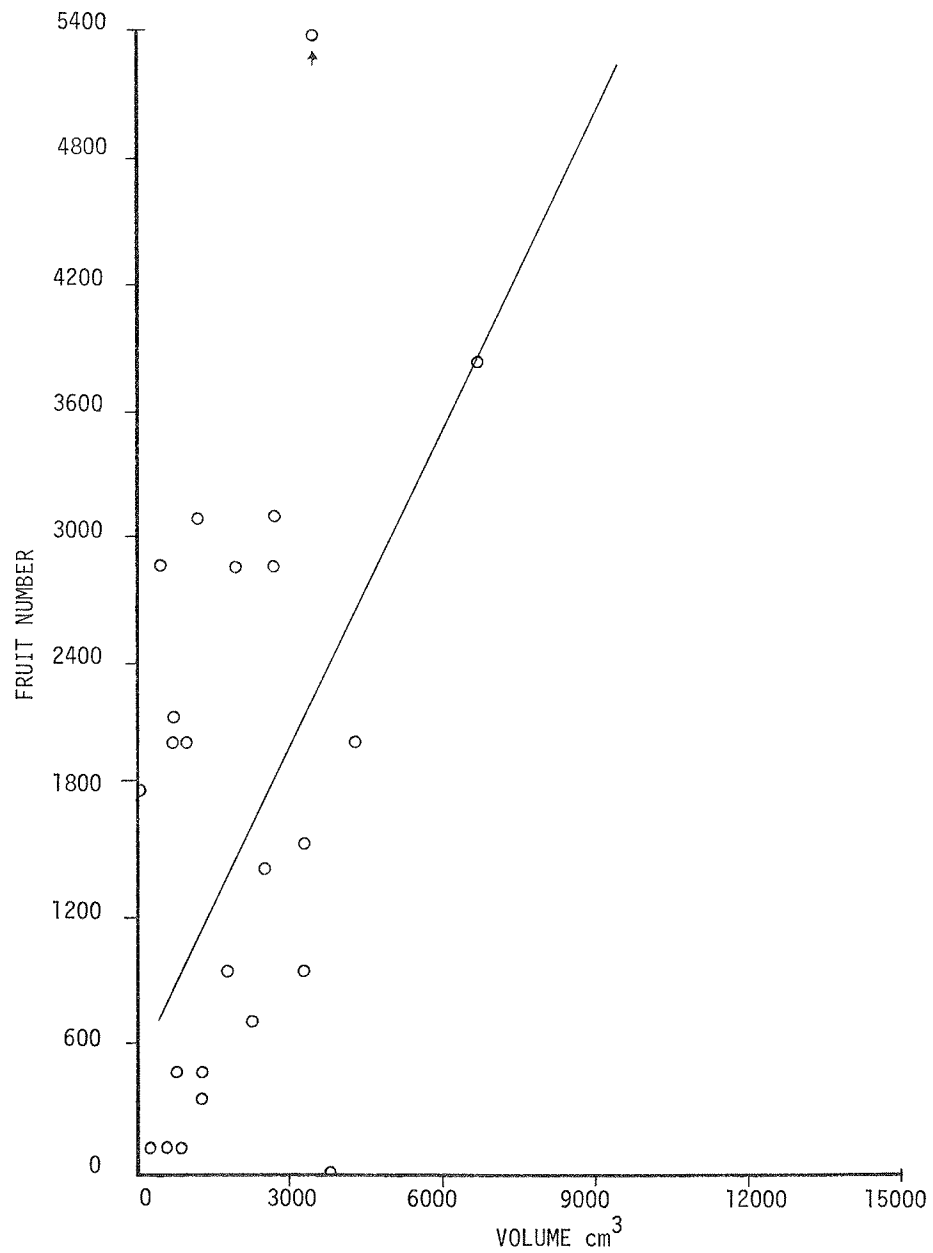


Figure 18. The relationship between fruit number and canopy volume in *Chenopodium incarum*. (DSCODE A3UEE14)

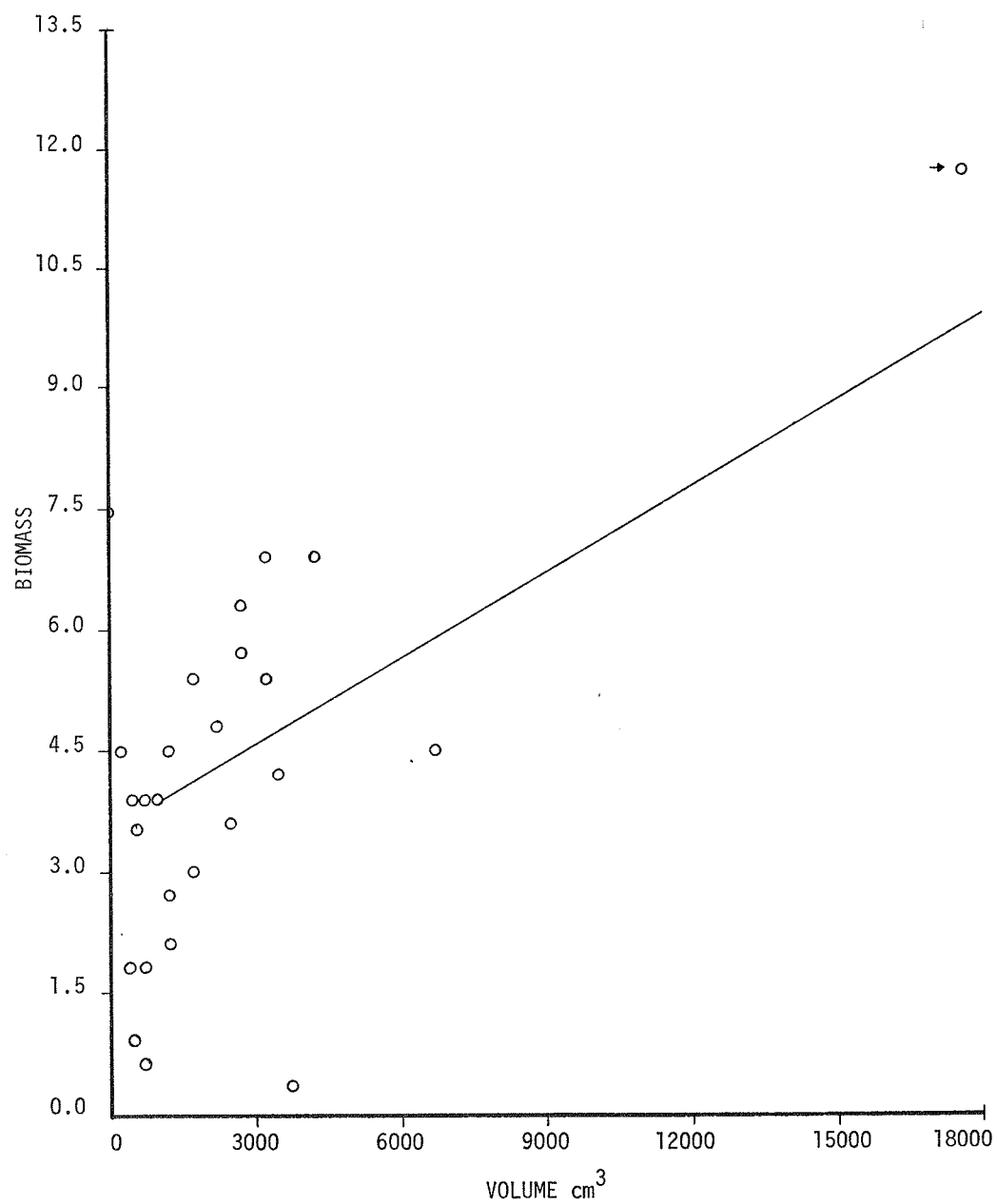


Figure 19. The relationship between above-ground biomass and plant volume in *Chenopodium incanum*. (DSCODE A3UEE14)

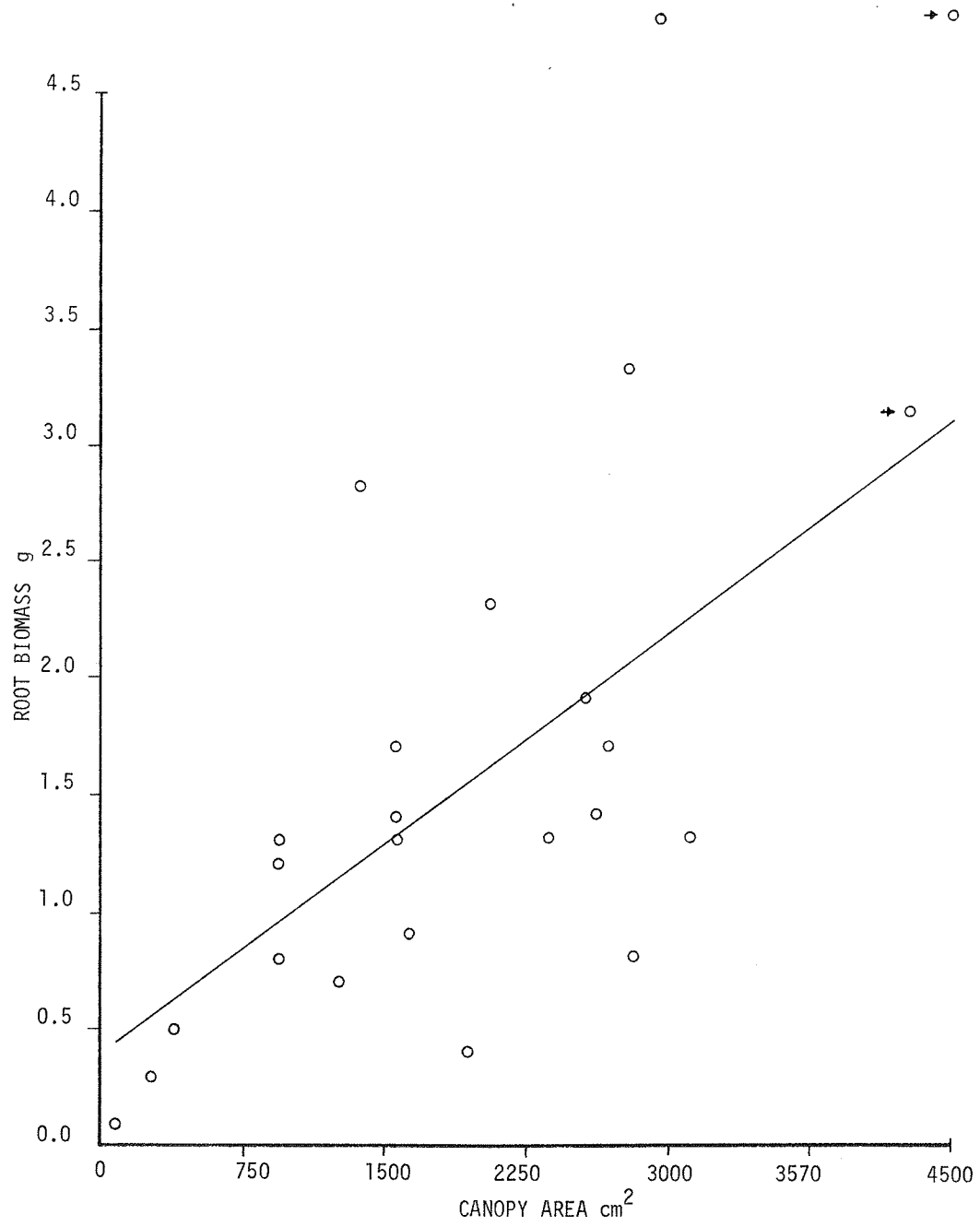


Figure 20. The relationship of root biomass to canopy area in *Bahia absinthifolia*. (DSCODE A3UEE14)

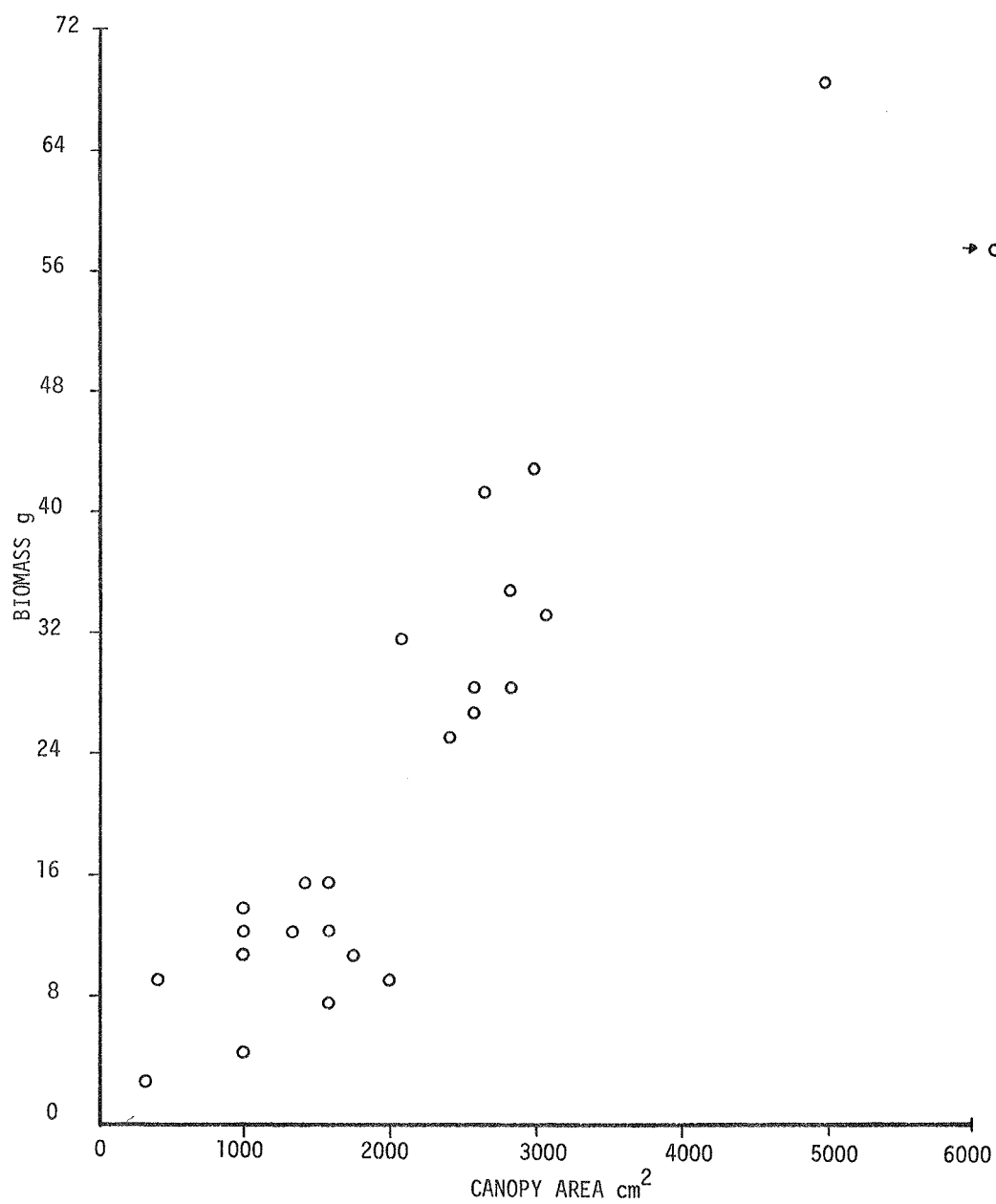


Figure 21. The relationship between above-ground biomass and canopy area in *Bahia absinthifolia*. (DSCODE A3UEE14)

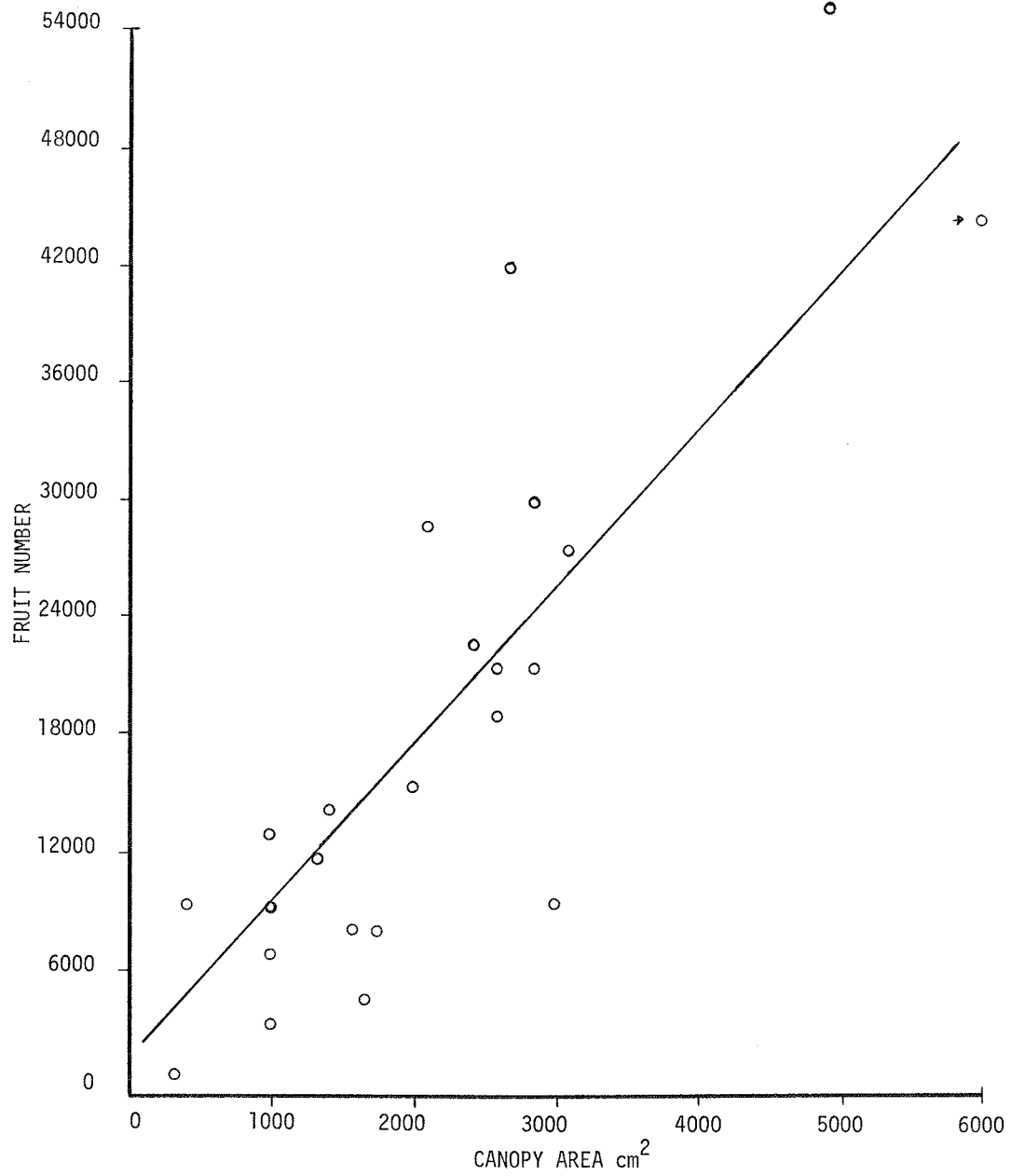


Figure 22. The relationship between fruit number and canopy area in *Bahia absinthifolia*. (DSCODE A3UEE14)

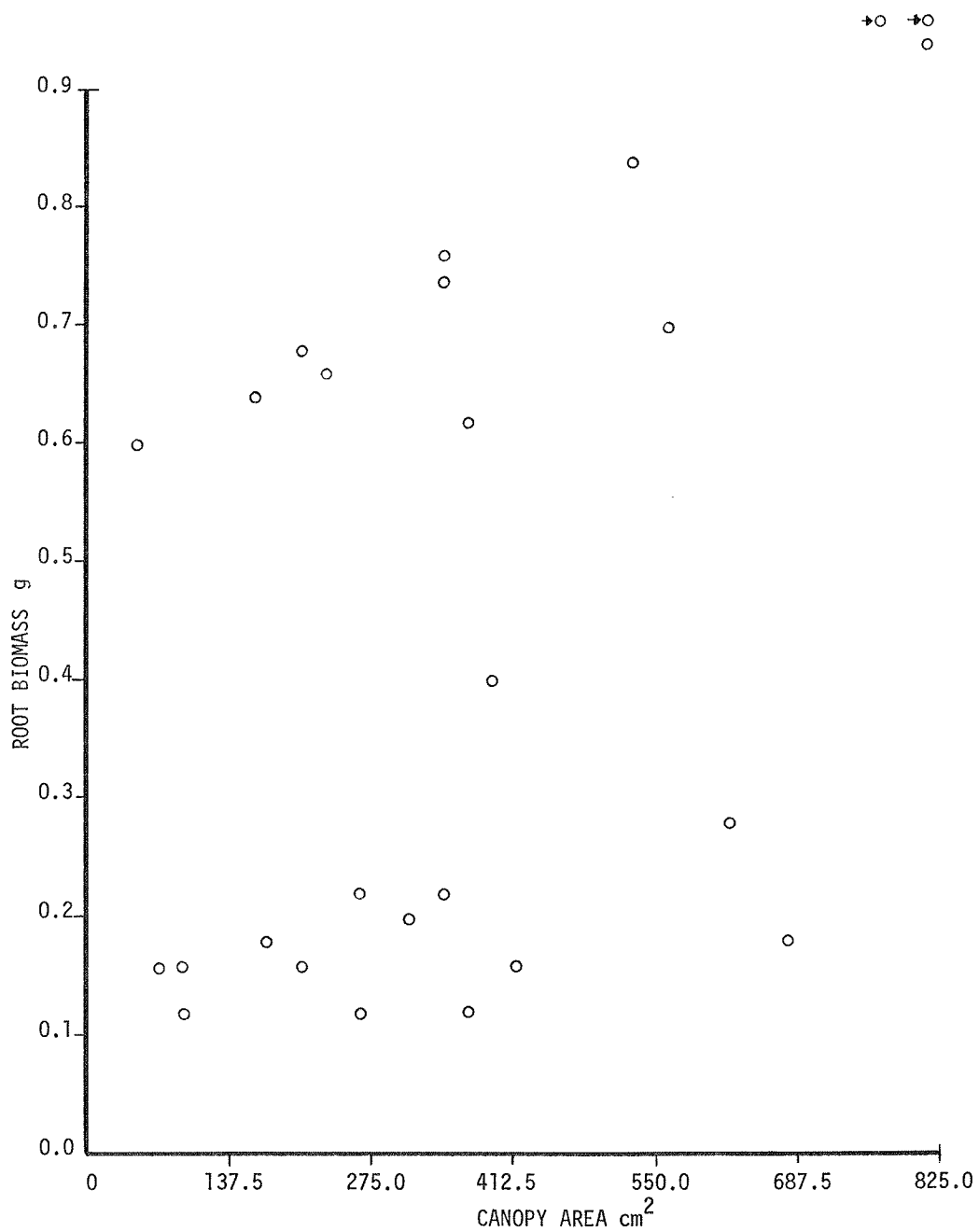


Figure 23. The relationship between root biomass and canopy volume in *Eriogonum abertianum* var. *abertianum*. (DSCODE A3UEE14)

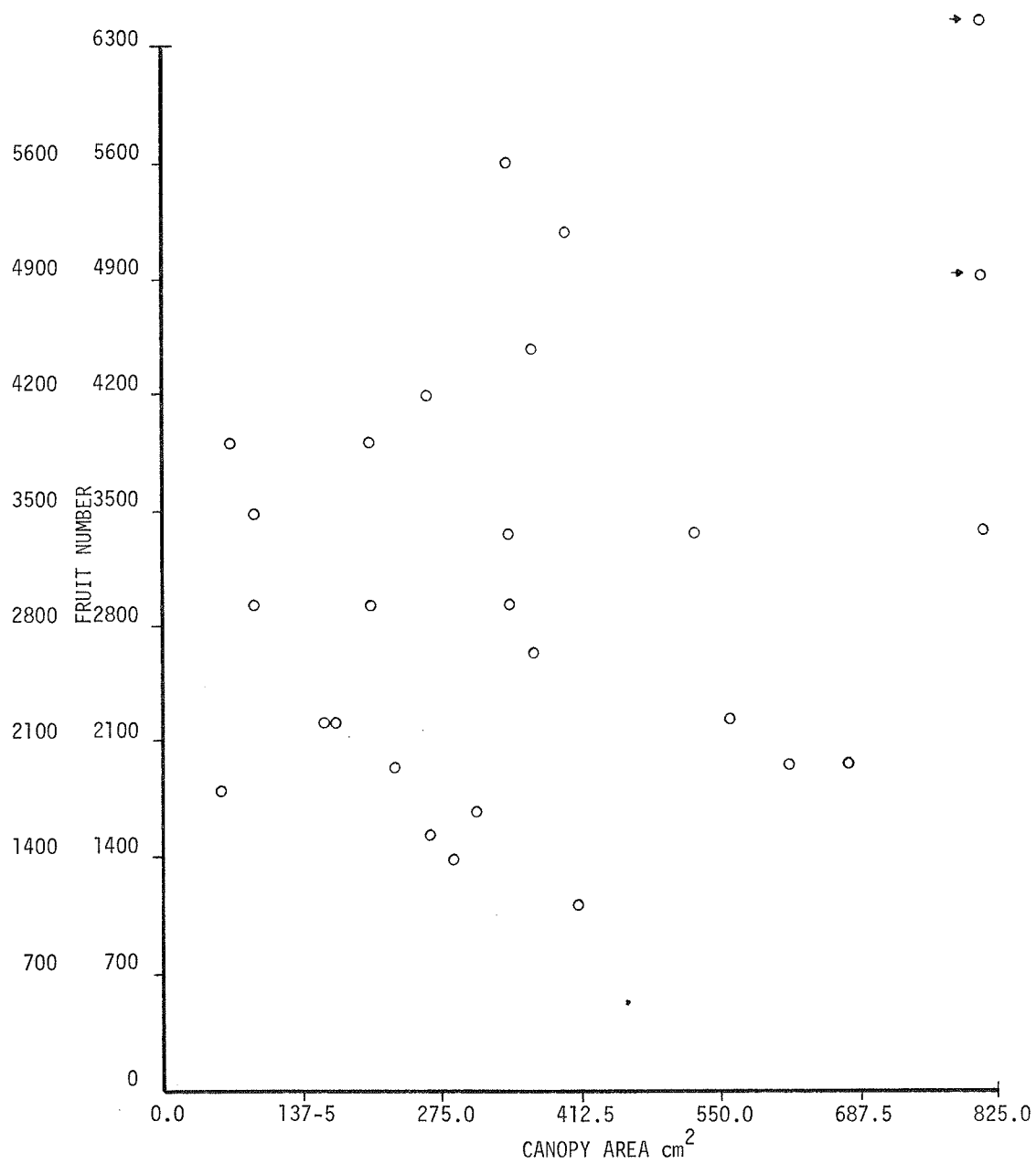


Figure 24. The relationship between number of fruits produced and plant volume in *Eriogonum abertianum* var. *abertianum*. (DSCODE A3UEE14)

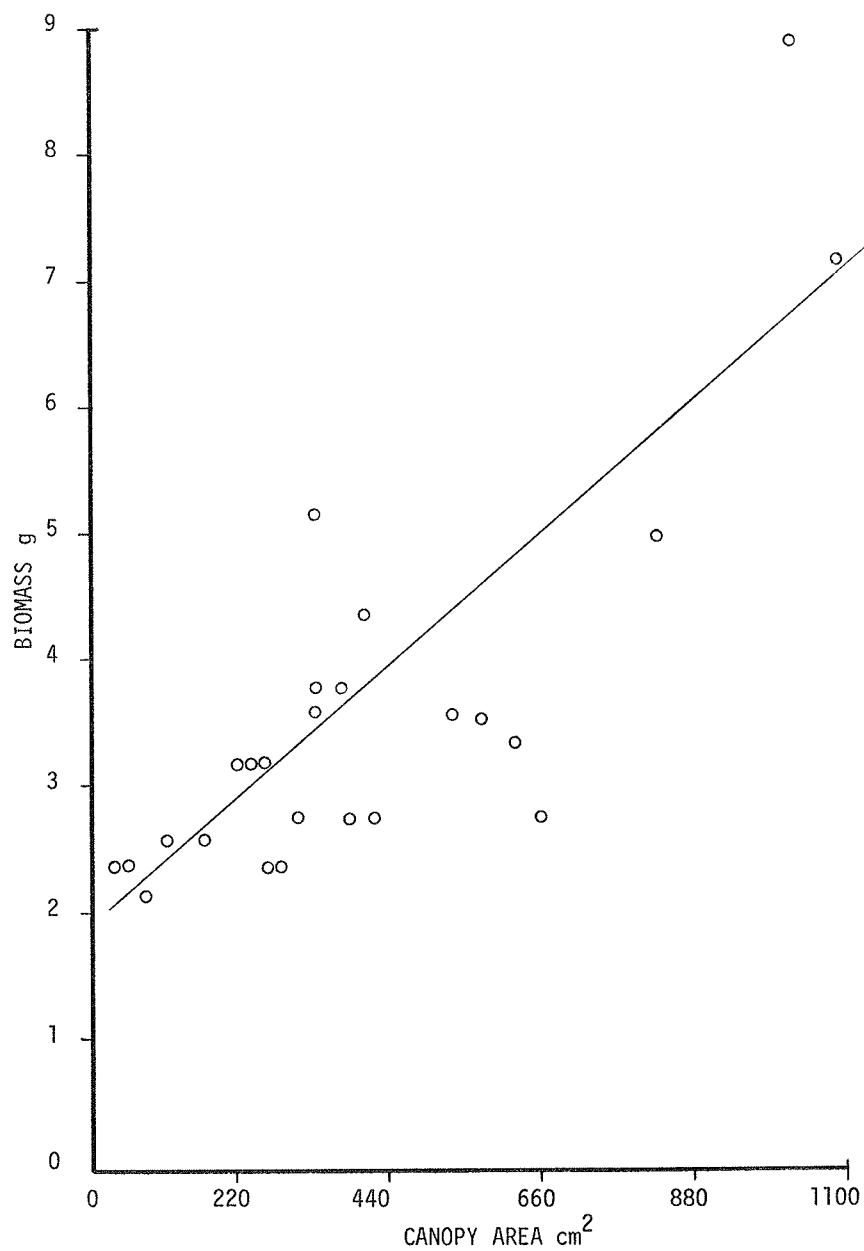


Figure 25. The relationship between above-ground biomass and canopy volume in *Eriogonum abertianum* var. *abertianum*. (DSCODE A3UEE14)

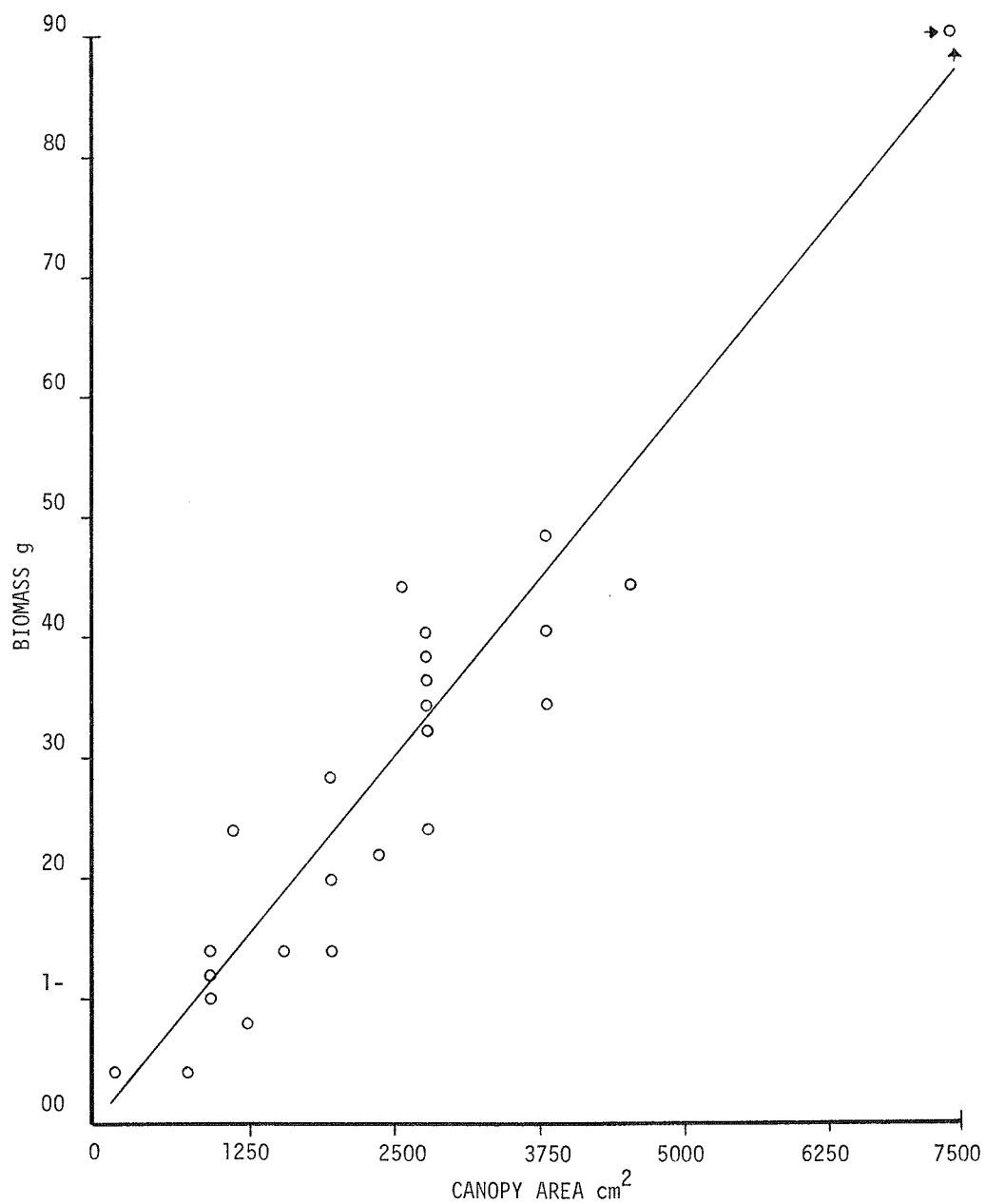


Figure 26. The relationship of above-ground biomass to canopy area in *Baileya multiradiata*. (DSCODE A3UEE14)

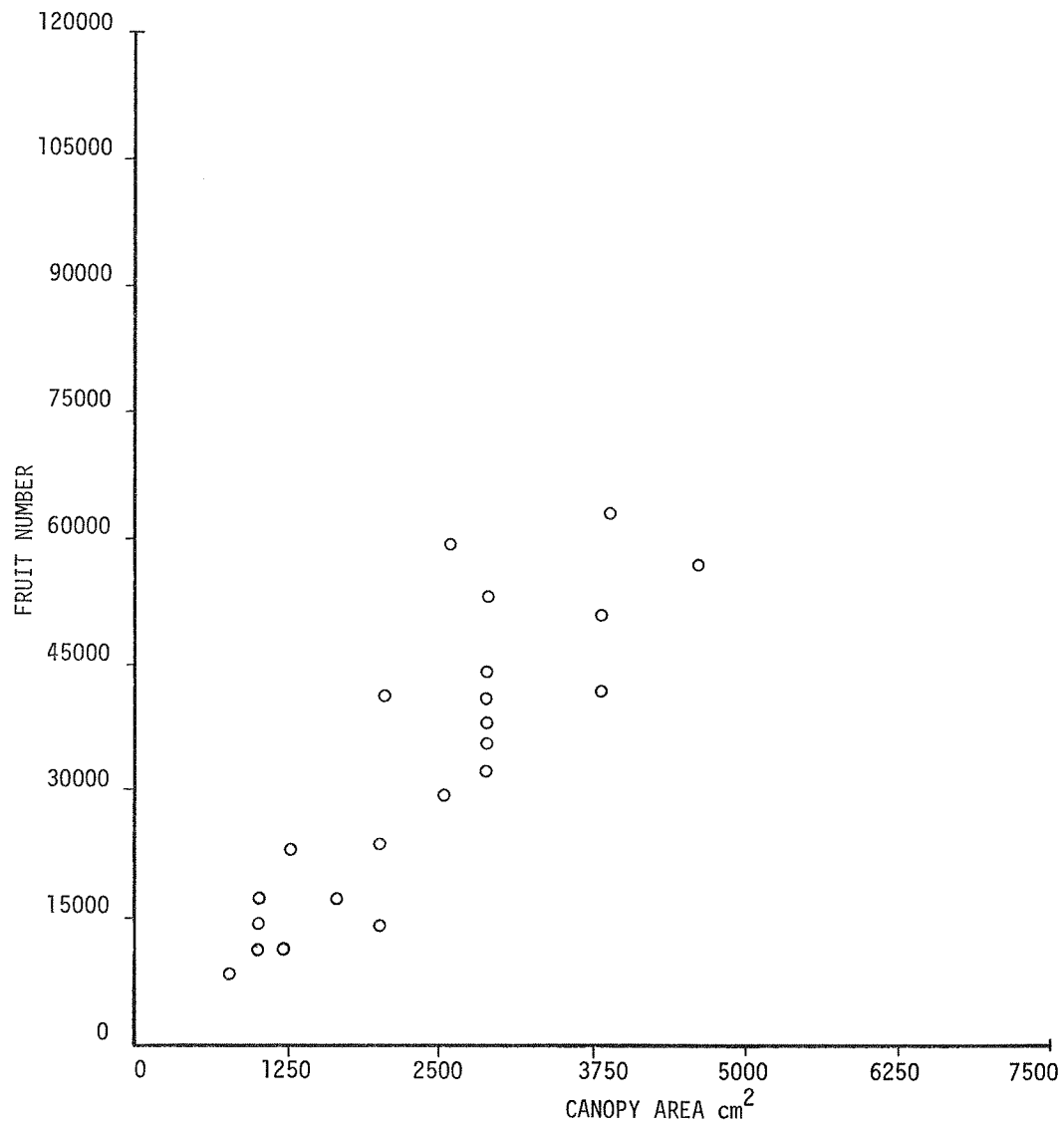


Figure 27. The relationship between number of fruits (based on total reproductive structure biomass) and canopy area in *Baileya multiradiata*. (DSCODE A3UEE14)

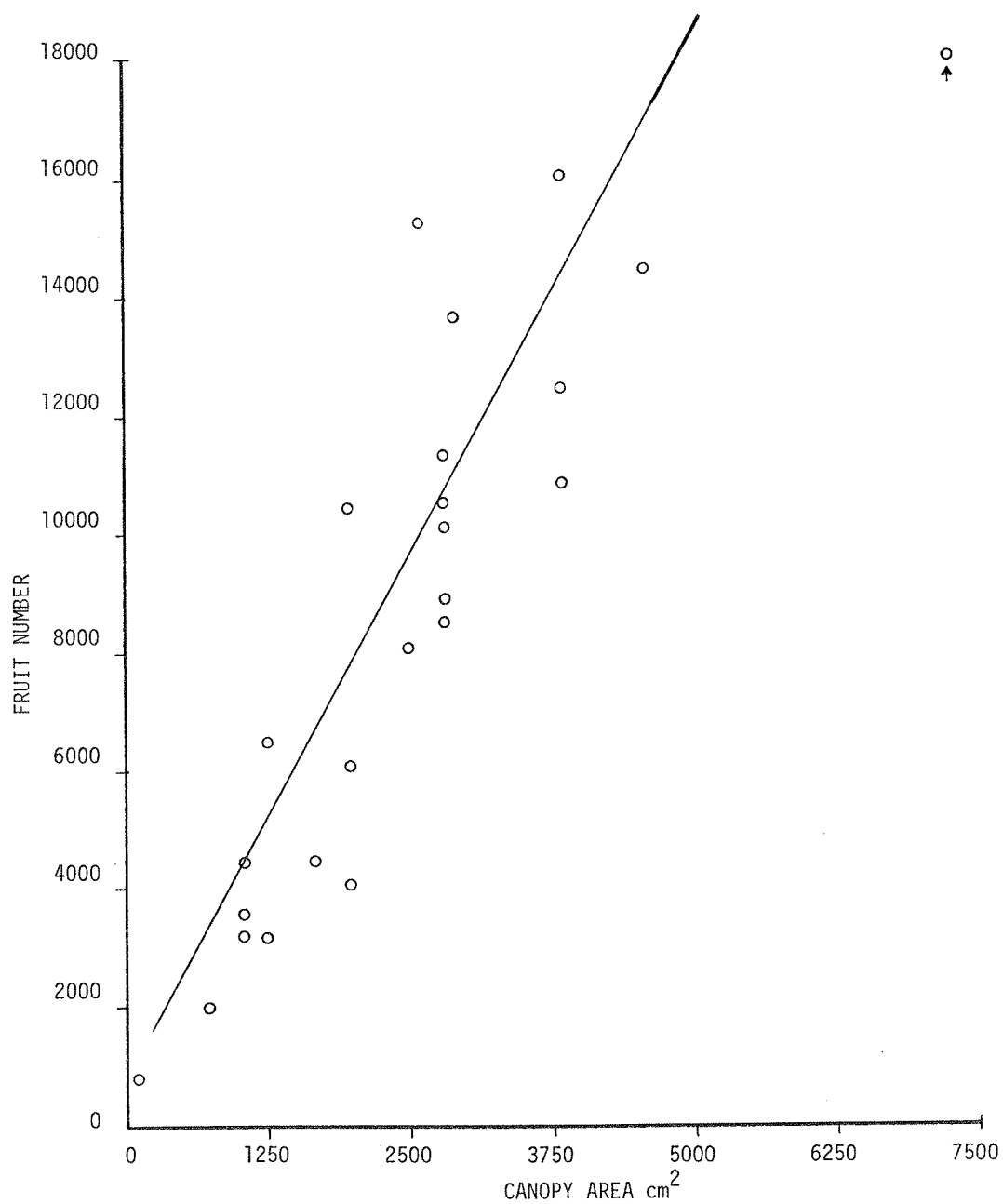


Figure 28. The relationship between fruit numbers (adjusted for non-seed parts) and canopy area in *Baileya multiradiata*. (DSCODE A3UEE14)

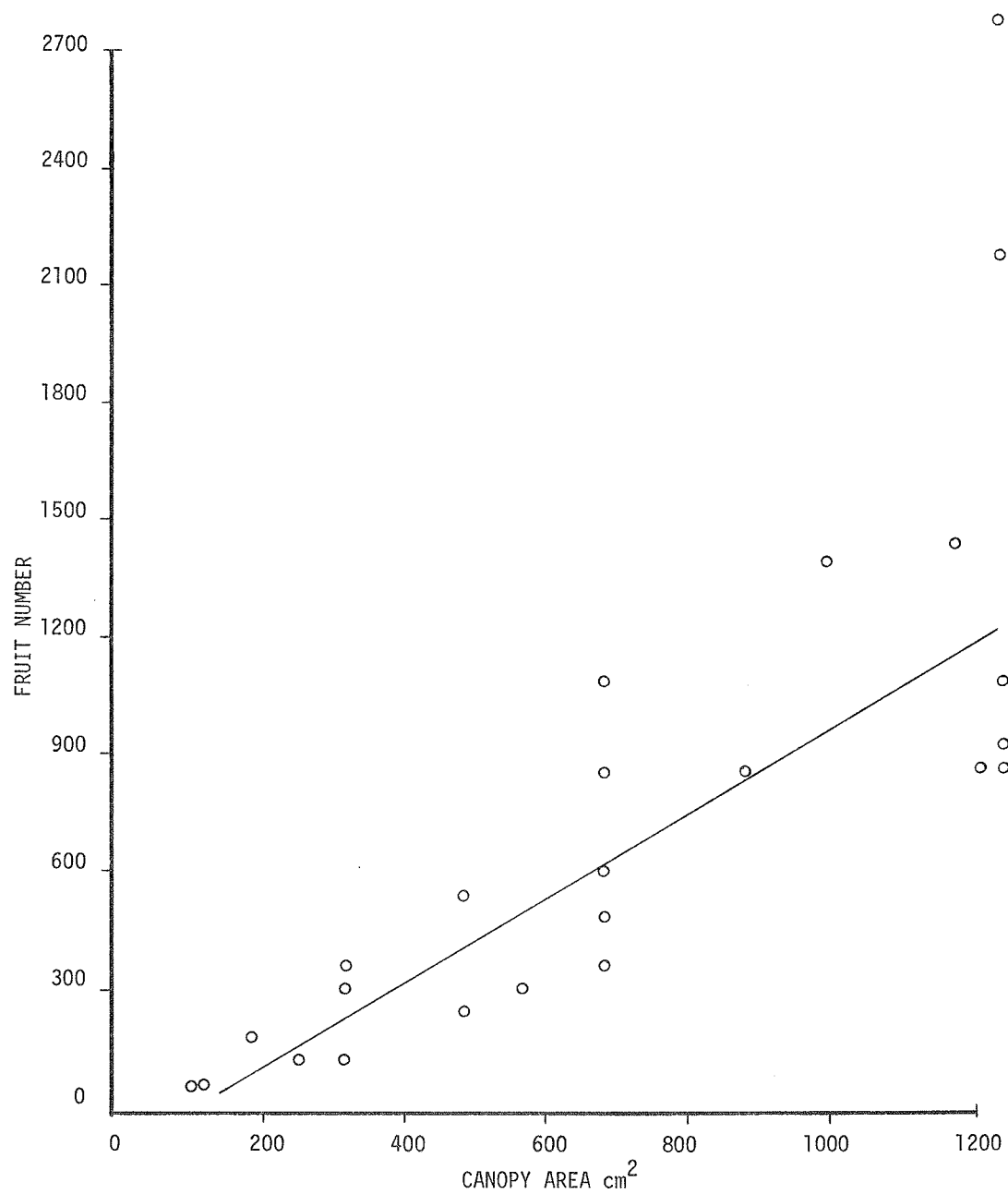


Figure 29. The relationship between fruit number (adjusted for non-seed parts) and canopy area in *Bouteloua barbata*. (DSCODE A3UEE14)

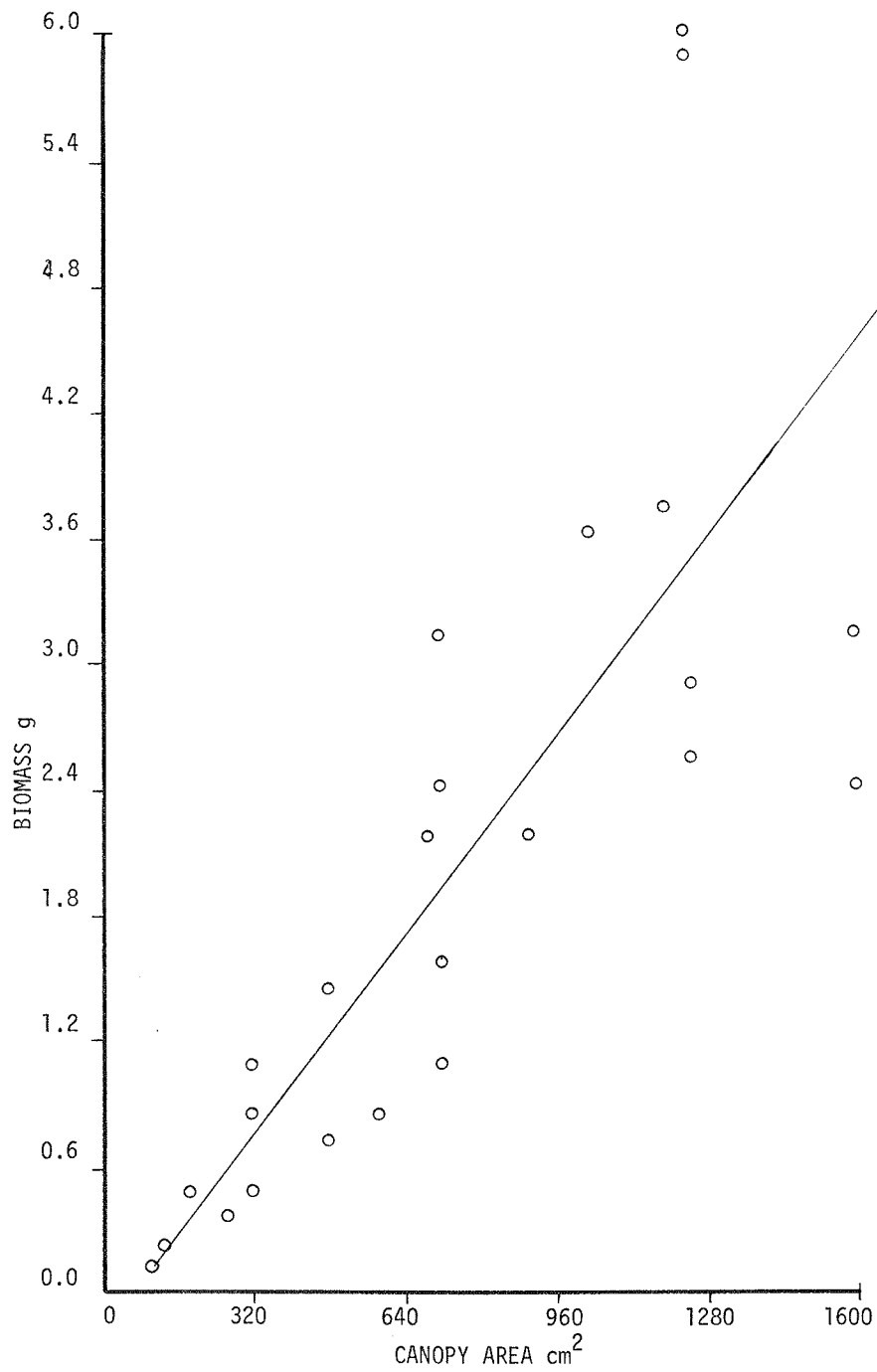


Figure 30. The relationship between above-ground biomass and canopy area in *Bouteloua barbata*. (DSCODE A3UEE14)

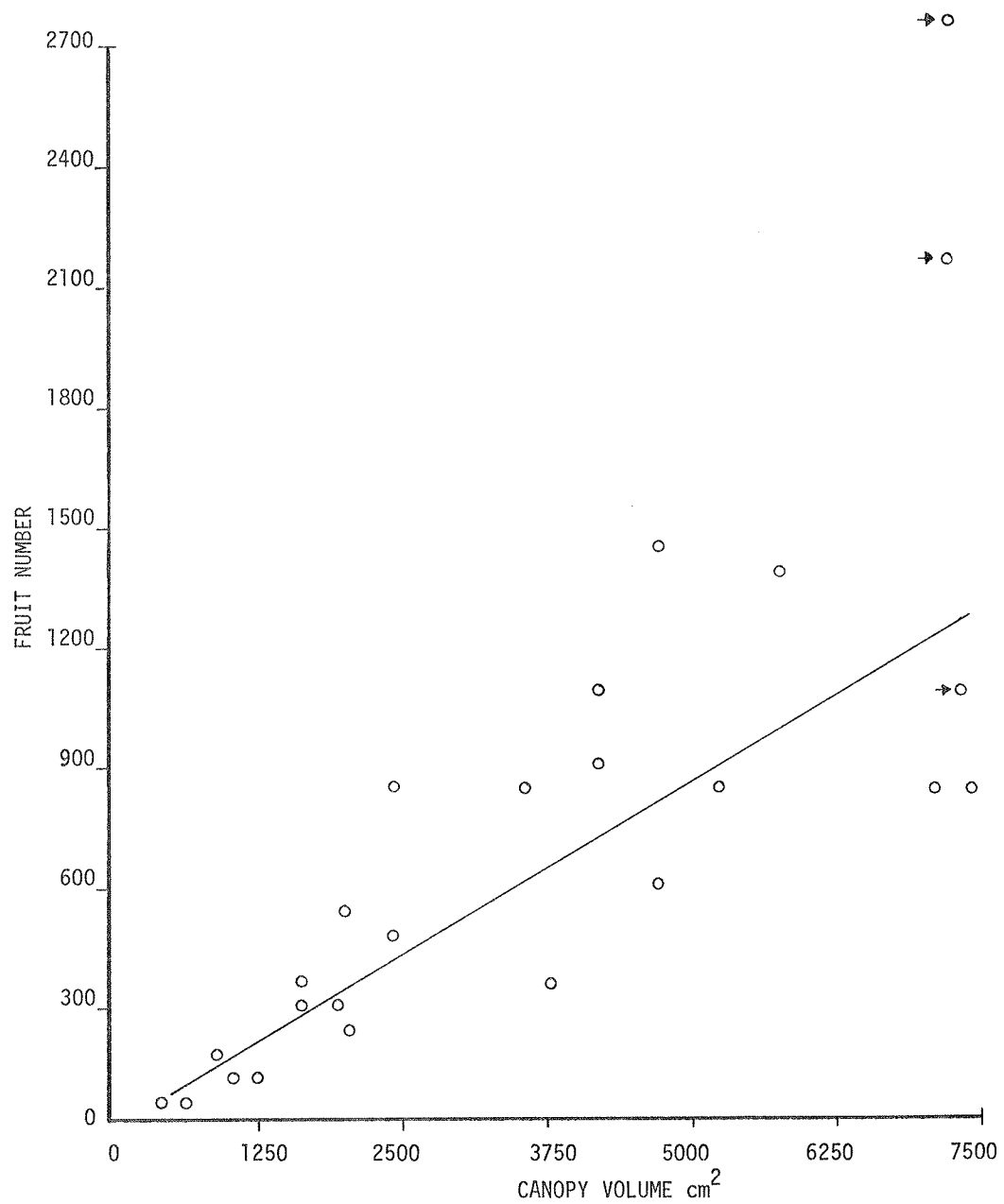


Figure 31. The relationship between number of fruits (adjusted for non-seed weight) and canopy volume in *Bouteloua barbata*. (DSCODE A3UEE14)

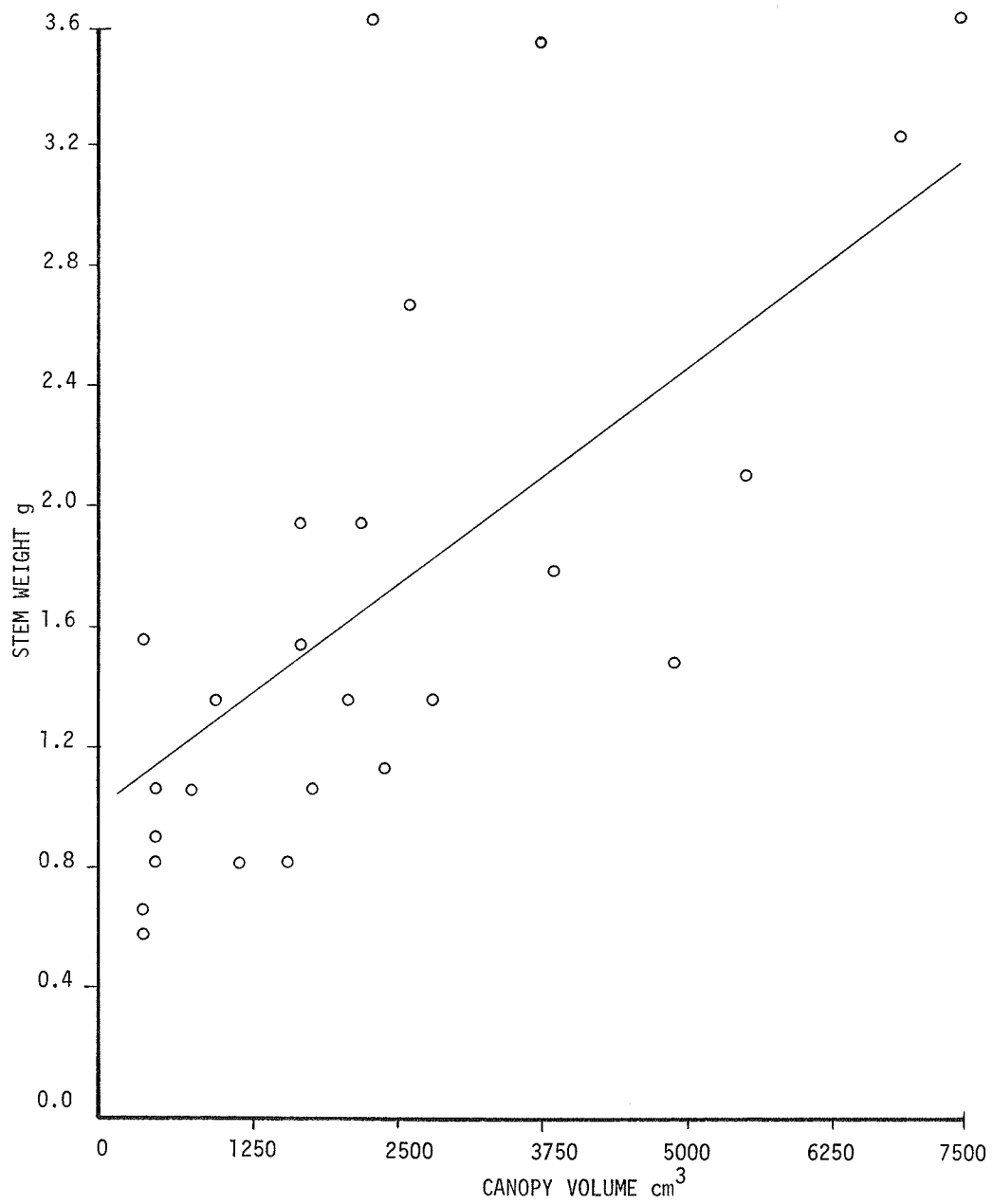


Figure 32. The relationship between stem weight and canopy volume in *Eriogonum trichopes*. (DSCODE A3UEE14)

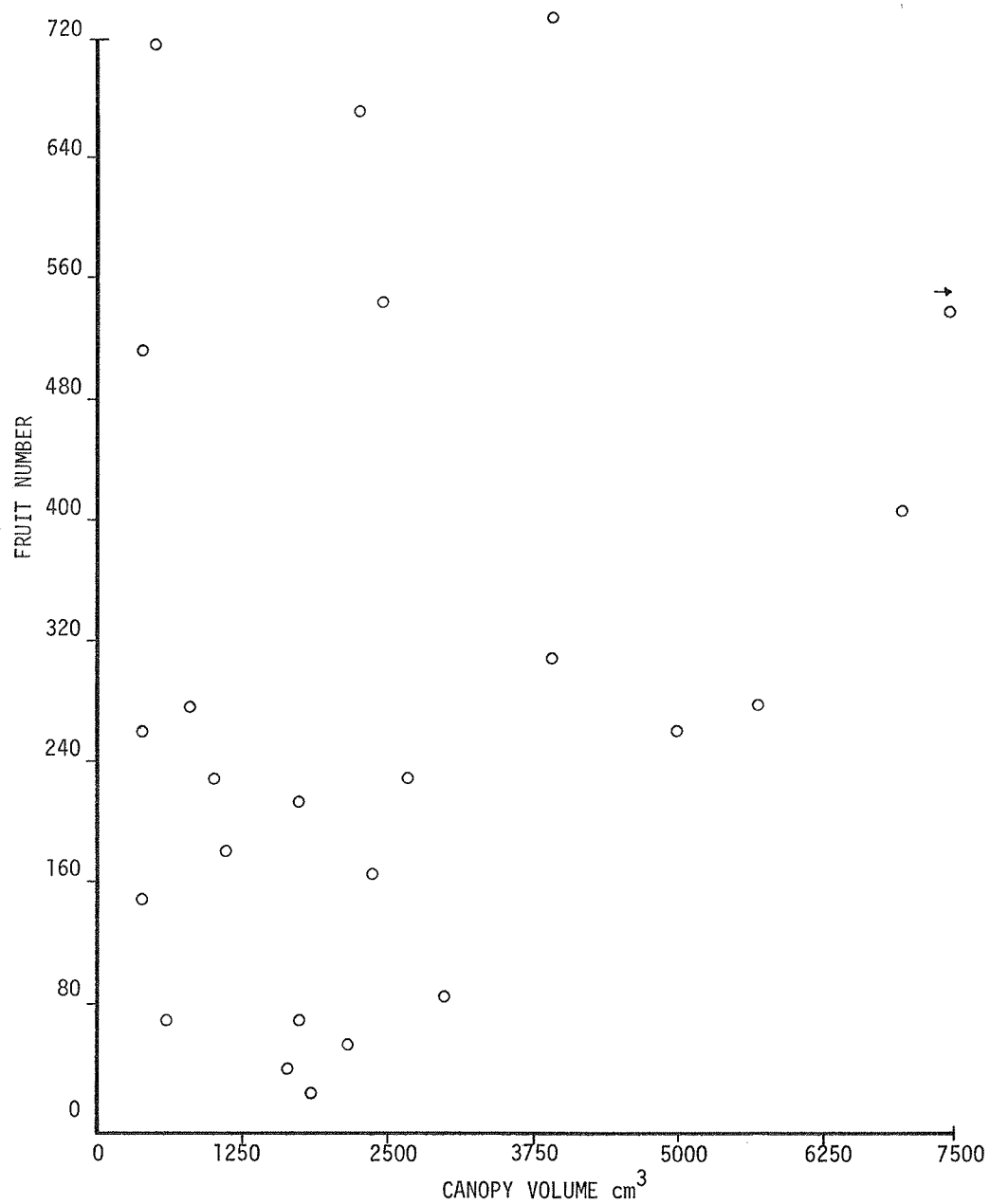


Figure 33. The relationship between fruit number and canopy volume in *Eriogonum trichopes*. (DSCODE A3UEE14)

Forager population estimates (A3UEE15) and total colony size

There was a seasonal trend in numbers of foragers in the foraging population, with peak numbers in July and August, months with the greatest seed production (Table 6). In *P. rugosus*, forager population size increased from approximately 350/colony in June to greater than 1,000 in July. The July and August estimates of forager populations of *P. californicus* and *N. cockerelli* also exceeded 1,000. *P. desertorum* colonies had forager population estimates less than 300.

Table 6. Estimated forager population numbers based on mark-recapture data *

MARCH - JUNE

<u>Pogrug</u>	<u>Novcoc</u>
3333	250
630	429
<u>1982</u>	<u>$\bar{x} = 340$</u>

JUNE

<u>Pogrug</u>	<u>Novcoc</u>	<u>Pogdes</u>	<u>Pogcal</u>
217	606		
218	400	260	337
824	549	184	613
479	557	277	$\bar{x} 475$
$\bar{x} 434$	236	$\bar{x} 240.3$	
SD 287	$\bar{x} 469$		
	SD 156		

JULY

<u>Pogrug</u>	<u>Novcoc</u>	<u>Pogdes</u>	<u>Pogcal</u>	<u>Pogbar**</u>	<u>Pogcal**</u>
1,044	1,391		557	2,535	2,040
1,464	1,863		1,464	2,849	2,256
6,063	2,208		1,103	82,102	$\bar{x} 2,136$
$\bar{x} 2,857$	$\bar{x} 1,820$		3,091	14,309	
			3,826	$\bar{x} 25,448$	
			$\bar{x} 2,008$		
			SD 1,387		

AUGUST

<u>Pogrug</u>	<u>Novcoc</u>	<u>Pogdes</u>	<u>Pogcal</u>
1,519	585	284	1,011
548	762		2,881
756	1,342		$\bar{x} 1,946$
734	1,650		
496	1,884		
479	$\bar{x} 1,245$		
818	SD 559		
$\bar{x} 764$			
SD 359			

* Estimate by Lincoln-Peterson Index. Pogrug = *P. rugosus*, Novcoc = *N. cockerelli*, Pogdes = *P. desertorum*, Pogcal = *P. californicus*, Pogbar = *P. barbatus*.

**Indicated data from Portal, Arizona

Total population estimates were obtained for three colonies of harvester ants which were completely excavated (see Descriptive notes section for details). The following population estimates were obtained:

- 30 Sept. '72-*Pogonomyrmex rugosus* #62;workers-1595,larvae-150
- 15 Sept. '72 *Pogonomyrmex rugosus* #18;workers-2195,larvae-180
- 10 Oct. '72 *Pogonomyrmex californicus* #35;workers-1932,larvae-0

Colony distribution (A3UEE12)

The data on density estimates and nearest neighbor analysis are summarized in Table 7. *N. cockerelli* exhibited a clumped distribution ($P < .05$, Grieg-Smith, 1964) and *P. desertorum* had a highly significantly clumped distribution ($P < .001$, Grieg-Smith, 1964). The distribution of *P. rugosus* colonies was found to be random. *P. californicus* had extremely low densities (4-6 colonies/hectare) in comparison to the other species and as a consequence no formal analysis of the distribution of this species was attempted.

Table 7. Nearest-neighbor analysis for harvester ant species in the study area*

Species	PD^2	ND^2	PD^2/ND^2	Colonies/hectare
<i>Novomessor cockerelli</i>	28333	20813	1.36	18.2
<i>Pogonomyrmex desertorum</i>	4075	1473	2.76	137.9
<i>Pogonomyrmex rugosus</i>	16422	13255	1.24	21.3

*P = point, D = distance, N = neighbor

Descriptive notes (A3UEE16).

The following is summarized from the notes of Tim Cox who was responsible for most of the excavation of the *Pogonomyrmex rugosus* colonies (Figs. 34 and 35).

Excavation of colony #18 was begun 24 August 1972. Most digging was done from dawn to approximately 1100 hrs. The flow of ants from the chambers was very constant in the first meter of excavation but became very sporadic below that depth. Below 1 m, the ants were extremely reluctant to leave the passage unless air was forced in on them or unless actually dug up. On the second morning many ants could be found outside the colony galleries at the new ground level, but they did not seem to attempt to forage as they did not leave the immediate vicinity of the new entrance by more than 0.3 cm.

Ants recovered in the top meter of digging were of uniform size and courage, the apparent primary foragers of the colony. After this depth, however, many unpigmented workers were captured and as the excavation continued, more and more larger, dark ants were taken. These ants were not only of an extremely large size (1/4 larger) but were very courageous and seemed to possess a better sense of direction as to danger. Many young, unpigmented workers were taken from this depth on. Their numbers increased with the depth and their size was the average "forager" size.

Excavation had proceeded to approximately 1.7 m by 26 August. The following morning a heavy rain (11mm) had fallen the previous night and had filled approximately 0.3 m of the hole. It appears that at the end of excavation the previous day we had been within 0.45 m of the queen's chambers and that the rain had forced the ants to make an emergency chamber or convert an already existing chamber into a temporary queen's chamber overnight, since a new entrance and mound of earth was found approximately 1.5 m from the original main entrance.

Upon excavation, the queen was taken at approximately 1 m depth primarily with young "white" workers, and some of the very large workers.

Larvae were found in two chambers approximately 0.6 m down and were found again only at the maximum depth of the excavation (1.7 m).

The colony 62 excavation incurred the same ant flow consistency, location and approximate number of larvae, approximate depth of excavation, and general characteristics of ant behavior. The only real difference was that the queen was taken at the maximum depth excavated and was found with many larvae and young ants in a prehibernation condition as excavation was in the early fall.

Pogonomyrmex barbatus: On 5 November 1972, we went to the Aguirre Springs area 35 km ENE of Las Cruces, Dona Ana Co., New Mexico to collect *Pogonomyrmex barbatus* for laboratory studies. At 1100 hr there was some foraging activity. The soil surface temperature was estimated to be between 20-30 C. The foragers were bringing fruits of

Bouteloua gracilis and *Bouteloua curtipendula* to the nest. One nest was excavated to the depth of 0.45 m (Fig. 36). Storage galleries were filled with fruits of *Bouteloua curtipendula*. Over 800 workers and larvae were removed from the galleries.

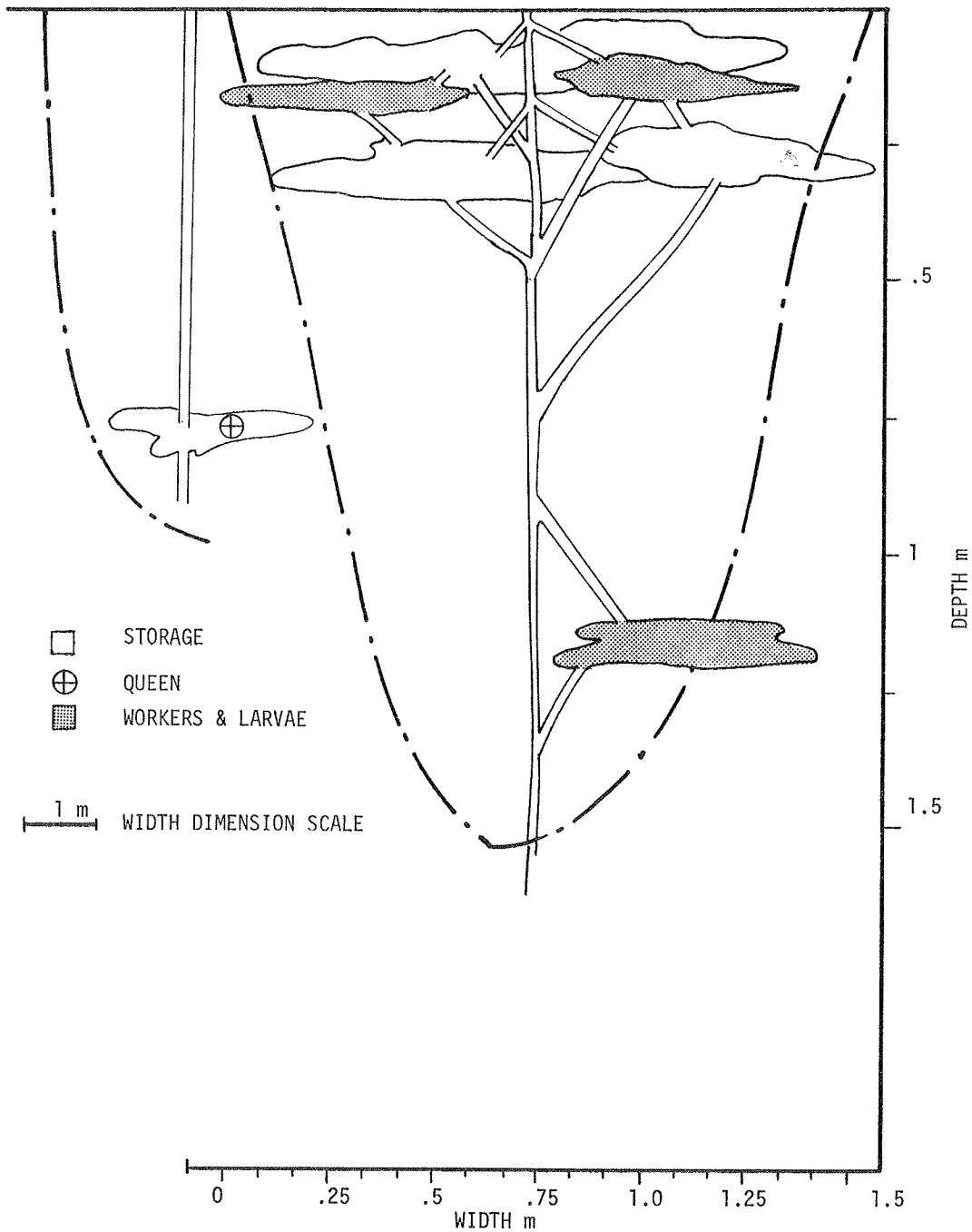


Figure 34. Relationships of storage and nest chambers of *Pogonomyrmex rugosus* colony 18, excavated in August, 1972. The depth and one width dimension are shown on the x and y axis, the second width dimension may be obtained by use of the width dimension scale.

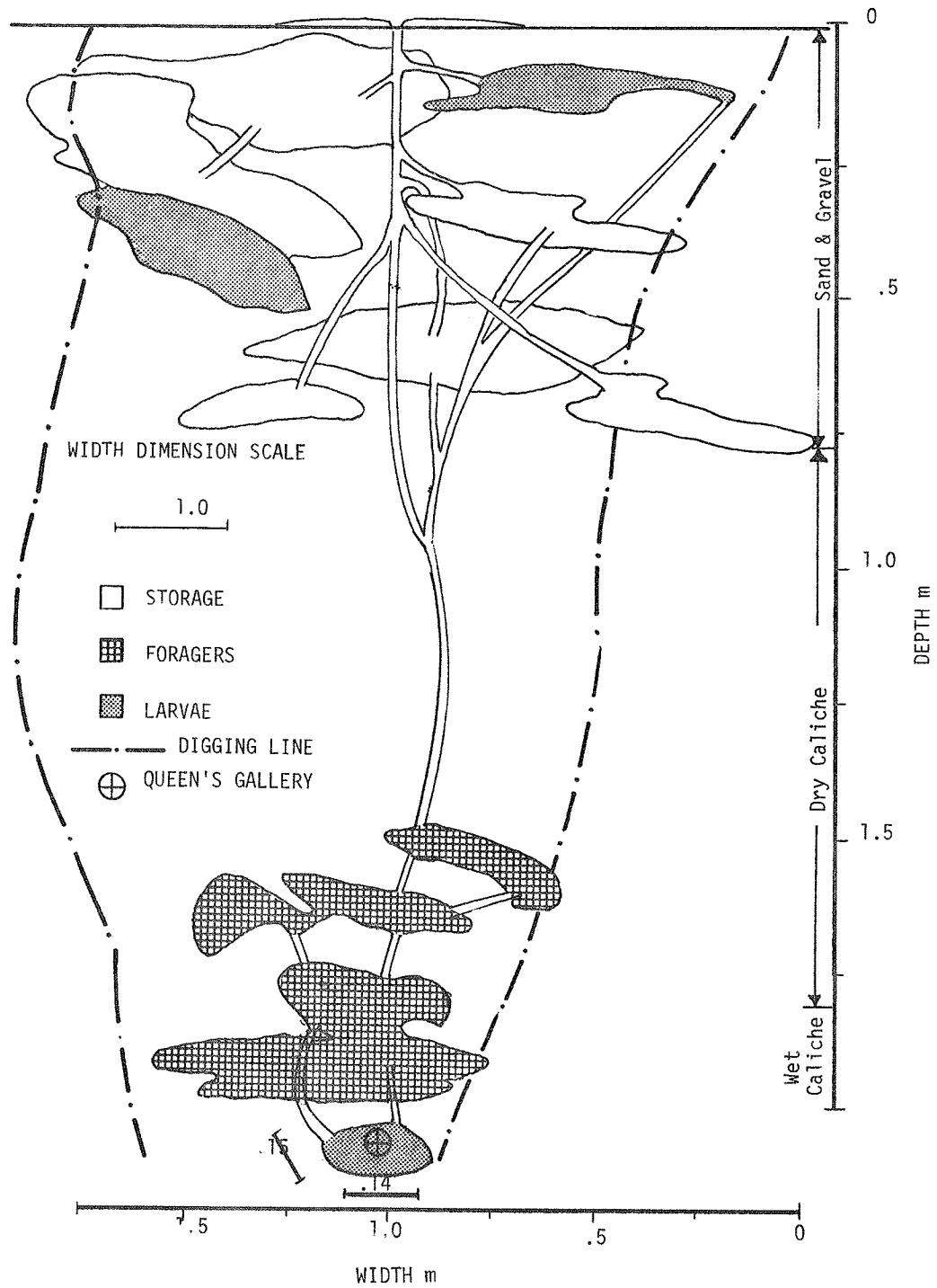


Figure 35. Relationship of storage and nest chambers of *Pogonomyrmex rugosus* colony 62, excavated in August, 1972. Method of presentation the same as in Figure 34.

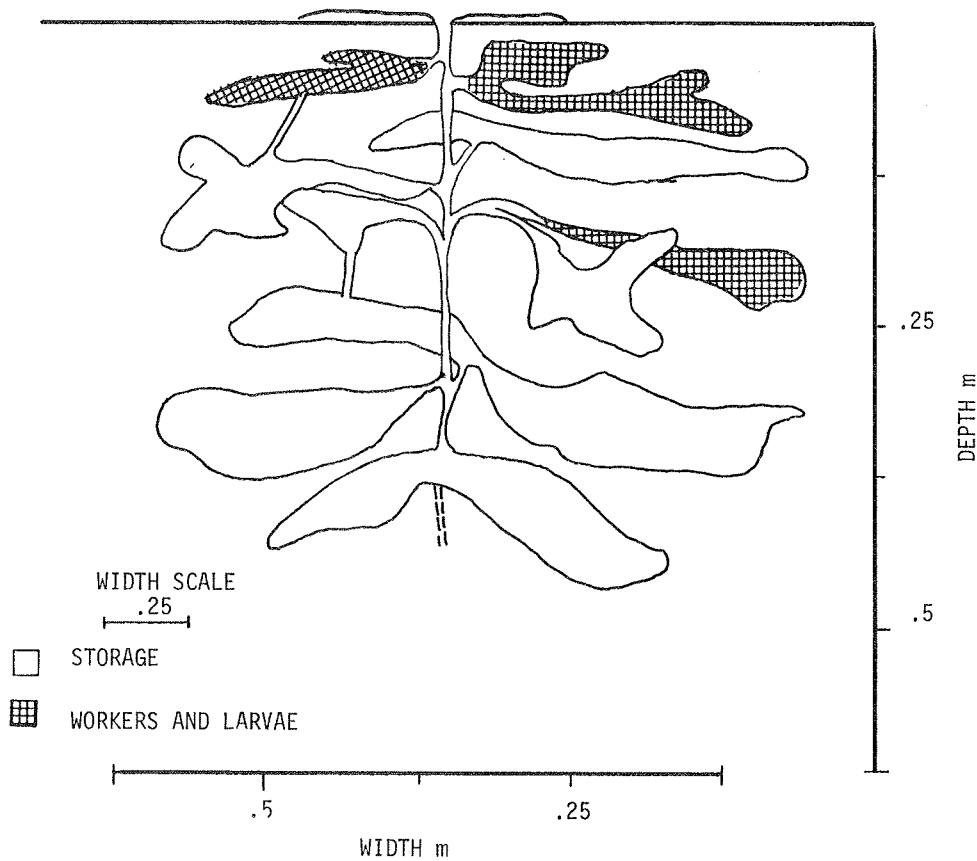


Figure 36. The relationship of nest chambers in a partially excavated colony of *Pogonomyrmex barbatus*.

A general survey of the area lower on the alluvial fan showed that *P. barbatus* was the only large harvester ant in the scrub oak-grass community. In drier sites at lower elevations in the grass-mesquite association, *P. rugosus* replaced *P. barbatus*, with *P. barbatus* extending into areas dominated by *P. rugosus* on the edges of larger watercourses. This suggests that *P. barbatus* requires moister habitats than *P. rugosus*.

Foraging and nest structure of *Pogonomyrmex barbatus*. (A3UEE03 and A3UEE16): The mesquite-acacia community near Portal, Arizona, supports dense populations of *Pogonomyrmex barbatus* (28 colonies/hectare). In July we spent several days in this area obtaining data on this species, primarily for comparison with *P. rugosus*. Unlike

P. rugosus, *P. barbatus* did not forage at night. Some data was obtained on foraging activity as affected by soil surface temperature and saturation deficit. The data in Table 9 show that foraging activity in this species is highest at soil surface temperatures between 25-40 C and at saturation deficits $<30 \text{ g/m}^3$. While making these observations at soil surface temperatures between 55-56 C, and a saturation deficit of 37 g/m^3 , I was able to stimulate emergence of foragers from *P. barbatus* colonies by casting a shadow on the mound. Foragers that departed the mound made a short excursion (less than 2 m) in the sun, then quickly sought shade. If trapped in the open, these ants would climb into the vegetation or remain in the shadow of a stick or rock, making but brief forays toward the nest then retreating quickly to the lower temperature environment. The soil surface temperature where my shadow was cast dropped quickly to 47 C, which was apparently low enough to result in egress of some foragers from the colony.

A 6 m circle was cleared around a *Pogonomyrmex barbatus* nest and some foraging behavior experiments were conducted with colored seeds. In experiments 1 and 2, seed distribution per unit area was uniform and in experiments 3 and 4, the 4 m line was saturated with dyed grain. The foraging behavior of *P. barbatus* was similar to that of *P. rugosus*. Intensity of foraging exhibited a log decay with distance from the nest and even forage distribution, but increased in response to greater forage concentration (Table 8).

Table 8. The effect of distance and forage concentration of foraging activity of *Pogonomyrmex barbatus**

Experiment Number	Distance to colony in meters		
	3m	4m	6m
Number to the nest/minute			
Pogbar #1 Exp. 1	4.2	1.2	.4
2	2.4	.8	1.2
3	3.4	2.9	.7
4	6.1	7.6	.6
	3m	5m	6m
Pogbar #2 Exp. 1			
2	1.4		
3	1.6		
4	6.1	.4	.2
	5.2	4.6	.4

*See text for details.

While these are scant data on which to base speculation, it is tempting to hypothesize that foraging response is the same to distance and forage concentration in all harvester ant species.

Table 9. The relationship of foraging activity and soil surface temperature and saturation deficit in *Pogonomyrmex barbatus**

Soil Surface Temperature	Saturation Deficit							
	0-5	6-10	11-15	16-20	21-25	26-30	31-35	36-40
16-20	29.5							
21-25								
26-30					188			
31-35					297	14.5		
36-40				214				
41-45							24.1	
46-50								
51-55							3.25	0
56-60							0	

*Table values are number to nest/minute.

DISCUSSION

Novomessor cockerelli exhibited the greatest difference in foraging pattern in the species investigated. In *N. cockerelli* maximum foraging activity was in the early evening, coincident with the activity of insects. While *N. cockerelli* will take seeds or fruits, arthropods and arthropod parts apparently are the preferred forage. Sufficient night samples of foraged materials were not obtained to compare with day samples for determination of significant differences in materials foraged at night in either *N. cockerelli* or *P. rugosus*. These data would be necessary to evaluate the significance of nocturnal activity in these species. It is possible that *P. rugosus* switches preference to arthropods when foraging at night. Nocturnalism is advantageous to an insect scavenger or predator in the desert, since there is a marked rise in insect activity after dark.

The forager activity patterns in the three species of *Pogonomyrmex* exhibit differences in the temporal components of the niches of these species. While there is coincidence in maximum foraging activity in the three species at 45 C, the foraging rate in *P. rugosus* dropped sharply at higher temperatures, while the rates of *P. desertorum* and *P. californicus* remained fairly high. The greater insensitivity of these species to high saturation deficits and temperatures greater than 45 C allow them to forage for the items preferred by *P. rugosus* with reduced competition. Although there is considerable overlap in food preference and time of foraging in the three species, their foraging behavior differs. *P. desertorum* and *P. californicus* frequently forage in the forbs,

cutting fruits from the plants and dropping to the ground with their booty. The heavier *P. rugosus* workers were observed foraging in the dense canopy of *Tridens pulchellus* but not on the sparsely branched forbs. *P. desertorum* and *P. californicus* appear to have greater niche overlap than either of these species with *P. rugosus*. However, in the intensive study area the density of *P. californicus* was considerably lower than *P. desertorum*. Aspects of competition and niche overlap in these species is the subject of the MS thesis of Helen Hart (R.A. on this study).

The large differences in soil temperatures at initiation of foraging in the spring and cessation of foraging in the fall were unexpected. We had assumed that soil temperatures at 40-50 cm would represent the thermal barrier for movement to the surface where mid-day soil surface temperatures are sufficiently high for foraging even in mid-winter. We had also assumed that the soil temperature barrier to movement would be the same for initiation and cessation of foraging. The first assumption need not be rejected but the second requires modification. If seasonal acclimation occurred, the minimum temperature for activity could be lowered, allowing an extended foraging period in the fall. This would be particularly adaptive in the Chihuahuan Desert, where late summer annuals are the most reliable source of forage, and fruit ripening of many species occurs in late September and October. We are currently investigating maximum and minimum activity temperatures (ACTmax and ACTmin) in the laboratory and will investigate the effects of acclimation on ACTmax and ACTmin.

The data clearly demonstrate that both saturation deficit (or some other measure of air water content) and temperature are parameters which must be considered in order to predict foraging activity in harvester ants. However, Eddy (1970) reported that relative humidity had no influence on activity in *P. occidentalis*. Other factors affecting activity probably act more as "on-off" switches than rate regulators. Light intensity appears to affect the behavior of some species. *P. californicus* and *P. desertorum* cease foraging at dusk, even when soil surface temperatures and saturation deficits are favorable for foraging. Eddy determined that *P. occidentalis* ceased activity at light intensities <300 ft. candles and above 7000 ft. candles. Box (1960) reported that *P. barbatus* in south Texas foraged mostly at night. In eastern Arizona, we found that *P. barbatus* ceased foraging at dusk although temperature and moisture conditions were favorable for foraging. This suggests the possibility of geographical differences in the behavior patterns of the same species.

Lavigne et al. (1971) analyzed factors affecting foraging in *P. occidentalis* and found that there were two peaks in activity as measured foragers egress from the colony. Bursts of egress activity were noted in our studies but the return rate of foragers did not result in bursts as such. Since we were interested in predicting the number of fruits brought to the colony per unit time, we felt the return rate to be a more meaningful number.

The technique of using dyed grain for studying foraging intensity and colony interactions was used by Willard and Crowell (1965) in studies of *Pogonomyrmex owyheei*. Their experiments showed that in *P. owyheei* complete overlapping of foraging occurred where mound density was high. They reported variation in foraging intensity as a function of distance and with direction from the nest. An evaluation of their data is complicated by small sample sizes and the extended periods of single observations.

The log decay of foraging effort as a function of distance from the colony indicates a random search pattern. However, when the concentration of forage resource was increased, the foraging effort was increased at that distance. Some foraging occurred at a distance greater than the highly concentrated forage. This indicates that some foragers probably act as scouts and always forage at great distances from the colony. Factors in addition to food concentration and distance may affect the foraging intensity of ants. Wallis (1964) presented evidence that the degree of hunger or satiation of a colony had a direct effect on the foraging intensity of *Formica fusca*. In our studies we found that foraging intensity decreased markedly after we had conducted our dyed seed experiments for several days in succession. When colonies 18 and 62 were excavated, the storage chambers were found filled with dyed grain. In *Pogonomyrmex* we hypothesize that foraging intensity may decrease when storage chambers are filled and/or all workers and larvae are satiated. This aspect of foraging behavior must be quantified before an accurate model of foraging in harvester ants can be constructed.

The variation in success rate of returning foragers is difficult to interpret since success rate was found to be independent of soil temperature, saturation deficit, and hour of the day. Further experiments examining success rate as a function of forage resource distribution may provide the answer to this question. However, this may also be an intrinsic part of the foraging behavior of *P. rugosus* and *N. cockerelli*. *P. californicus* and *P. desertorum* foragers return to the colony at a lower rate than *P. rugosus* and *N. cockerelli*, but few, if any, unsuccessful foragers were observed in the former two. We might hypothesize that foragers of *P. rugosus* and *N. cockerelli* search for a fixed period and return to the nest if unsuccessful and that *P. californicus* and *P. desertorum* search until successful. Experiments designed to test this hypothesis will be conducted in 1973.

There appears to be little if any direct aggressive interaction between workers of different colonies of the same species or of different species. The degree of overlap of foraging territories and the shapes of foraging territories cannot be explained by interaction between colonies. If foraging of colonies were random and unaffected by the foraging activities of adjacent colonies, foraging territories would be circular or nearly so. However, this is not the situation in *P. rugosus* and *N. cockerelli*.

Distortion of the foraging territory appears not to be the result of interaction between colonies. The foraging territory of colony 50 did not change after colony 18, which had a foraging area overlapping with 50, had been completely excavated. The constancy and distorted shapes of foraging territories require explanation but no reasonable hypothesis can be offered.

Forage preferences of *Pogonomyrmex* were not a simple function of seed availability. There appeared to be a correlation between phenology and relative abundance of seeds and their importance as forage items. *Eriogonum trichopes* and *E. abertianum* var. *abertianum*, which set fruit in early June and continued to flower and fruit throughout July and August, were the most important. In July, when *Chenopodium* matured, the fruits of this species increased in importance. These relationships suggest that forage preference may be a function of the forage item previously brought in. Thus both phenology, abundance and rate of maturation of fruits appear to be considerations in forage selection in *Pogonomyrmex*. Selectivity of forage items in *Veromessor pergandei* was reported by Tevis (1958), who pointed out that this species did not gather the most abundant seeds.

The data in this study support the contention of Tevis (1958) that, while the foraging activity of harvester ants has a small effect on the total seed production of annuals, their activity can be significant by affecting the seed reserves of preferred plant species (e.g., *Eriogonum trichopes*). Willard and Crowell (1965) provided a list of plant species foraged by *P. owyheeii*, ranked as to relative abundance in storage chambers excavated, but provided no data on abundance or seed production of plants in the area. Eddy (1970) found that *P. occidentalis* foragers brought in seeds of almost every species of plant in the area and that there was a high correlation between the rank of cover of a plant species and the number of seeds of that species foraged. Additional studies of foraging habits of species of harvester ants in relation to seed production may confirm this hypothesis.

The foraging strategy of *N. cockerelli* appears to be more like that reported for *V. pergandei* (Went et al., 1972), which brings almost anything back to the nest: sticks, leaves, good and bad fruits, dead insects or parts, and fecal material. Foragers of *N. cockerelli* carried a similar spectrum of materials to the colony. Examination of these materials revealed that a preponderance of the foraged items was invaded by fungal hyphae. Even the whole fruits of *Eriogonum* spp. were predominantly infected with hyphae. Examination of the materials excavated from the upper meter of a *N. cockerelli* nest by Crawford and Wooten in their millipede study (1973), revealed numerous large balls of organic material and hyphae in the upper chambers. In addition, there appears to be increased fungal invasion of the soil surrounding chambers of this species. As a consequence of these observations, we suggest that *N. cockerelli* may be culturing fungi as a food source.

2.3.3.2.-60

All of the harvester ant species studied foraged on termites when these were available, and also brought in insect carrion. This is probably important to the health of such colonies by providing a protein source for peak reproduction and growth. With further study we may be able to assess the role of harvester ants as termite predators.

In the species of annuals sampled to obtain predictive equations for plant parts as a function of some easily-measured length dimension, good correlations were obtained for most species except for fruit numbers in *E. trichopes* and *E. abertianum*. These species of *Eriogonum* exhibited nearly continuous growth pattern and fruit production during about 90 days of the growing season. Consequently, when these plants were sampled at a supposed peak in fruit maturity, many of the fruits had been lost even as the plants were growing. This problem can be overcome by placing seed fall traps around the bases of a number of these plants at the beginning of the growing season to obtain data on rate and sum of fruit production, which can be regressed on canopy volume or area. In the other species of annuals, fruit maturation on any one plant was fairly synchronous. Therefore, the relationship of fruit numbers to a canopy dimension could be predicted with fair reliability.

The technique of allometric analysis of annuals and perennial forbs to provide equations for predicting biomass of plant parts appears to have some general applicability, especially where fairly frequent periodic sampling without removal is desirable. Coupling these equations with a plotless technique (point-quarter) for estimating density provides a method for rapid estimation of biomass production, seed production, etc., in an area regardless of the density of annuals. In exceedingly dry years, such as 1971 at the Jornada, the sparsity of annuals makes quadrat sampling an unreliable method for estimating production of annuals, but this is not a criticism of the plotless method.

Forager population and colony size estimates (A3UEE15). The peak forager population sizes recorded in July may in fact reflect the magnitude of total colony size. Two colonies of *P. rugosus* and a *P. californicus* colony excavated in August and September had total populations of approximately 2000 individuals. Mobilizing essentially the entire adult population for foraging at times of peak fruit production and favorable climatic conditions would be an important feature of the social behavior of desert seed-foraging insects. The behavior would insure maximum storage of food items at peak availability. Since ants are limited to selection of seeds or fruits on the soil surface or on plants, wind or water can reduce the available food base very rapidly. We noted virtual disappearance of fruit caches around the base of *Eriogonum* plants following heavy rains. These fruits apparently are transported by surface flow and buried in places where plant materials obstruct sheet flow. These observations suggest that

harvester ants must maximally exploit these resources before they are dispersed or made unavailable by climatic events. We have two sets of soil surface samples obtained prior to and following a sheet flow event. These samples are currently being processed to determine changes in seed availability.

Brian (1971) criticized nest excavation as a means of getting at colony size, stating that with regard to large diffuse colonies, it is easy to be persuaded that the whole colony has been discovered. We are certain that our excavation of the two *P. rugosus* colonies recovered all but an insignificant number of the colony members. Since we were unsuccessful in obtaining the queen in the *P. californicus* excavation, we are not as confident of that colony size estimate.

Brian (1971) also provided a critique of mark-recapture methods. He pointed out that ants and termites remove paint. However, if such studies are conducted over a 24-48 hr period, sufficient paint marks remain to identify recaptures. Consequently we feel that our estimates of forager population size are fairly reliable.

Laboratory experiments in 1971 indicated that rhodamine- (a fluorescent vital stain) dyed food might provide reliable estimates for whole colony populations. In 1972, we attempted to apply this technique to field populations. Metal cone barriers were built to place around colonies to starve them prior to providing rhodamine-dyed seeds. Problems encountered in retaining the colony within the barriers caused this approach to be abandoned in order to obtain other kinds of data.

To the casual observer there appears to be a degree of regularity in the distribution of harvester ant colonies. Our analysis showed a clumped distribution in *Novomessor* and *P. desertorum* and a random distribution in *P. rugosus*. The high degree of clumping in *P. desertorum* may indicate multiple entrances to the same colony. We did not place sufficient emphasis on mark-recapture and excavation in this species to provide an answer to this question. The factors resulting in a clumped distribution in these species require further analysis.

EXPECTATIONS

1. The colony density of harvester ants of the genus *Pheidole* appears to be fairly high in numerous areas in the hot deserts. We shall apply the techniques devised for studies of the larger harvester ants to evaluate the effects of climatic factors on foraging, forager population numbers and foraging preferences.

2. Dr. George Ettershank has continued to experiment with rhodamine-tagging techniques. With his assistance, we will continue field assessment of this technique for estimating population size.

3. We recognize the need for more data on the foraging habits of *N. cockerelli* and *P. rugosus* at night. These studies will be scheduled at regular intervals in 1973.

4. In order to test the generalizations of foraging habits and predictability of preferred species of forage we will study the food habits-plant production relationships in several different plant communities.

5. We will attempt to fill in gaps in our understanding of the foraging behavior of *P. barbatus* and attempt to obtain some data on the enigmatic *P. apache*.

6. The relative success of our 1972 mark-recapture program suggests that continued efforts with that technique plus removal studies may provide reliable estimates of population size.

7. We will continue our studies of oxygen consumption, water loss and temperature relationships to the harvester ant species in our laboratory colonies.

ACKNOWLEDGEMENTS

Special recognition is due George Ettershank, co-author of the 1971 report, who has continued to make significant contributions to this work by his suggestions and continuous input of ideas. James Zimmerman directed the work on this project while I was on sabbatical leave in the spring. Linda Whitford assisted with data summarization. Paul Whitson, John Ludwig and Richard Spellenberg provided valuable ideas for studying annual plants and identified plants and seeds. The diligent efforts of my field assistants are gratefully acknowledged. Their sweat and muscle provided the bulk of the data: Helen Hart, Rebecca Delson, Barry O'Laughlin, Tim Cox, Ken Rall, Fred Dax, Hank Becker, and Beverly Stock. Special thanks are due to my son Brett for providing the simple and very workable idea of clearing circles around ant colonies to study foraging behavior.

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1972 PROGRESS REPORT

COLONY CHARACTERS OF TERMITES AS RELATED TO POPULATION
DENSITY AND HABITAT

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Research Memorandum, RM 73-30

MAY 1973

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Report Volume 3

Page 2.3.3.3.

A B S T R A C T

The balance is shifting from field studies in the Tucson basin, which relate termite populations to the occurrence of dead plant material, toward laboratory work on food-energy relationships and the role of termites in the detritus cycle. Eleven species of termites have been found on the two sites: two dry-wood and three subterranean species at Sil erbell, and three dry-wood has now been accomplished.

Five major woody plants and many lesser species have contributed an estimated accumulation of 2,589 kg/ha of fallen dead wood at Santa Rita. Foraging populations and biomass estimates for the four most important species of termites are as follows: *Amitermes wheeleri* (subterranean), 19.0 foraging groups, 2,375 foragers or 1.1 g/ha; *Paraneotermes simplicicornis* (dry-wood), 7.5 groups, 4,683 foragers or 11.0 g/ha; *Heterotermes aureus* (subterranean), 95,750 foragers or 33.1 g/ha; *Gnathamitermes perplexus* (subterranean), 705,200 foragers or 484.7 g/ha. Incipient colonies of *Marginitermes hubbardi* (dry-wood), started from paired alates, attained a mean colony size of 6.42 individuals (range 3-14) after one year at 32 C.

Paraneotermes consumed 6.70 mg wood/hr/g-dry weight; *Heterotermes* 4.98 mg, both at 28 C. Alates of two dry-wood species contained ca. 10.5% total body nitrogen, and a sample of immatures of one of these produced 5.73 kcal/g, all on a dry weight basis. Amino acid analyses of two species of dry-wood termites indicated that termite protein is similar to other animal proteins in terms of amino acids present.

This continuing accumulation of data now requires that the facts be refined and fitted together to assess the role of termites in the detritus cycle and their importance in producing large seasonal swarms of alates as food for a variety of predators, both vertebrate and invertebrate.

I N T R O D U C T I O N

Complementary field and laboratory work has continued to provide new information on the demography and activity of termite populations, including their relationships with some of the biotic and abiotic factors in the Sonoran Desert. Research begun in 1970-71 for relating these populations to their food supply -- superficial and standing dead wood -- is essentially complete for the Santa Rita site, while determination of annual production rates of dead wood will continue into 1973. Other studies, begun during the same period, have produced data of varying reliability on the estimation of termite populations and biomass, and the determination of foraging territories, periods of foraging activity, plant hosts, and colony development characteristics. Since such information depends heavily on the abundance and accessibility of the different species, refinement of the data can be expected from an extension of pertinent studies well into 1973.

Both dry-wood and subterranean termites subsist on cellulose from a variety of sources, so that it is obviously desirable to document their role in the comminution and decomposition of plant debris. The decision to measure rates of wood consumption by termites, as well as related details of wood utilization, was mentioned briefly in the 1972 proposal and reinforced as a result of interaction with the Problem-oriented Modeling Group. This area of study will be expanded in 1973 and should provide information which is directly related to other Desert Biome projects broadly concerned with the detritus cycle, nutrient cycling, soils, plant growth, and predators.

Further items of research proposed earlier, and to continue into 1973, include analyses of accumulated data on daily and seasonal foraging activity, soil movement and modification by subterranean termites, and seasonal alate production.

O B J E C T I V E S

A number of lesser annual objectives combine to support broad, long-term objectives of the continuing project. Those for the whole project are:

1. To determine the patterns of growth, maturation and decline in colonies of a representative dry-wood and subterranean termite as functions of environmental variables in the Tucson Basin.
2. To study the annual production and dispersal of winged forms of the same two species of termites as functions of colony size and environmental variables, with reference to their availability as food for vertebrates and other arthropods.

Objectives detailed under previously proposed procedures, and which guided the research in 1972 are:

1. Determine the quantity of fallen dead wood available to termites by major woody plant species/ha. Continue estimation of dead-wood production rates.
2. Provide best possible estimates of size, composition, density and biomass of subterranean foraging groups. Data collection for similar estimates on complete colonies of dry-wood species is in progress.
3. Determine daily and seasonal foraging intensities for two subterranean species in terms of hr/yr, based on area foraged and limiting environmental factors (continuing).
4. Evaluate the pattern of colony growth and development for one dry-wood species, including reproductive capacity of founding pairs, appearance, maturation and longevity of castes at constant laboratory temperatures. Continuing, with some data available for one year.
5. Make laboratory determinations of wood-consumption rates by one dry-wood and one subterranean species, in terms of mg wood consumed/hr/g of termite, on a dry weight basis. Determine details of wood utilization by analyzing composition of specific woods, termites, and their fecal material. Continuing, with some data available.
6. Determine chemical and physical changes in samples of soil moved to the surface and worked by subterranean termites (continuing).

METHODS

Fallen Dead Wood Available to Termites

DSCODE A3UNE02. All superficial dead wood in randomly chosen 50-m² circles is plotted, measured and weighed. Other dead plant material is not considered. Each item containing a termite colony or foraging group is bagged in the field, and the termites later extracted and processed according to DSCODE A3UNE04. Data are analyzed to provide estimates of the dead wood available to termites by major woody plant species/ha. Fifty circles have been completed, with several samples/mo between 71 05 03 - 72 06 06, on the natural plot, Santa Rita site. Termite data are recorded on A3UNE04.

Termite Colony or Foraging Group Characteristics

DSCODE A3UNE04. Complete groups of termites collected under A3UNE02 are extracted from the wood, identified, sorted by sex and caste, and counted. Occasional samples of each sex and caste are dried to constant weight at 60 C. Data provide a basis for estimates of size, composition, density and biomass of foraging groups or colonies according to species.

2.3.3.3.-4

DSCODE A3UNE06. Estimates of foraging populations of two subterranean species, *Heterotermes aureus* and *Gnathamitermes perplexus*, have also been made from data collected during activity-environmental studies on the Santa Rita chained plot between 71 10 15 - 72 10 13. Twelve 10 x 10-m plots of toilet paper rolls (100 rolls/plot) were set out with rolls on a grid at 1-m intervals (Figure 1). The surface of the area was first raked clear of all dead wood and each roll wrapped with tape to prevent raveling. *Heterotermes* and *Gnathamitermes* began feeding on the rolls within the first week of the study. Twelve plots were used so that rolls could be examined according to schedule with a minimum of disturbance of the termites. Every roll in a different block of 100 was quickly examined visually at two-hour intervals, during one 24-hour period, once each week. Evidence of past termite activity and an estimate of the number of foragers present in each roll (in size classes of 1-5, 6-50, 51-150, 151-250, 251 +) were recorded. Several environmental variables were also recorded on DSCODES A3UNE07-08.

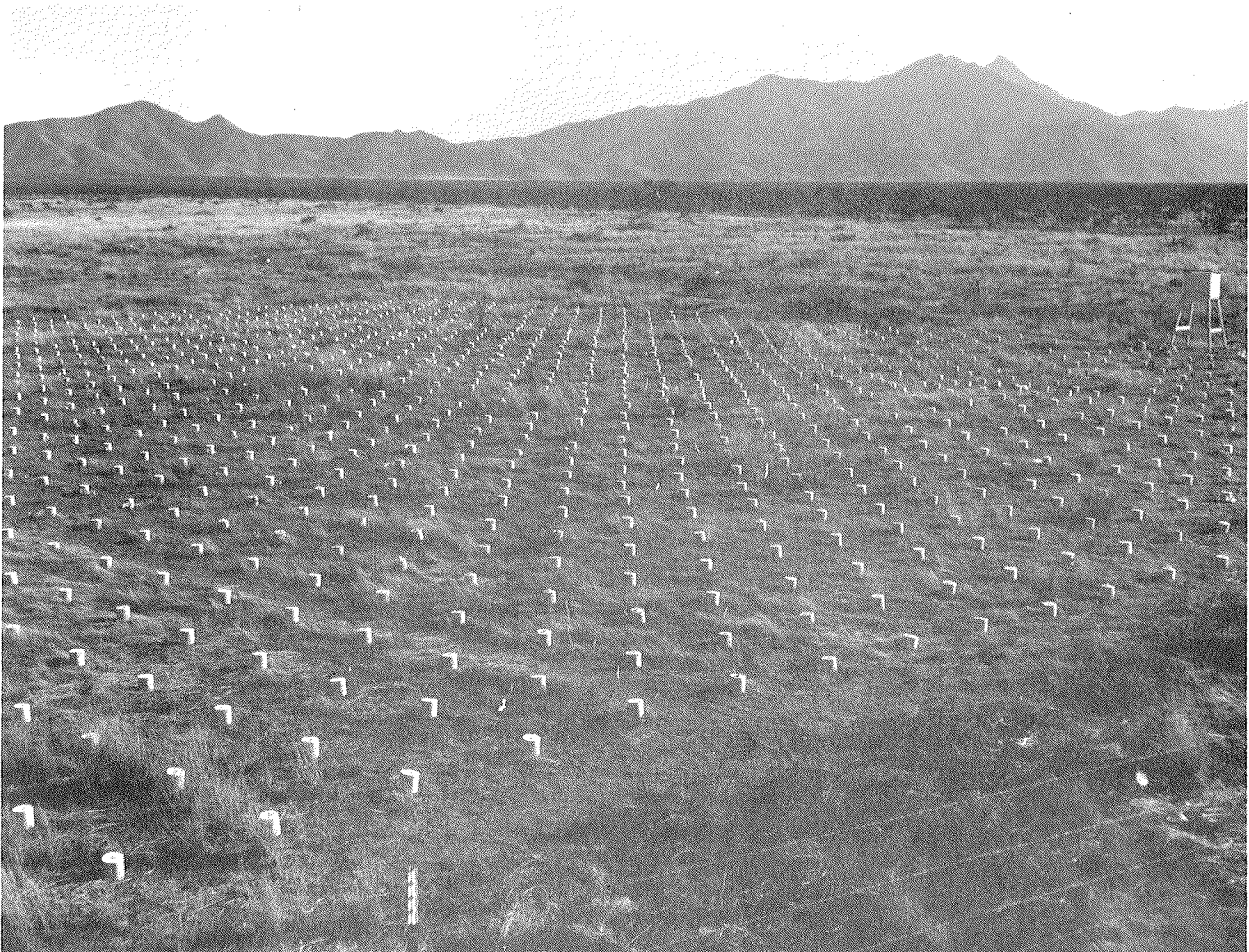


Figure 1. Area for studying subterranean termite foraging behavior on the Santa Rita Site. The lighter area in the foreground was chained about 18 months previously to remove large standing vegetation. (DSCODES A3UNE06-8).

Colony Growth and Development of Dry-wood Termites

DSCODE not yet submitted. In the laboratory, alates of two dry-wood species (*Marginitermes hubbardi* and *Pterotermes occidentis*) were collected during summer flights and paired on weighed pieces of appropriate species of wood (Figure 2). The development of colonies from these pairs is being followed for periods varying from one to three years at several temperatures and 100% RH. The time of appearance, maturation and, hopefully, longevity of the instars and castes are being determined. Data on wood consumption and fecal pellet production from these groups will be used in studies of wood utilization by dry-wood termites.

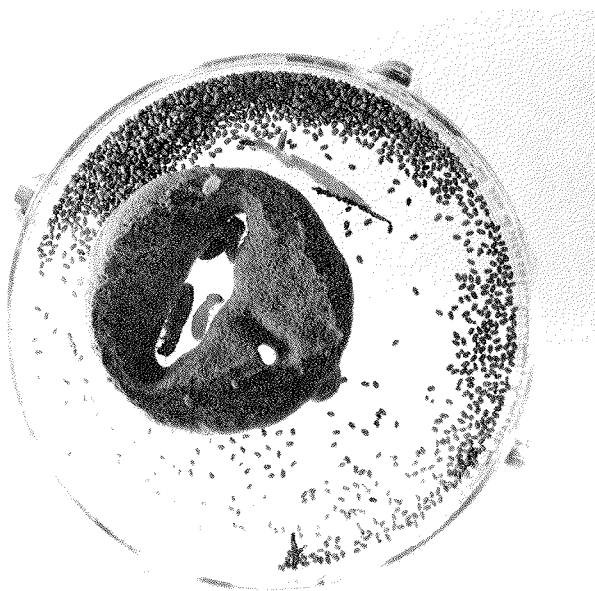


Figure 2. Incipient colony of *Marginitermes hubbardi*, started from reproductive pair, after one year on birch disc at 32 C and 100% RH. The petri dish is 5 cm in diameter and the small particles are fecal pellets.

Food-Energy Relationships

Wood consumption rates of termites. DSCODE not yet submitted. The dry-wood termite, *Paraneotermes simplicicornis*, and the subterranean *Heterotermes aureus* were used to determine rates of wood consumption in the laboratory as functions of temperature and appropriate species of wood. Three replications were made for each species of wood at each of six temperatures (4° intervals from 16-36 C) for 28 days.

Paraneotermes was tested on blocks of wood (*Acacia greggii*, *Opuntia fulgida*, *Prosopis juliflora*) measuring 6 x 25 x 25 mm in pint jars containing 40 ml sterile sand moistened with 16 ml distilled water. Forty-four termites, in typical caste proportions, constituted individual test groups.

Heterotermes was tested on blocks of wood (the same species plus *Cercidium floridum*) measuring 6 x 12 x 12 mm in five-dram vials containing 10 ml sterile sand and 4 ml distilled water. One hundred termites, in typical caste proportions, made up the test groups.

Drying the wood blocks to constant weight at 105 C before and after the tests provided the raw data for calculating consumption rates to varying degrees of refinement.

Nitrogen content of termites. No DSCODE submitted. Total nitrogen content of the alates of two species of dry-wood termites, *Pterotermes occidentis* and *Marginitermes hubbardi*, was measured in several different groups of each species by the micro-Kjeldahl method.

Amino Acid Analyses of termites. No DSCODE submitted. The amino acid balance of total termite protein was determined with a Beckman Automatic Amino Acid Analyzer, Mod. 121. Alate samples of two dry-wood termites, *Marginitermes hubbardi* and *Pterotermes occidentis*, were prepared for analysis by hydrolysis in constant-boiling HCl (ca. 6N) under nitrogen for four hours at 145 C. Several adequate samples of each species were used which varied in dry weight from 5.2-85.7 mg, depending on the availability of the alates during the flight season.

Caloric content of termites. No DSCODE submitted. Gross energy content of a single sample of larvae and nymphs of *Marginitermes hubbardi*, with a dry weight of 0.881 g, was determined in a Parr Oxygen Bomb Calorimeter.

RESULTS

2.3.3.3.-7

List of Termites Found on Sonoran Desert Sites

Data filed in DSCODES A3UNE01-04 have provided the following list of four dry-wood and seven subterranean termites found on the Santa Rita (SR) and Silverbell (SB) sites to date. The most important species are starred (*).

SUBTERRANEAN	DRY-WOOD
<i>Amitermes emersoni</i> (SR)	<i>Incisitermes banksi</i> (SR)
<i>Amitermes minimus</i> (SR)	* <i>Marginitermes hubbardi</i> (SB)
<i>Amitermes silvestrianus</i> (SR)	* <i>Paraneotermes simplicicornis</i> (SR)
<i>Amitermes wheeleri</i> (both sites)	* <i>Pterotermes occidentis</i> (both sites)
* <i>Gnathamitermes perplexus</i> (both sites)	
* <i>Heterotermes aureus</i> (both sites)	
<i>Tenuirostritermes tenuirostris</i> (SR)	

Several species, particularly of *Gnathamitermes*, *Heterotermes*, *Marginitermes*, *Paraneotermes* and *Pterotermes*, have been used rather opportunistically in experimental studies depending on their abundance, ease of maintenance, and survival or other characteristics.

Fallen Dead Wood Available to Termites

Analysis of the dead-wood data from the 50 circles completed on the natural plot at Santa Rita is presented in Table 1. This part of the study is complete, but additional data in A3UNE02, locating the wood in each circle, might eventually be used to relate the dispersion of termite colonies to that of the dead wood.

Table 1. Field weights of fallen dead wood by species, based on fifty 50-m² circles completed. Santa Rita Undisturbed Site DSCODE—A3UNE02

Species	Mean wt/circle ± 95% CI	Range/circle kg	Est kg/ha
<i>Acacia greggii</i>	3.534 ± 2.515	0-42.412	707
<i>Opuntia fulgida</i>	2.303 ± 1.419	0-21.489	461
<i>Prosopis juliflora</i>	2.046 ± 1.490	0-33.680	409
<i>Opuntia joints</i>	1.942 ± 0.998	0-15.621	388
<i>Opuntia spinosior</i>	1.936 ± 0.635	0- 9.724	387
<i>Cercidium floridum</i>	0.858 ± 1.225	0-30.873	172
<i>Celtis pallida</i>	0.105 ± 0.167	0- 4.224	21
<i>Opuntia engelmannii</i>	.068 ± 0.063	0- 1.077	14
<i>Ephedra trifurca</i>	.060 ± 0.047	0- 0.964	12
Cow chip	.009 ± 0.012	0- 0.225	2
Other*	.084 ± 0.084	0- 2.031	17
Total	12.945 ± 3.120	0.595-45.303	2,589

* "Other includes *Aloysia wrightii*, drift *Echinocereus fendleri*, *Encelia frutescens*, *Ferocactus wislizenii*, *Gutierrezia sarothrae*, rabbit pellets, and a few unidentified perennials.

† Biomass based on the following dry weights: larva-worker, 0.336 mg; soldier, 0.479 mg; nymph, 1.053 mg; larva, 0.264 mg.

Termite Colony or Foraging Group Characteristics

A detailed analysis of the foraging population of *Heterotermes* at Santa Rita is presented in Table 2. Although this termite is extremely common in the Sonoran Desert, estimates of mature colonies numbering in the tens of thousands and of the underground force outnumbering foragers by 10:1 remain rather speculative.

Table 3 summarizes our best estimates on populations of the four species which are apparently most abundant on the Santa Rita site. The two foraging population estimates for *Heterotermes* are encouragingly close in spite of the different experimental designs of the two methods of estimation. The same certainly cannot be said for the estimates for *Gnathamitermes*. The disparity in the estimates made by the two methods may reflect differences in foraging behavior patterns: *Heterotermes* forages intensively within relatively stable and limited areas, while *Gnathamitermes* seems to forage over wide and changing areas.

Table 2. Composition, density and biomass of 40 foraging groups of *Heterotermes aureus* collected in fifty 50-m² circles. Santa Rita Undisturbed Site.
DSCODE— A3UNE02, -04

No. circles	50
Avg. no. groups/circle	0.80
Avg. group composition:	
Larva-workers	418.8 ± 195.7 (±95% CI)
Soldiers	6.7 ± 3.3
Nymphs	4.6 ± 6.2
Larvae	0.5 ± 0.7
Total	430.5 ± 198.7
Ave. group weight, mg	148.9
Est. groups/ha	160
Est. termites/ha	68,880
Est. biomass/ha,g [†]	23.824

Table 3. Foraging group size, density, biomass and nitrogen content¹ of four species of termites on the Santa Rita Site. DSCODES—A3UNE02, -04, -06

Species	Ave Group Size	Ave Group wt, mg	Est Groups /ha	Est Termites /ha	Est Biomass /ha,g	Est N In Biomass /ha,g
<i>Gnathamitermes perplexus</i>	--	--	--	705,200 ²	484.7 ²	50.89 ¹
	55	37.8	64.0	3,520 ³	2.4	0.25
<i>Heterotermes aureus</i>	--	--	--	95,750 ²	33.1	3.48
	431	148.9	160.0	68,880 ³	23.8	2.50
<i>Paraneotermes simplicicornis</i>	624	1,470.9	7.5	4,683 ³	11.0	1.20
<i>Amitermes wheeleri</i>	125	57.4	19.0	2,375 ³	1.1	0.12

¹ See METHODS and RESULTS sections on Food-Energy Relationships: Nitrogen Content of Termites.

² Based on maximum no. of foragers found in Plot 1 of Toilet Paper Plots, A3UNE06.

³ Based on average figures from groups found in fifty 50-m² circles, A3UNE02.

Colony Growth and Development of Dry-wood Termites

Of 145 pairs of *Marginitermes* set up in August, 1971, 61 survived for one year at 32 C and 100% RH. Some of these were then terminated and the rest examined and allowed to continue for another year. Fifty-three of these contained one or two reproductives and should continue (or should have continued) as viable colonies. The remaining eight contained no reproductives and probably would not have survived. Eggs appear to be laid periodically, even under constant conditions, since initial production occurred within approximately the first three weeks and resumed eight to ten months later for several weeks. The composition of an average one-year colony is given in Table 4. Colony development of termites beyond the first two or three years can probably be worked out from complete counts of natural colonies. Such data are being accumulated in A3UNE04.

Table 4. Average caste composition of an incipient colony of *Marginitermes hubbardi* after one year at 32 C and 100% RH, based on 53 colonies

Caste	Mean no., \pm 95% CI	Range
Reproductive	1.53 \pm 0.17	0- 2
Larva	4.04 \pm 0.61	0-11
Soldier	0.85 \pm 0.15	0- 2
Egg	0.28 \pm 0.25	0- 5
Total	6.42 \pm 0.69	3-14

Food-Energy Relationships

Wood consumption rates of termites. Consumption rates of different woods by test groups of *Paraneotermes* (44/group) and *Heterotermes* (100/group) were determined in three different ways: mg of wood consumed/group/28 days, mg of wood consumed/group/days survived, and mg of wood consumed/hr/g-dry weight of termites. Total test means of these rates at each temperature, and of each host species at all temperatures, are listed in Table 5. Total group consumption rates are not especially accurate since they do not consider termite survival. Percent survival (Table 5) was rather low, especially for *Heterotermes*, but certainly considerably lower than in a field situation. However, survival has been accounted for in the daily and hourly rates so that these values should be more accurate. Consumption/hr/g-dry weight of termites will permit direct comparisons on a species basis and can serve as rates for modelling purposes.

As expected, both species consumed more wood as temperature increased. The increase appears to be linear within the limits of 16-32 C (Table 6). Although survival of *Paraneotermes* decreased with rising temperature, there is little suggestion of an optimum temperature within this range for *Heterotermes*. This may be related to *Paraneotermes*' habit of working buried wood, and *Heterotermes*' apparent preference for superficial wood.

Wood consumption has also been measured for 20 of the 53 colonies of *Marginitermes hubbardi* which have successfully completed one year of development. The mean value of wood consumed by these one-year colonies at 32 C was 622.24 \pm 96.03 mg (CI₉₅). For eight other colonies, wood consumption and fecal pellet production were measured and plotted in Figure 3 to show the positive correlation between the two processes.

Table 5. Wood consumption by two species of termites, *Paraneotermes simplicicornis* and *Heterotermes aureus*, at several temperatures, on various species of wood, for 28 days

Treatment	Percent Survival	Mg wood Consumed/grp (Survival Disregarded)	Mg wood Consumed /grp/day (Survival Considered)	Mg wood consumed /hr/g-dry wt of Termite
<i>Paraneotermes simplicicornis</i> (group size = 44)				
All woods at:				
16 C	91.16 a *	151.40 b	5.398 c	2.21 c
20	95.71 a	243.79 a	8.684 bc	3.56 bc
24	91.92 a	321.52 a	11.484 ab	4.70 ab
28	61.36 ab	324.04 a	16.439 a	6.70 a
32	66.92 ab	345.76 a	13.971 a	5.82 a
36	53.79 b	298.01 a	15.739 a	6.54 a
All temperatures on:				
PROJUL**	68.56 a	303.37 a	15.088 a	6.20 a
ACAGRE	77.50 a	306.37 a	11.899 b	4.88 b
OPUFUL	84.34 a	232.40 b	8.870 c	3.68 b
<i>Heterotermes aureus</i> (group size = 100)				
All woods at:				
16 C	26.08 a	50.18 c	1.89 c	2.34 b
20	47.67 a	55.53 bc	2.37 bc	2.93 b
24	59.42 a	77.85 ab	3.27 ab	4.06 a
28	44.92 a	78.23 ab	4.04 a	4.98 a
32	58.92 a	97.53 a	4.13 a	5.09 a
36	55.83 a	97.97 a	3.51 a	4.33 a
All temperatures on:				
CERFLO	53.83 a	140.77 a	5.05 a	6.23 a
OPUFUL	58.67 a	65.69 b	2.78 b	3.44 b
PROJUL	39.39 a	42.02 c	2.60 b	3.21 b
ACAGRE	43.33 a	56.37 bc	2.37 b	2.93 b

*Means followed by the same letter are significantly different at the 95% level by Student-Newman-Keuls' test.

**Species of wood: ACAGRE, *Acacia greggii*; CERFLO, *Cercidium floridum*; OPUFUL, *Opuntia fulgida*; PROJUL, *Prosopis juliflora*.

Table 6. Regression equations and coefficients for wood consumption (all wood species lumped) by *Paraneotermes simplicicornis* and *Heterotermes aureus* against temperature (16-36 C)

Variable	Equation	Coefficient
<i>Paraneotermes</i>		
Mg wood consumed/grp (Survival disregarded)	$y = 7.45x - 87.06$.77 ^{NS*}
Mg wood consumed/grp/day (Survival considered)	$y = 0.52x - 1.52$.90**
Mg wood consumed/hr /g-dry wt of termite (Survival considered)	$y = 0.22x - 0.73$.91**
<i>Heterotermes</i>		
Mg wood consumed/grp (Survival disregarded)	$y = 2.61x + 10.98$.97†
Mg wood consumed/grp/day (Survival considered)	$y = 0.10x + 0.58$.84**
Mg wood consumed/hr /g-dry wt of termite (Survival considered)	$y = 0.12x + 0.73$.84**

*NS = non-significant regression

**Regression significant at the 95% level.

†Regression significant at the 99% level.

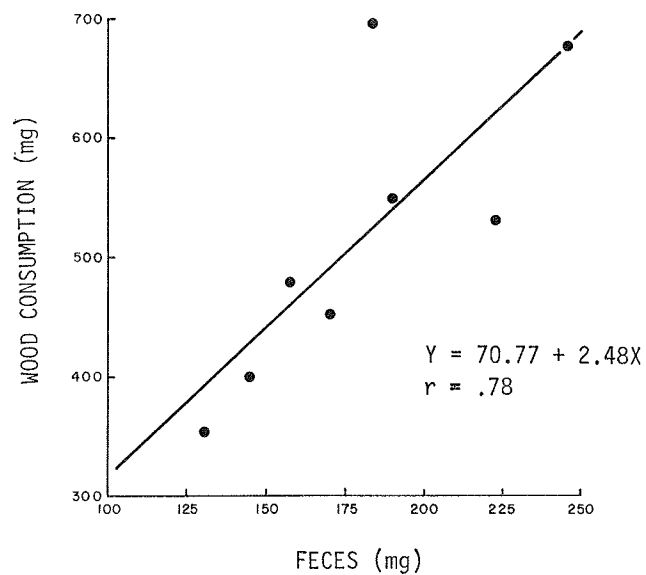


Figure 3. Regression of wood consumption on fecal material production for eight one-year colonies of *Marginitermes hubbardi* reared on birch discs at 32 C.

Nitrogen content of termites. The studies included below on nitrogen content, amino acid balance and caloric content are only a beginning but, since such information is scarce or simply not available, the results are considered important enough to include here. The percentages of nitrogen in winged forms of two dry-wood species are given in Table 7. The best current estimate of total body nitrogen, ca. 10.5%, has therefore been taken as a basis for reporting grams of nitrogen/ha for the four important species in Table 3.

Table 7. Total body nitrogen (N) on a dry weight basis for alates of two dry-wood termites

Species	Sex	No. of Alates	No. of grps	Total Dry wt mg	Total N, mg	Total N% \pm 95% CI
<i>Pterotermes occidentis</i>	M	32	4	266.4	26.48	9.94 \pm 0.85**
	F	24	3	207.0	21.36	10.32 \pm 1.54
<i>Marginitermes hubbardi</i>	M	194	9	586.4	64.09	10.93 \pm 0.66
	F	92	8	283.3	31.05	10.96 \pm 0.51

*Number of *Pterotermes* alates used, 8/group; of *Marginitermes*, 8 to 80/group.

**Mean percentage of total N based on group means of each species.

Amino Acid analyses of termites. The amino acid balance of total protein in two species of dry-wood termites has been determined (Table 8). The balance for each species is very similar although absolute values differ, perhaps as a result of differences in fat content.

Caloric content of termites. The heat of combustion produced from a single sample of the dry-wood termite, *Marginitermes hubbardi*, (larvae and nymphs) was equivalent to 5.73 kcal/g-dry weight. This value may be expected to vary considerably from caste to caste, and with seasonal changes in body fat content.

Table 8. Analysis of total body amino acids present in alates of two species of dry-wood termites

Amino Acid	Mean % of Dry Weight, All Samples	
	<i>Pterotermes occidentis</i> *	<i>Marginitermes hubbardi</i> **
Lysine	3.540	1.805
Histidine	1.702	0.855
Arginine	3.419	1.677
Aspartic acid	4.669	2.369
Threonine	2.262	1.155
Serine	1.973	1.005
Glutamic acid	7.303	3.691
Proline	3.833	2.000
Glycine	6.955	2.664
Alanine	5.011	2.401
Valine	3.720	1.901
Methionine	0.920	0.450
Isoleucine	2.692	1.200
Leucine	4.427	2.203
Tyrosine	3.311	1.723
Phenylalanine	2.181	1.142

*Based on four samples ranging from 10.0-18.3 mg (dry wt).

**Based on six samples ranging from 5.2 - 85.7 mg (dry wt).

DISCUSSION

Segments of work on the Santa Rita site begun in 1971 or earlier are practically complete, namely those dealing with the population characteristics of the termites, and with the quantities of superficial dead wood available to them. As a natural extension of these subjects, emphasis shifted during 1972 to several details related to the role of termites in the detritus cycle. Mark Westoby's model "TERMITE", designed to answer questions about the interactions between termites (4 species), dead wood (4 species) and critical abiotic factors (temperature at present) for a period of something like 20 years, has provided a helpful framework for much of the field and laboratory work.

The list of ten species of termites for Santa Rita contains most of the species expected, except perhaps for two or three highly specialized subterranean species of *Amitermes*. Good estimates of foraging populations and biomass have been made for four of the important species; however, the best that can be said about total populations of the subterranean species is that the foragers may represent about 10% of the total.

Although termites apparently attack all types of dead plant material, the accumulation of superficial dead wood at Santa Rita (2,589 kg/ha) and its production rate (current estimate, 349.4 kg/ha/yr) are impressive. Determinations of wood consumption rates by a subterranean species (*Heterotermes*), 4.98 mg/hr/g-dry weight of termite, and by a dry-wood species (*Paraneotermes*), 6.70 mg/hr/g-dry weight of termite at 28 C, compare favorably with rates reported in the literature. *Mastotermes darwiniensis* (closely related to the dry-wood termites) consumes 1.96 mg/hr/g-dry weight (Gay et al., 1955), and *Reticulitermes flavipes* (subterranean), 7.08 mg/hr/g-dry weight of termite (Smythe and Carter, 1970). These values have been adjusted for comparison with our own, although they were determined at 26 C and do not include corrections for survival. In general it appears that wood consumption rates are inversely related to termite body weight. What is next needed is to relate termite populations to the availability and dispersion of dead wood, and to determine their share in its decomposition.

A search for details of food-energy relationships among the invertebrates reveals a broad information gap for the insects in general and the termites in particular. In order to describe or predict increase in biomass for the problem-oriented models -- "TERMITE", for example -- one should know the portion of gross food energy ingested which is available to a termite population for maintenance and production, i.e., net energy. Studies on the year-by-year development of dry-wood termite colonies, reported on here for one year, will eventually provide data on the metabolizable energy available in one species of wood. Nitrogen retention studies in progress will be useful in determining the nitrogen requirements of termites. Amino acid balance is being determined in anticipation of further work on amino acid requirements, sources of amino acids in wood, quality of termite protein as food for predators, and related nutritional studies.

The rather high percentage of nitrogen reported here indicates that the nitrogen requirements of termites are comparable to those of other animals. All amino acids tested for have appeared in appreciable quantities in the two species examined, indicating that termite protein is similar to other animal proteins in terms of amino acids present. A suitable conversion factor for adjusting total nitrogen to total protein has not yet been established for termites.

An estimate of food energy content, calculated by the Atwater factors for protein, fat and total carbohydrate by difference, was given for a dried sample of unstated caste and species of an African termite (Leung, 1968, p. 175). The value reported, 6.56 kcal/g-dry weight, cannot be compared directly with our figure as it represents metabolic rather than gross energy. The dried termites contained a high percentage of fat (54.3%), suggesting that alates were used for the caloric determination.

The continuing accumulation of facts in all of these areas requires that the facts be refined and fitted together to assess the role of termites in the detritus cycle and their importance as producers for a variety of predators, both invertebrate and vertebrate. This can probably best be done within the framework of a submodel, such as "TERMITE", which has not only sharpened the direction of certain studies but improved the basis for assessing their priority and required levels of accuracy as well.

EXPECTATIONS

The following research, largely an extension of work begun in 1972 or earlier, is planned for 1973. A substantial amount of time needs to be spent in analyzing and preparing for publication the data already at hand.

1. Complete data collection and determine production rates, by species, of fallen dead wood at Santa Rita.
2. Refine information on foraging group and colony characteristics: composition, size, density and biomass based on field data, and dynamics of early colony development from laboratory colonies of selected dry-wood species.
3. Determine rates of wood consumption for additional species and relate rate to body weight for these and other species reported in the literature.
4. Analyze activity-environmental data (toilet paper plot) on *Heterotermes* and *Gnathamitermes* with respect to:
 - a. Environmental restraints on foraging activity.
 - b. Foraging intensity, area covered, time of day and year.
 - c. Cellulose consumption.
 - d. Soil movement, and modification of its chemical and physical characteristics by termites.
5. Alate production per colony and per hectare for some of the important species.
6. Investigate certain food-energy relationships, with emphasis as follows:
 - a. Determine metabolic energy values for several termite-wood combinations.
 - b. Conduct nitrogen retention studies and relate nitrogen requirements to sources of nitrogen for at least one dry-wood termite.
 - c. Determine gross energy values for several species and castes.

ACKNOWLEDGEMENTS

We appreciate the assistance and inspiration provided by the Problem-oriented Modelling Group, especially Mark Westoby, who built "TERMITE" in response to some of our early questions about the interactions between termites, dead wood, and critical abiotic factors.

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1972 PROGRESS REPORT

THE ROLE OF *Orthoporus ornatus* MILLIPEDES
IN A DESERT ECOSYSTEM

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Research Memorandum, RM 73-31

MAY 1973

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A B S T R A C T

The role of the large and abundant desert millipede, *Orthoporus ornatus*, is being studied at the Jornada Validation Site, and also at sites in Big Bend National Park, Texas, and at Albuquerque, New Mexico. Because of its size and abundance *O. ornatus* is assumed to be an important detritivore, and therefore of consequence in nutrient cycling in the desert.

Periods of major activity coincide with rainfall occurring during the warmer months of the year. Early warm-season rains appear to trigger annual molting and surface appearance. Once on the surface, the opportunity exists for dispersal, mating, oviposition, and feeding. Eggs are laid in underground caches and small instars are seldom seen above ground. During most of the year *O. ornatus* remains underground in a relatively quiescent state. A substantial proportion of the Jornada population overwinters in the nests of the harvester ant, *Novomessor cockerelli*.

Potential fecundity ranges from about 330 eggs to 400 eggs. Mature females usually represent only a small portion of a population. Age structure as determined by frequency distributions of midsegment widths varies considerably with different populations.

Surface density estimates range from a mean of 67/ha (Jornada) to 733/ha (single Big Bend estimate). Standing crop in the latter estimate compares favorably with published values for dense populations of woodland millipedes.

The desert millipede ingests mainly dead organic material (often including bark of desert shrubs), as well as moist soil. It feeds most often between about 20 C and 30 C; ingestion rates more than double in this range. Assimilation percentages are high for a detritivore, ranging from about 24% to 38% at these temperatures. Monthly respiratory metabolism is somewhat temperature dependent, but rises out of proportion to temperature increase during surface activity, when respiratory energy expenditure is nearly 500 cal/g.

INTRODUCTION

The role of soil invertebrates in turnover of organic matter and nutrients is beginning to be understood, especially in mesic ecosystems (Edwards et al., 1970). These animals are instrumental in disintegrating, chemically changing, and increasing the surface area of plant litter so that it can be utilized by decomposer organisms and thereby recycled within the system.

Prominent among the detritivorous soil invertebrates are millipedes (Arthropoda: Diplopoda). These can reach very high population densities (Banerjee, 1966; Blower, 1970; Dowdy, 1968; Saito, 1967; and Shaw, 1968). Although complete life histories are known for relatively few millipede species (Blower and Gabbut, 1964; Blower and Fairhurst, 1968), there have been a number of studies detailing aspects of their population energetics (Byzova, 1967; O'Neill, 1968; Phillipson, 1967; and Saito, 1967).

Little is known of invertebrate soil detritivores in desert ecosystems; however, IBP-supported process studies on ants will probably reveal that some desert species play an important role in the turnover of organic materials. Extensive work on termite activity is now being conducted in the Sonoran Desert by Nutting, as part of an IBP process study.

One of us (C.S.C.) acted as a consultant for the IBP/Desert Biome on preliminary studies of the desert millipede *Orthoporus ornatus* (Diplopoda: Spriostreptidae) during the summers of 1970 and 1971 at the Jornada Validation Site. From observations made then it was concluded that *O. ornatus* was large and abundant enough to warrant further investigation as a desert detritivore of considerable potential. It has a unique ability (for a millipede) to resist desiccation (Crawford, 1972), which enables it to remain on the desert surface and feed for a matter of days following summer rains. Consequently, we began to study its general role in the desert, assuming that when sufficiently abundant it could play an important part in the flow of nutrients in the desert.

Because of information herein reported, we continue to adhere to the view that *O. ornatus* can be an important desert detritivore. In the coming year we hope to obtain data that will show the extent to which a population actually removes and processes nutrient material in a desert ecosystem.

OBJECTIVES

These are essentially the same as in the original process study proposal. They are given below, together with qualifications more recently added.

1. To reveal various details in life history. Recent emphasis has been on phenology and reproductive attributes.
2. To estimate potential fecundity.
3. To estimate diel activity in terms of periodicity and surface dispersal.
4. To estimate density and biomass. Preliminary density estimates have been made; biomass studies are being deferred until next year. Age structure estimates have been and will be made in connection with these studies.
5. To record kinds of food eaten in the desert and to measure attributes of ingestion.
6. To determine assimilation values as a prerequisite for the establishment of an energy budget. This objective was not specifically stated as such in the original proposal.

METHODS

Life history

Field observations at the Jornada Validation Site, on the West Mesa in Albuquerque, N.M., and at Big Bend National Park, Texas, were used to record life history data. Phenological information was made possible in large part by monthly excavations with shovels of *Novomessor cockerelli* harvester ant nests (except for July) at the Jornada site in order to obtain samples for respiratory metabolism (DSCODE A3UCF01). In addition, a trip was made in late May and early June to Big Bend to study density and to make observations on life history. Excavations in the soil were made with spoons and revealed sites of egg chambers.

Potential fecundity

Estimates of potential fecundity were accomplished by dissecting large females and counting enclosed eggs when present. Size categories of these eggs were based on measurements with an ocular micrometer (see DSCODE ACU3F01).

Diel activity

Aside from general observations on this phenomenon with respect to ambient conditions, one of us (R.C.W.) spent two diurnal sessions recording millipede activity in a

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marked hectare plot near the Jornada playa. Indirect evidence from laboratory feeding experiments was used to demonstrate nocturnal feeding.

Density

Density estimates were made by the following methods: 1) ant nest excavation mentioned above, 2) single counts of surface-located specimens made on 1.6 km of dirt road (3.5 m wide) near the Jornada playa, 3) single counts of all specimens in a given plot on either the Jornada site or in Albuquerque, and 4) a regression method in which cumulative removal is plotted against numbers removed each time from a sealed-off area (Petrusewicz and Macfadyen, 1970, p. 73).

Age structure has so far been estimated by width measurements of middle segments made with a micrometer (see DSCODE A3UCF01).

Food, ingestion, and assimilation

Field observations were made of different materials eaten.

Ingestion rates were studied in experiments also designed to measure assimilation percentage. The procedure first involved drying sections of *Ephedra* (Mormon tea) stems at 60 C for 24 hr. These were previously cut to equal lengths. *Ephedra* bark is a common food of *O. ornatus* at the Jornada site, where all specimens used in feeding tests were obtained.

Each experimental unit was treated in the following manner: After being placed in a desiccator until a constant weight was reached, 4 *Ephedra* sections were then placed, together with a millipede and 2 g of soil (treated initially as was the *Ephedra*), in a large plastic shoe box. Several series of millipedes were so treated; they had been initially conditioned to an identical situation for 5 days. Twice a day 1 cc of water was added to the soil in each box. Temperatures and photoperiods were controlled.

Ephedra bark consumption over the ensuing 5-day period was determined by weighing the *Ephedra* sections before and after the experiment. A correction factor for atmospheric absorption of water was obtained from control sections and used to adjust ingestion values. Soil consumption was measured by weighing the uningested soil following drying at 60 C for 24 hr.

A muffle furnace was used to determine the ash-free weights of food consumed and feces produced. *Ephedra* bark collected at the same time as that used for food was ashed at 500 C for 18 hr, and feces produced were ashed under the same conditions

after first being ground in a Wiley mill. The ash-free value of soil was determined similarly, but without grinding. All ash-free values were determined from material that was previously at a constant dry weight.

Methods of calculating ingestion rates and assimilation percentages are indicated in Table 6.

Respiratory metabolism

Monthly metabolic rates were determined by use of a Gilson differential respirometer (see DSCODE A3UCF01). Specimens to be tested were acclimated for at least 48 hr in soil maintained at approximately mean ambient soil temperature for that time of year. Specimens were then each exposed to three, 1-hr respirometer runs at that temperature. When the runs were complete each specimen was acclimated for another 48 hr at 20 C, and then tested in the respirometer as before, but at 20 C. Averages of the 3-hr runs were used in expressing respiration rates.

Measurement of carbon dioxide production for respiratory quotient (RQ) estimation was accomplished by recording pressure changes in the respirometer in the absence of the usual carbon dioxide absorbent (Ascarite) from the reaction vessels. The difference between oxygen consumption (in microliters) and the change recorded in the absence of Ascarite constituted carbon dioxide production.

Conversion of recorded values of oxygen consumption to caloric values was performed by using the estimated RQ value and tables of caloric values in Brody (1945).

RESULTS

Life history

Mating was observed on several occasions in the daytime on the soil surface and in shrubs at Big Bend in late May. It was also seen once in mid-August on the soil surface 56 km west of Lordsburg, N.M. On both occasions heavy rains had fallen the previous day and many millipedes were on the surface. Mating can proceed for at least 0.5 hr. Mating pairs were intermittantly noted when many mature *O. ornatus* were kept together in a collecting container.

Oviposition by a captive female (from Big Bend) occurred once. She deposited about 30 eggs, each covered with a fecal coating, in a group beneath the soil. At

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Big Bend 3 caches of between 100 and 200 eggs were discovered in separate chambers about 15 cm beneath the surface of a mound that was probably formed at the base of an old *Opuntia* cactus plant. All of the eggs at Big Bend appeared to be old, many having small holes in the fecal covering. Attempts to properly incubate eggs have not yet resulted in hatching.

Emergence of early instars from the mound described above took place in late May following heavy rains. These small specimens appeared too large to have just emerged from the eggs found in the mound and may have hatched a year earlier. These and other groups of small instars exhibited a decidedly clumped dispersion. They were feeding on debris and on dead leaves of a plant tentatively identified as *Senecio*. They were only present on the surface when the surface was moist.

Overwintering takes place underground; in fact, as Table 1 shows, about three-fourths of the year is spent in subterranean residence. As is indicated below, a diapause-like state exists during the coldest part of the winter. At the Jornada site probably no more than half of the specimens over 3 cm in length overwinter in nests of *Novomessor cockerelli* (see Table 4), where they are coiled adjacent to galleries. Sexually mature specimens are rare in these nests but extensive digging has not revealed them elsewhere.

Molting at the Jornada site occurred in late spring following the first major precipitation of the year (Table 1). Just prior to that time appears to be a critical period relative to survival: all 12 premolt specimens collected on June 5 died within 2 days in Albuquerque, whereas the 6 postmolt specimens simultaneously collected did not.

The relationship of precipitation to surface phenology of *O. ornatus* is depicted in Table 1.

Potential fecundity (see DSCODE A3UCF02)

Mature females were not common in *Novomessor* nests. Therefore, the apparent progression of maturity with season shown in Table 2 may be somewhat misleading. Table 2 does suggest, however, that egg maturation occurs significantly only after molting has occurred (see also Table 1).

Data from Tables 2 and 3 indicate that mean potential fecundity in this species over a wide geographical range approximates 400 eggs, with the value for Jornada specimens being about 330. At times of collection no more than about half of those eggs were mature.

Table 1. Surface phenology of Jornada *Orthoporus ornatus* in 1972

Date	Events observed	Recent precipitation*	Soil conditions (means)			
			Date of measure	Temp (C)	Moisture pot. (bars)	45cm
6/3	First surface specimens		5/16	19	23	-112
6/4	First molts	31mm 6 days before, 103mm 20 days before	6/16	21	24	-26
Late June	Few large surface specimens	606mm in June (total)	6/21	28	28	-7
7/7	Few small surface specimens	75mm 3 days before, 62mm 15 days before	7/6	27	29	-93
7/21-24	Maximum surface specimens	246mm 2 days before, 426mm in previous 10 days	7/28	29	30	-17
8/24	All subterranean	31mm in previous 16 days	8/16	29	28	-108
						-86

*Between 1/1 and 5/13 only 59mm were recorded.

**45cm soil temperatures previously recorded were 23C (5/13), 20C (4/08), 16C (3/11), and 6C (2/4).

Table 2. Egg counts from dissected female *Orthoporus ornatus* dug from *Novomessor cockerelli* nests on Jornada Experimental Range, N.M. (DSCODE—A3UCF02)

1972 Collection dates	No. of females collected & examined	Mean diam. width (mm)	Mean no. of eggs/female		Mean total no. of eggs/female
			Immature (<0.5mm)	Developing (0.5-1.5mm)	
March 18	1	5.1±0.0	299.0±0.0	----	299.0±0.0
April 15	4	4.8±0.2	312.5±27.6	----	312.5±27.6
May 20	0	----	----	----	----
June 9	2	8.3±0.0	332.5±4.5	43.0±9.0	375.5±4.5
July 6	9	7.1±0.7	258.7±36.3	97.3±3.0	331.4±13.5
				121.0±29.7	

Table 3. Egg counts from dissected female *Orthoporus ornatus* in 1972 (DSCODE—ACU3F02)

Places & dates on collection	No. of females collected & examined	diam. width (mm)	Mean no. of eggs/females		Mean total no. of eggs/female
			Immature (<0.5mm)	Developing (0.5-1.5mm)	
Big Bend, 5/30-6/2	9	9.3±0.2	106.6±17.3	65.0±9.4	215.0±19.7
Jornada*, 3/18-7/6	16	6.5±0.5	283.9±22.2	75.6±13.9	121.0±51.4
Lordsburg, 8/11	3	8.1±0.0	124.0±3.8	127.0±12.7	216.0±6.8
Albuquerque, 7/25	4	8.0±0.0	201.5±10.7	167.5±4.8	80.0±13.7

*All specimens from Jornada Experimental Range, N.M., were dug from harvester ant (*Novomessor cockerelli*) nests.

Diel activity

Hourly counts of numbers of *O. ornatus* on the ground, inactive, and feeding are given in Fig. 1. Values were recorded on a 1-ha plot on the playa fringe at the Jornada site on July 24. Activity information recorded the next day was similar. Figure 1 probably represents typical millipede activity on a hot day shortly after heavy rainfall. Feeding activity did not occur between 1000 hours and 1400 hours, and about half of the above-surface population was feeding at any one time. Laboratory and field observations have confirmed that feeding also takes place at night.

Density and biomass

A mean of 2.67 ± 0.27 millipedes was excavated from *Novomessor* nests (excavation depth: 1m; diameter at top of hole: 1.5m) in monthly trips between January and September (except for July) to the Jornada site. Eighty three nests were excavated and 222 specimens found. An approximate calculation of the dispersion parameter k (Southwood, 1966) by the formula $k = \frac{\sum x^2 - \frac{(\sum x)^2}{n}}{n-1}$ shows $k = 2.066$, where k is about 70% efficient. Although this is a relatively low density population, this information suggests that the millipedes in ant nests assume a clumped dispersion and are therefore not dispersed among the nests on the basis of chance alone.

Density estimates from the Jornada site, from Albuquerque, and from Big Bend are given in Table 4. Standing crop estimates from counts made in 2 areas are given in Table 5 and are compared with those from published studies.

Age distribution expressed in terms of midsegment width is given for counts made at the Jornada site and Big Bend (Fig. 2), and for counts made on two 929 m² plots and a single hectare plot in Albuquerque (Fig. 3). At each site the frequency distributions are different, reflecting possible differential mortalities in the past. Arrows indicate approximate midsegment width of the smallest females in each population found to contain some mature eggs.

The relationship between live and dry weights shown in Fig. 4 indicates a respective 3:1 ratio of these basic units of biomass. This and all other regression relationships shown in this report have highly significant correlation coefficients ($p < 0.01$). Specimens obtained for this comparison came from surface collections at the Jornada site in late July.

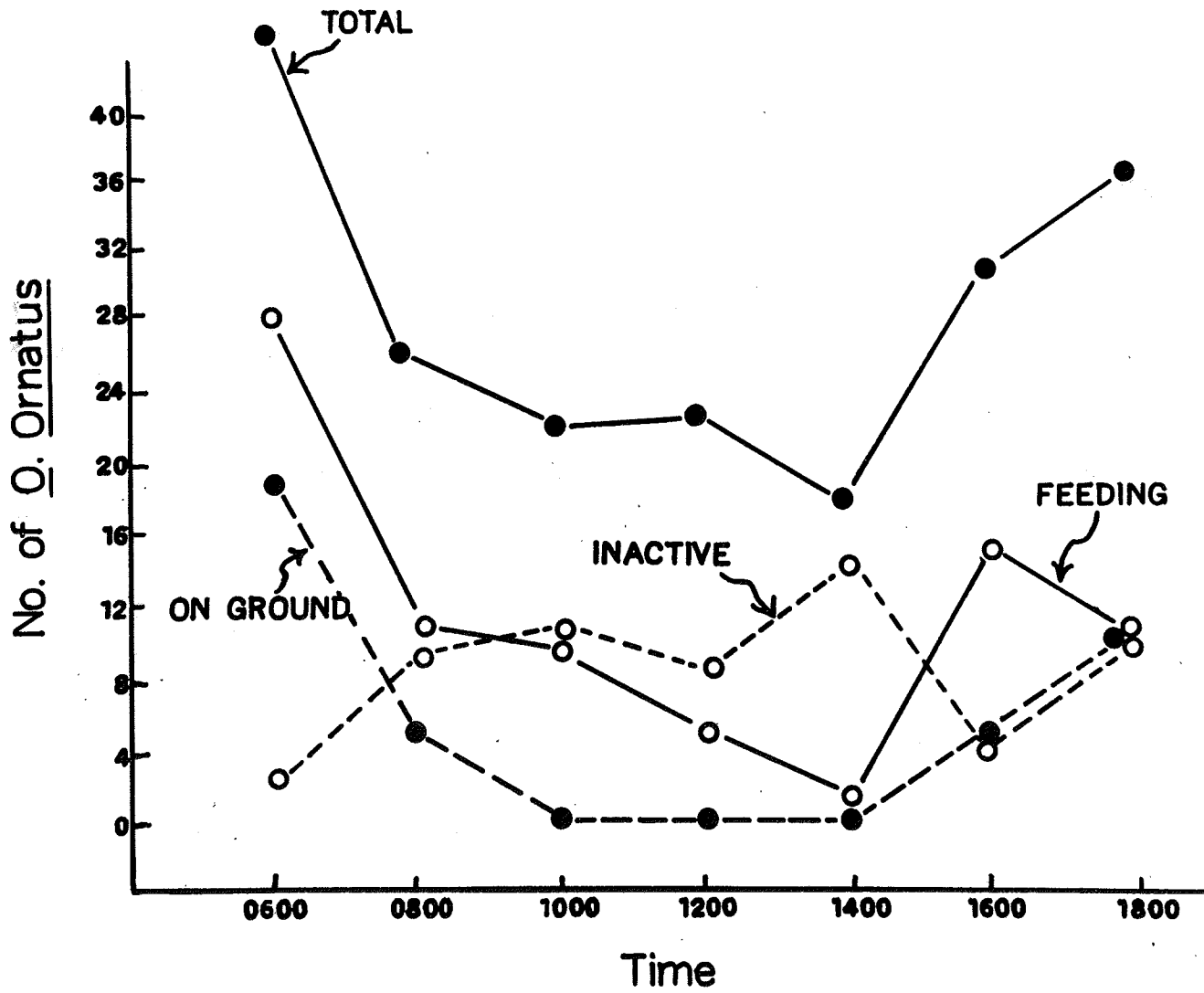


Figure 1. Hourly counts of *Orthoporus ornatus* engaged in different activities on a 1-ha plot (Jornada Validation Site; July 24, 1972).

Table 4. Preliminary density estimates of *Orthoporus ornatulus* >3mm width

Place	Method	No. ha ⁻¹
Jornada	Mean 1972 <i>Novomessor</i> nest count	17
"	Highest 1972 playa fringe count	44
"	Highest 1971 road count	85
"	Single 1972 900m ² enclosure estimate	121
	Mean estimate: 67	
Albuquerque	Single 1972 hectare count	183
"	Mean of 2, 1972 929m ² counts	387
	Mean estimate: 258	
Big Bend	Single 1970 900m ² enclosure estimate	733

Table 5. Some comparative standing crop (live weight) estimates

Species	Individual wt. (mean or range in g)	Standing crop (g m ⁻²)	Situation	Source
<i>Japonaria laminata</i>	0.044	0.323	Adults, Jan. 1966-Jan. 1967	Saito, 1967
<i>Iulus scandinavius</i>	0.028-0.077	0.801	Overwintering instars VIII-XI	Blower, 1970
<i>Orthoporus ornatulus</i>	1.95 (n=35)	0.003	Highest single 1972 Jornada road count	Present study
<i>Orthoporus ornatulus</i>	6.31 (n=63)	0.763	Single 900m ² Big Bend enclosure	Present study

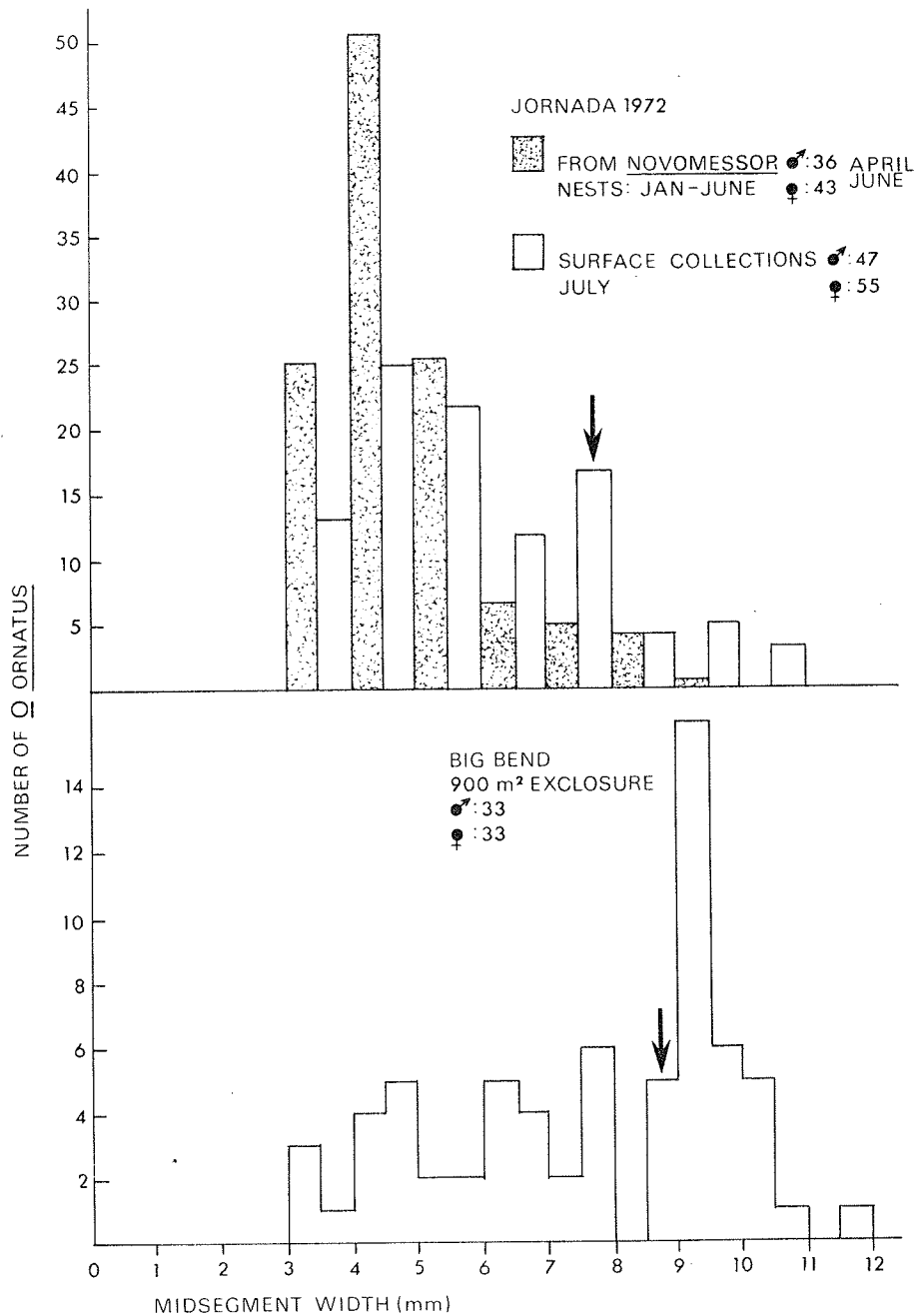


Figure 2. Age distribution expressed in terms of midsegment width of *Orthoporus ornatus* populations from the Jornada Validation Site and from Big Bend National Park. Arrows indicate approximate midsegment width of smallest females found to contain mature eggs.

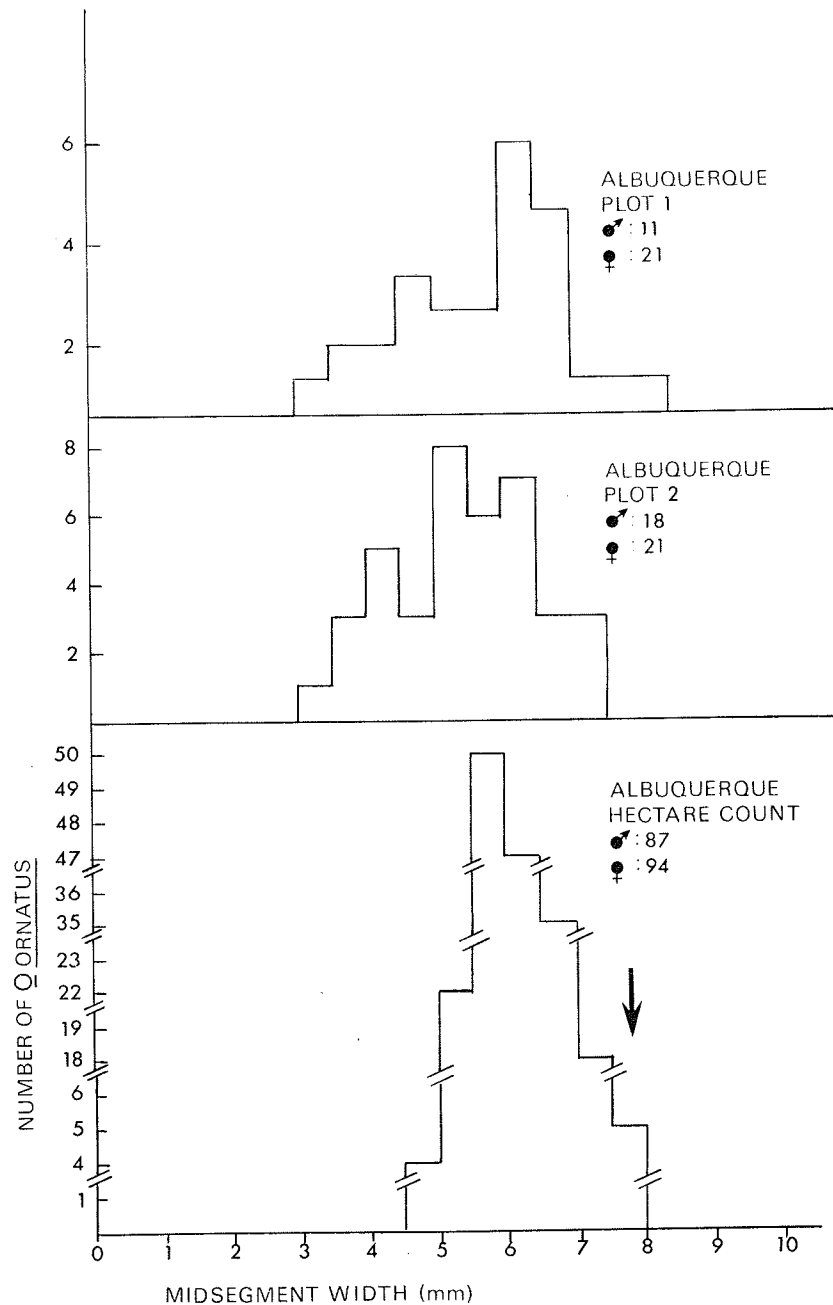


Figure 3. Age distribution expressed in terms of midsegment width of *Orthoporus ornatus* from 3 different plots on the West Mesa, Albuquerque, N. M.

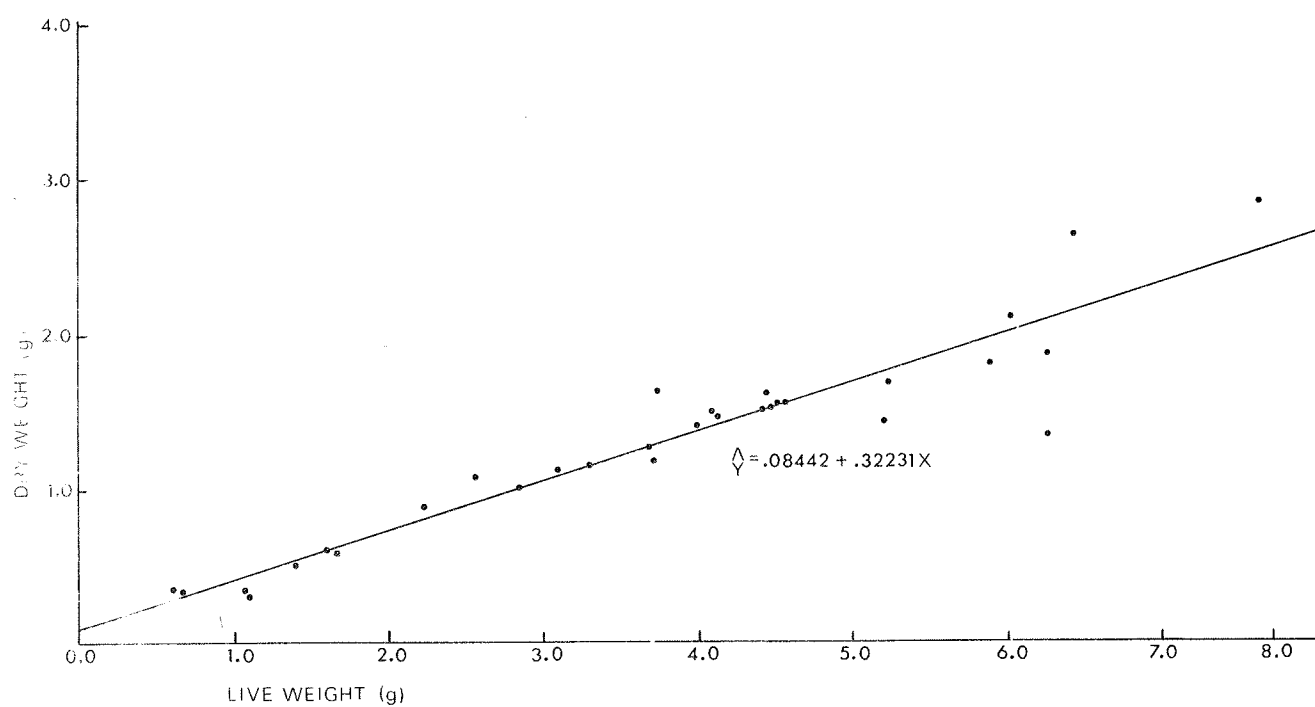


Figure 4. The relationship between live weight and dry weight of *Orthoporus ornatus* (collected from Jornada Validation Site; late July, 1972).

Food and ingestion

A complete list of food items seen in the process of being eaten is not as meaningful as the statement that diet in *O. ornatus* has considerable range. Diet in nature can be summarized as follows: new shoots of annuals and animal feces (infrequent); virtually any kind of dead plant tissue and superficial tissues of shrubs (frequent). The latter category includes mainly dead bark; however, the bark is not always dead and the tissue is not always bark. For instance, superficial tissues of a type of *Opuntia* are common food at Big Bend. In Albuquerque the bark of *Salsola* (tumbleweed) is a frequent food. At the Jornada site the barks of *Ephedra* and *Prosopis* (mesquite) are readily eaten. However, the bark of *Larrea* (creosote bush) appears rarely eaten.

Consumption of moist soil is a prerequisite for ingestion of dry *Ephedra* bark. Analysis of soil ingestion is not yet complete.

Ingestion rates of *Ephedra* bark are inversely related to dry body weight (Fig. 5). Expressed as g food ingested/g dry weight over a 5-day period, they more than double between 20 C and 30 C (Table 6). Such temperatures are considered a reasonable approximation of the range in which *O. ornatus* feeds in the field.

Assimilation

As shown in Table 6, assimilation percentage ranges from about 24 at 20 C to about 38 at 30 C.

Table 6. *Orthoporus ornatus*: estimates of ingestion and assimilation

Parameters	20 C (N=12)	24 C (N=15)	30 C (N=10)
Ingestion rate*	0.020±0.003	0.034±0.004	0.050±0.010
Assimilation %**	23.6±4.0	31.4±2.3	37.6±3.5

*g food ingested/g dry wt x 5 days

**calculated as $\frac{\text{food ingested} - \text{feces}}{\text{food ingested}} \times 100$; all values ash-free dry wt.

Respiratory metabolism

Oxygen consumption is inversely related to body weight (Fig. 6), as is Q_{10} from summer animals during a change from 25 C to 35 C (Fig. 7). Specimens weighing between 3.2g and 5.9g had a mean Q_{10} of 1.45, while those weighing between 0.8g and 1.8g had a mean Q_{10} of 2.38.

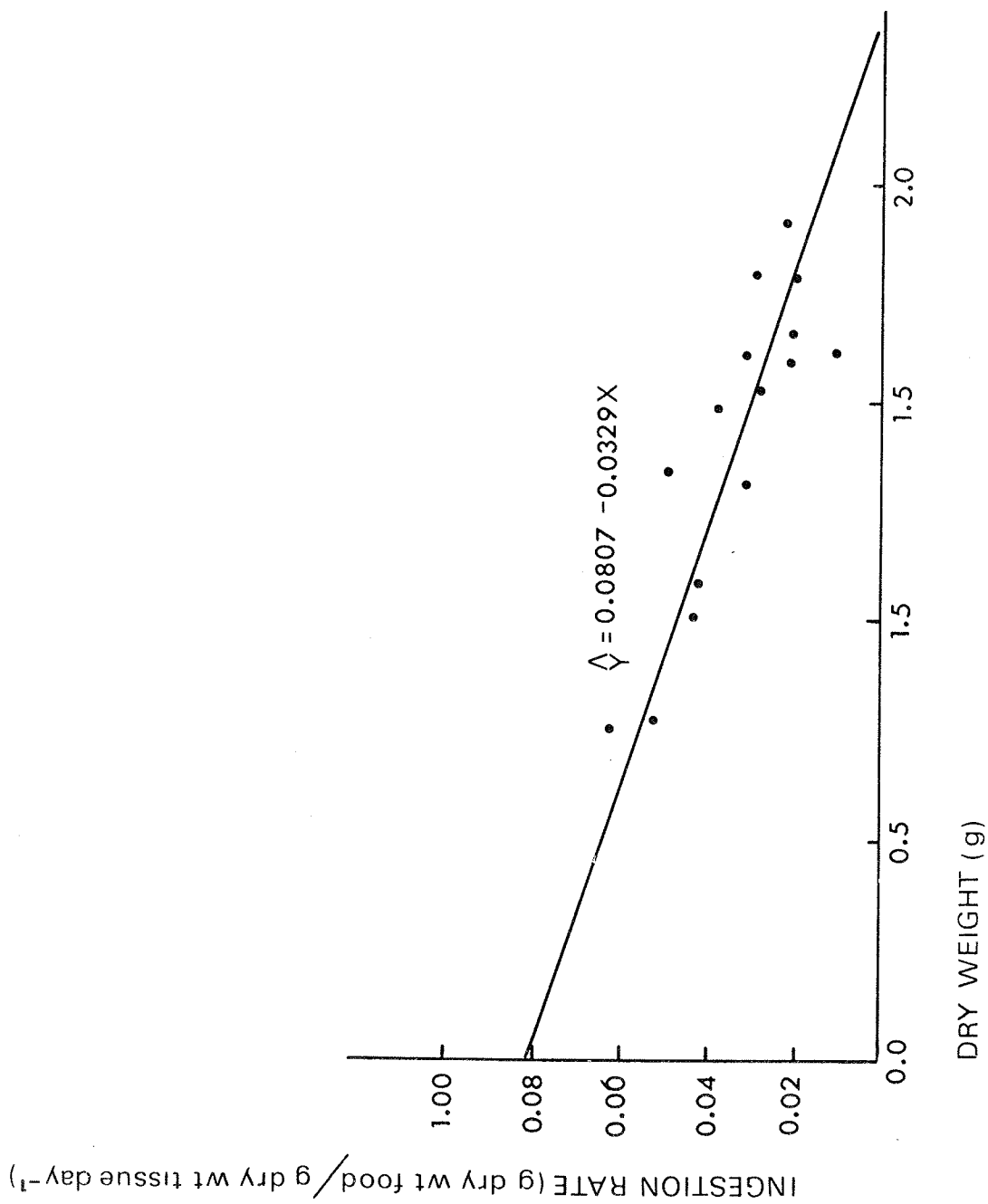


Figure 5. The relationship between ingestion rate of *Orthoporus ornatus* at 24 °C (collected from Jornada Validation Site; late July, 1972).

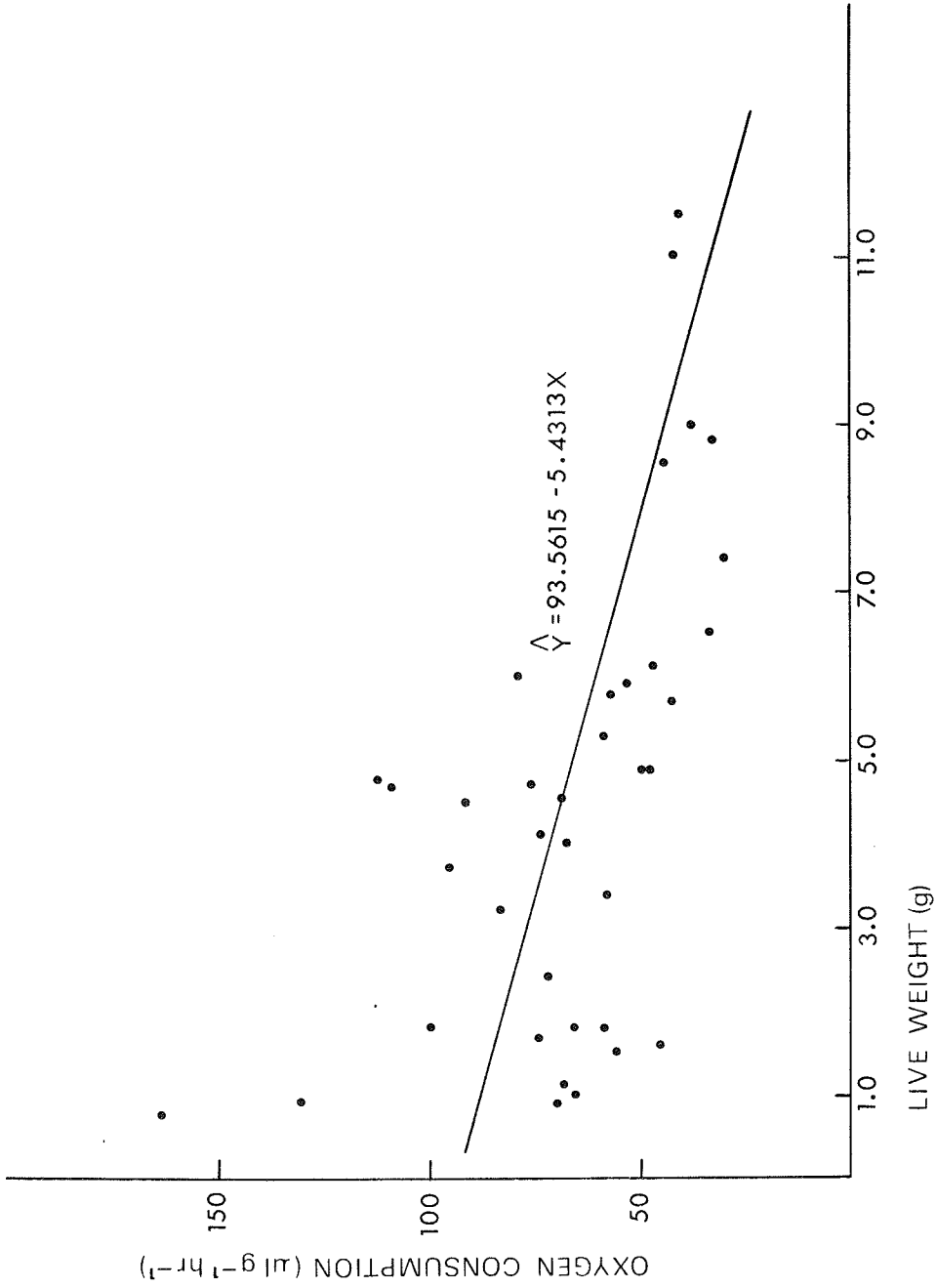


Figure 6. The relationship between oxygen consumption at 24 C and live weight of *Orthoporus ornatus* (collected from Jornada Validation Site; late July, 1972).

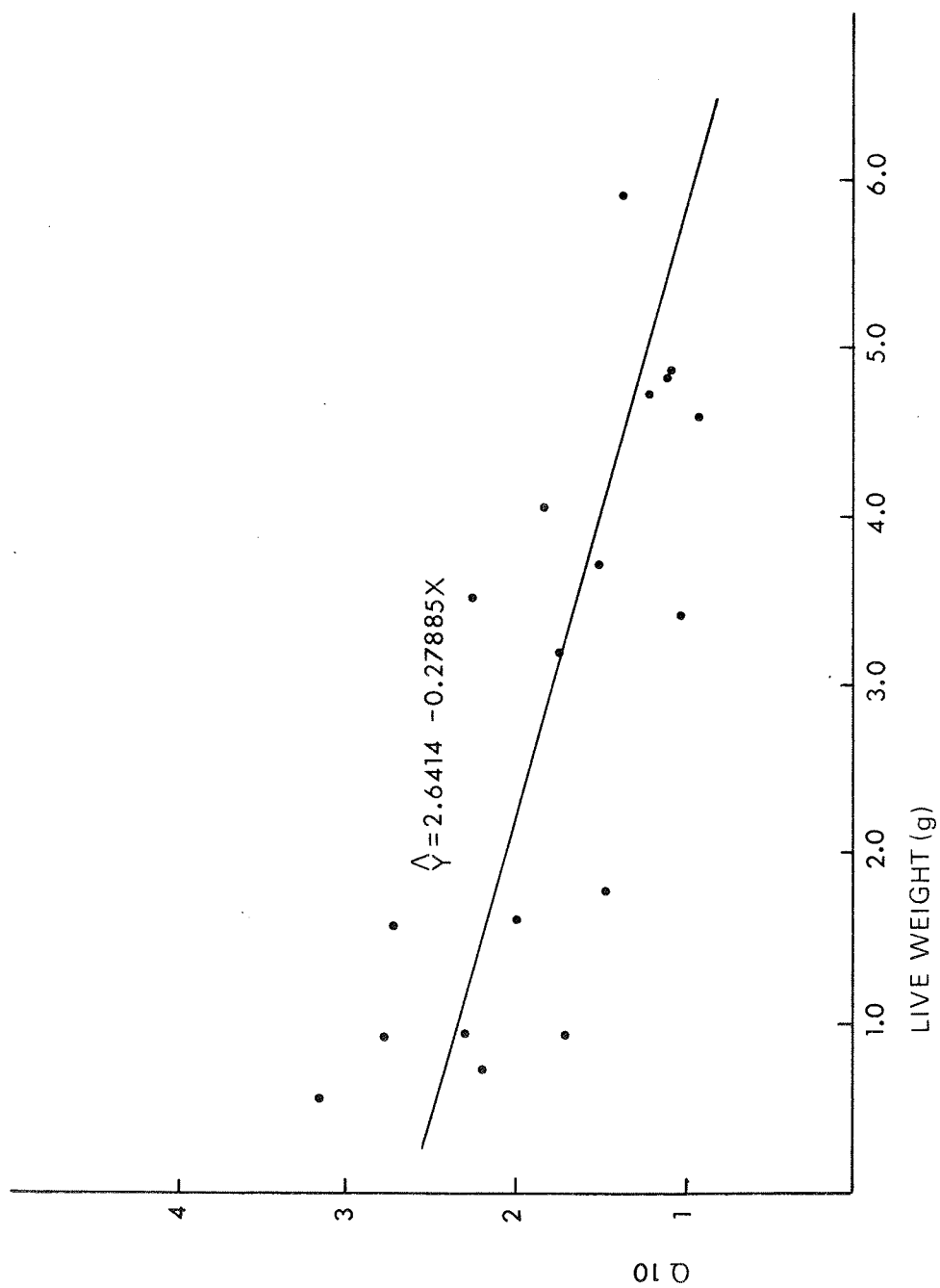


Figure 7. The relationship between Q 10 for a change from 25 C to 30 C and live weight of *Orthoporus ornatus* (collected from Jornada Validation Site; late July, 1972).

Monthly values for oxygen uptake are given in Fig. 8. Following relatively steady rates at 20 C between January and early June just prior to molt, *O. ornatus* appeared to depart from a diapause-like state between late June and September, at which time specimens had probably been underground for at least a month.

Oxygen uptake values of ambient temperatures reflected such temperatures to some extent; however, the increase after molting is out of proportion to a mean ambient temperature rise of only 3 C. October values suggest that the diapause-like state begins in late fall.

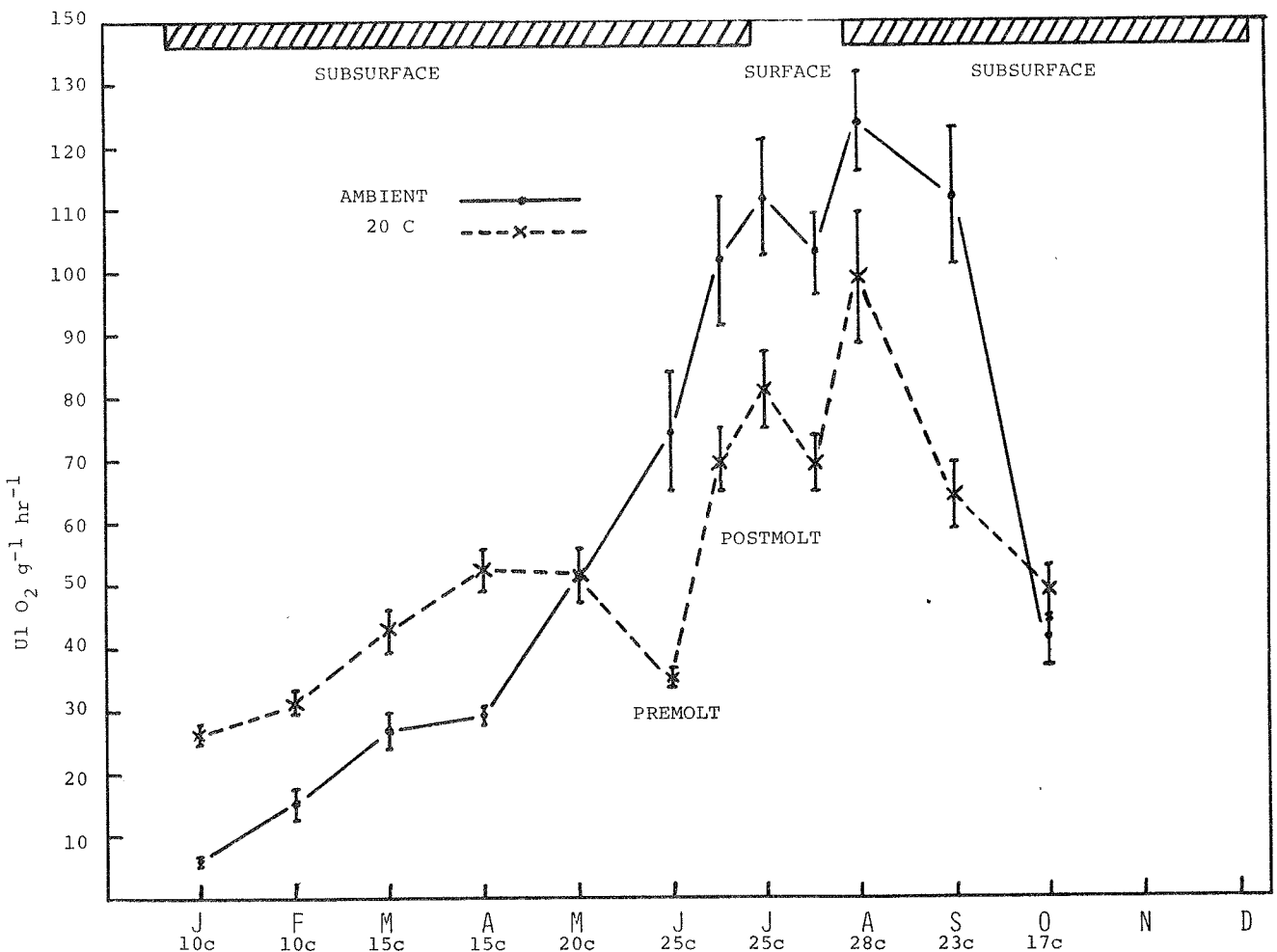


Figure 8. Monthly values of oxygen consumption per unit of live weight for *Orthoporus ornatus* collected from *Novomessor cockerelli* nests (except for July surface specimens) at the Jornada Validation Site (DSCODE A3UCF01).

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When expressed in terms of cal g^{-1} , respiration at ambient field temperatures also showed an annual curve (Table 7). All values in Table 7, except for those of July, were calculated from one half of each of the recorded mean values of oxygen uptake (in $\mu\text{l g}^{-1} \text{hr}^{-1}$) that were recorded each month. The reason for this is that in reaction vessels specimens tend to move about, and therefore metabolize more than when in their soil-bound state. This procedure seems to give a reasonable estimate of oxygen uptake for an animal at rest.

Caloric values were calculated using a measured RQ value of 0.83.

Table 7. *Orthoporus ornatus*: annual respiratory metabolism (DSCODE A3UCF01)

Month	N	cal g^{-1*}	Temp. (C)
Jan.	12	27.8	10
Feb.	14	38.6	10
Mar.	15	48.1	15
Apr.	16	50.2	15
May	15	90.9	20
June	16	178.6	25
July**	33	470.6	25
Aug.	16.	253.5	28
Sept.	17	222.3	23
Oct.	15	72.5	17

*Live weight

**Surface individuals

DISCUSSION

The results to date substantiate preliminary conclusions that *O. ornatus* is at times an abundant desert detritivore. The term "detritivore" is not completely appropriate, however. The desert millipede's diet is also to some extent that of a herbivore.

Perhaps the most striking aspect of this animal's life is that it appears to feed for a very limited part of the year, unlike millipedes living in forest litter. Several key adaptations seem to allow this kind of existence. First, responsiveness to a reasonably predictable rainfall pattern during the warmer part of the year has obviously evolved in this species. Early rains during late spring appear to trigger an annual molt and to arouse the otherwise quiescent millipedes to a state allowing later surface foraging. Responsiveness to early rains probably also involves ovarian maturation in large females.

Early and late rains can trigger movement to the surface, where dispersal, reproductive activities and foraging take place. For a detritivore, *O. ornatus* has relatively high assimilation efficiency; it is approximately twice that of a woodland millipede, *Narceus americanus*, that feeds on dead wood (O'Neill, 1968). This high rate, together with the ability to resist desiccation and to ingest water rectally (Crawford, 1972), enables the desert millipede to feed on the surface during periods that would be rapidly fatal to most other millipedes.

It is during these periods of surface foraging that *O. ornatus* probably makes its main contribution to nutrient flow in the desert, because after a short duration of high energy expenditure, a semi-dormant state is once again entered beneath the surface.

EXPECTATIONS

By December, 1972, monthly measurements of respiratory metabolism will be complete. These measurements, together with the new available assimilation and ingestion values, allow rough estimates of *O. ornatus* activity during the year. It remains to be demonstrated precisely how much nutrient material is processed by a given population in a feeding season, and also to what extent this produces additional millipede biomass. For IBP modelling purposes, we feel that a complete description of a millipede energy budget is desirable, but of secondary importance. Therefore, most of the emphasis during the coming year will be directed toward answering the two points raised above.

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Basic to both points is a reasonable approximation of population density and age structure. More accurate measurements of biomass as seasons change are needed as well. In addition, daily feeding activity requires further analysis, and annual growth increments must be estimated. Finally, renewed attempts should be made to estimate potential and actual fecundity (birth rates and death rates are also desirable population parameters to know, but will be very difficult to ascertain).

In the coming year density at the Jordada site will be measured by making repeated daily counts of individuals on the surface of hectare plots. The regression technique will also be used at the Jornada site and will employ areas set off with lawn edging material. The same approaches will be used at Big Bend and perhaps at Albuquerque. Personnel will be present to make such measurements on days when millipedes are active.

Age structure will be analyzed after fixing millipedes in ethanol to obtain maximal body contraction (Blower and Gabbut, 1964). This seems the best remaining approach to the problem. The method will hopefully produce size discrepancies between any two instars and will therefore indicate longevity with relatively little error (recall that *O. ornatus* molts once a year).

Biomass will be estimated by drying specimens seasonally at 60 C until a constant weight is reached. Cuticular and gut-content components of biomass (as opposed to tissue biomass) will be estimated if possible.

Daily feeding activity will be estimated as before, and careful attention will be paid to the daily progression of ambient temperatures at different places in the feeding area.

Annual growth increments will be estimated by 1) weighing specimens kept in cohorts out of doors at yearly intervals (the first weighing has taken place), and 2) weighing laboratory specimens before and after molting.

Potential fecundity studies by dissection will be continued. Actual fecundity will be estimated where possible by counting eggs laid by females.

ACKNOWLEDGEMENTS

The assistance and cooperation of Dr. Walter Whitford and his colleagues, especially Dr. John Ludwig who provided weather data, is much appreciated. Officials at Big Bend National Park have allowed us to work in the park. Tamara Coombs, Leola Gonzales, Wayne Riddle, and Felix Nunez provided invaluable technical assistance. *Orthoporus onatus* was identified for us by Dr. Richard L. Hoffman, Radford College, Radford, Virginia.

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1972 PROGRESS REPORT

CONSUMPTION OF *Larrea* BY CHEWING INSECTS

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Research Memorandum, RM 73-32

MAY 1973

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A B S T R A C T

The variety of chewing insects feeding on *Larrea* in the vegetation of the Silverbell Validation Site is limited to, at the most, 13 species. *Boottettix puotatus* are scarce herbivores on the terminals of the creosote bush. *Ligurotettix coquilletei* Kunzei (desert clicker grasshopper) is conspicuous on the site but populations are small -- one pair of insects per large clump of *Larrea*. The katydid, *Insara covilleae*, is a nocturnal species that consumes tender parts including blossoms, fruits and galls. *Diapheromera covilleae* (stick insect) and *Thyridopteryx meadi* are present in small numbers, while *Semiothisa pallidata* are fairly abundant at night and prefer leaves and blossoms to terminal shoots. *Synglochis perumbraria* and two coleopterans occur sporadically on *Larrea*, as do two Homopterans. A gall fly, *Asphondylia auripila*, was reared from several fresh galls on creosote bush.

INTRODUCTION

The decision to transfer major effort in the Tucson Basin from the Santa Rita Validation Site to the Silverbell Validation Site changed the complex of plants to be monitored and added *Larrea* to the list. Since creosote bush is one of the dominant plants of the hot North American deserts, anything that consumes it should be of interest, not only to the modelling effort here but to persons studying it elsewhere.

What is reported is somewhat preliminary, but should serve as a point of departure for future studies. Unfortunately for the project, Mr. Alan Olsen accepted a permanent position at the end of the summer and left Tucson. His departure occasioned a reappraisal of the project and a decision to terminate it at the end of the first year. This decision was somewhat difficult, but was occasioned in part by our discovery that *Larrea* is not a heavy contributor to the biomass of chewing insects on the Silverbell site (indicated by a fecal pellet drop of no more than 3 g/m² of *Larrea* cover in 1972), in comparison with the leguminous shrubs and trees. Some of the insect species proved extremely difficult to handle in the laboratory. Unless we could obtain eggs, a meaningful rearing program was impossible. Rather than make another attempt, with another round of failures possible, we decided to turn our activities in another direction in 1973.

OBJECTIVES

The objectives stated for 1972 were:

1. To establish the life cycle of the individual species of chewing insects that consume portions of *Larrea* during the year.
2. To establish the food preferences of these species from instar to instar, including the possibility that they may consume other plant species.
3. To establish the amount of plant material consumed in each instar under laboratory and field conditions, as well as the extent to which there is plant damage beyond actual consumption.

Some progress was made on all three of these objectives, plus one of recording activity cycles during the 24-hr day for some species.

METHODS

Rearing at constant temperature was accomplished for several species in refrigerators converted to climate chambers by the addition of a heating element, fluorescent lights,

fans, and appropriate regulators. The best containers for small species were small plastic petri dishes, with a change of a small piece of *Larrea* daily. Larger insects were kept on bouquets in larger cages, up to 0.4 m^3 for adult stick insects.

Observation cages for the behavioral studies were of two sizes. Collapsible $0.3 \times 0.3 \times 0.45 \text{ m}$ (0.4 m^3) screen cages, with included bouquets or potted plants, were used extensively. These Mr. Olsen set up on a plastic-enclosed porch at his home where he could readily continue observations for 24-hr periods. In addition some large cages ($1.8 \times 1.8 \times 0.9 \text{ m} = 3 \text{ m}^3$) were built near the trailer at the southeast corner of the Silverbell research area. These were used for several series of observations. The odd metric dimensions are the result of the use of standard black window screening of 36" width in their construction. Black screening is much easier to see through than aluminum or galvanized, but was almost impossible to obtain.

RESULTS

A complete listing is made here of the chewing insects on *Larrea* that we know of in the Tucson area.

Orthoptera

Boottettix punotatus Scudder, F. Acrididae. Creosote bush grasshopper. Scarce but present at Silverbell, detectable by the faint stridulation of the male. Both sexes spend their time in terminals of the plant, where their green, brown and white color pattern conceals them admirably. Immatures were not found. Individuals in a large cage containing only *Larrea* survived for weeks, an indication that they consume the plant. Males stridulate through the daylight hours. One round of nocturnal observations, July 26/27, Data Set A3UWH09, indicates that they stridulate all night as well; temperatures recorded went down to 25 C. Very little other nocturnal activity was recorded, except that the one female was observed feeding once on a leaf. One male, of three, moved from one quadrant of the cage to another, but this was the only movement recorded.

Ligurotettix coquillettei kunzei Caudell. F. Acrididae, the desert clicker grasshopper is conspicuously present on the Silverbell site, because of the stridulation of the males. We had expected that it would prove to be a major consumer of this plant. It is active throughout the daylight hours, and especially noticeable during the hottest hours. Males are usually located by their stridulation, on the larger *Larrea* stems. A search of the plant may then reveal a female in the same plant. Despite their conspicuousness, populations are not large, at most one pair per large clump. A nocturnal run

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of observations, as in the last species (Data Set A3UWH09) indicated that males stridulated all night, and that there was some movement and feeding on *Larrea* leaves during the night. All three males and four females observed moved into the leaves by 2200 hrs and stayed there until about 0540, when they returned to the branches. There was feeding during this period, and continued stridulation.

These observations of nocturnal feeding on *Larrea* provide the first substantial information on the food of the species, at least in the adult stage. The bushes in the field cages that were heavily stocked with clickers received substantial defoliation, a condition that would not occur in nature. *Franseria deltoidea* bushes in the cages were not affected. We were unable to find nymphs of this species either, but there must be eggs in the soil in the field cages and we may be able to recover nymphs from them in the spring of 1973.

Insara covilleae Rehn and Hebard. F. Tettigoniidae. Creosote bush katydid. Activity of adults and nymphs of this species is entirely nocturnal. A series of observations, Data Set A3UWH09, confirms this statement. Feeding, stridulation, courtship, oviposition, and movement are confined to the hours of darkness. The adults spend their time among the leaves of the terminals, resting on stems or leaves. When they start to feed, they consume all tender parts, including small stems, blossoms, fruit, and galls, before moving on to a new feeding locus (Data Set A3UWH10). One confined on *Prosopis* would not eat this plant (Data Set A3UWH10).

Oviposition seems to take place one egg at a time. The usual site seems to be in clumps of leaves, but there is one record of oviposition in the soil. The eggs are exceedingly difficult to find, and were not found in the field. Those observed being laid in the observation studies did not hatch, perhaps because they were infertile.

Diapheromera (Ceratites) covilleae Rehn and Hebard. F. Phasmidae. Creosote bush stick insect. While Mr. Olsen had been successful in rearing one individual from egg to adult before the project started, very high mortality in the early instars interrupted an attempt to get growth rate in relation to temperature. Everything about this insect proceeds slowly. It moves little, either day or night, unless it is disturbed. The females kept in cages produced large numbers of eggs, which just drop as they are laid. The species was more abundant at Silverbell than we had anticipated. A transect in which 48 randomly-selected bushes were beaten on June 9, 1972, produced five males, and one individual contributed fecal material to the frass trap samples for a short period. Mr. Olsen recorded two rounds of activity observations, Data Set A3UWH09. One female observed in a cage started laying eggs at 1400 hrs on June 20 and was still laying eggs at midnight when the observations were terminated. One pair observed remained in copulation from 1940 hrs until past midnight, then fed from 0240

to 0450, as did the other three individuals in the cage. In one observation leaves, blossoms and terminals were consumed, seeds were not, Data Set A3UWH10.

Lepidoptera

Thyridopteryx meadi Hy. Edw. F. Psychidae. Collection of cases from all of the known areas resulted only in amassing dead pupae and odd inhabitants. No viable eggs were found. So we were unable to observe the hatching stimulus or development, as we had anticipated. We did find a few half-grown larvae at Silverbell, and have a record of some activity in a cage for one, (Data Set A3UWH09). It moved very little and was observed feeding on leaves for short periods four times over several days.

Semiothisa pallidata Packard. F. Geometridae. Adults of this species are fairly abundant at night in the Tucson area, but the larva and its food were unknown. Larvae were found on *Larrea*, reared to the adult stage, and a second generation reared on the same plant. Larvae were found on *Larrea* from February through May, but are apparently more abundant in the spring.

Rearing of a few individuals to the adult stage was accomplished at controlled temperatures of 15, 25 and 35 C, Data Set A3UWH11. The results are as follows: 15 C: 1-larva 41 days; 25 C: 4-larvae 21, 22, 22, 31 days, mean 24, S.D. 4.69; pupa 9, 11, 11, 12 days, mean 10.75, S.D. 1.26; 35 C: 3-26, 26, 26 days, mean 26, S.D. 0; pupa 5, 7, 7 days, mean 6.33, S.D. 1.15. The total production of fecal pellets during all larval instars was as follows: 15 C, 25.9 mg; 25 C, 133.5, 40.4, 160.1, 120.2 mg; 35 C, 157.2, 32.7, 124.8 mg. The mean would be 105.86 mg, S.D. 56.63, if all records were combined. However, it is very likely that the last entry for fecal pellets was omitted for the three lightest weights. All other weights were entered 4 or 5 times, these only 3. The mean without these is 142.3 mg, S.D. 18.21

The problems of maintaining satisfactory rearing conditions were such that there was very high mortality at 35 C, perhaps because of humidity problems. Development took so long at 15 C that the rearing had to be stopped in favor of other projects after the 41 days. The figures obtained can be used for an approximation, but would have to be refined for a detailed study. A small part preference study was accomplished with DSCODE A3UWH10. This indicated a preference for leaves and blossoms, and general avoidance of terminals.

Synglochis perumbraria Hulst. F. Geometridae. Larvae of this species were also reared on *Larrea*, from specimens taken on this plant in the spring. They were less abundant than *Semiothisa*, and disappeared by summer. This species has been reported as reared from *Larrea* by Rindge (1959), but the larva has not been described.

Coleoptera

Eupagoderes marmoratus. F. Curculionidae. We had anticipated that weevils of this genus would be important at Silverbell. However, very few were found in the area in 1972, at least during the spring and summer. They may be important in some years and in some places.

Epicauta lauta (Horn). F. Meloidae. Adults were taken several times at Silverbell, feeding on *Larrea* flower buds and blossoms. Others had been taken in emergence traps during 1971. Larvae of *Epicauta* eat grasshopper eggs in the soil. The food preference of this species, abundant in the Sonoran Desert and frequent in the Chihuahuan, was previously unknown.

Homoptera

These are sucking insects, and were not covered, except incidentally. Some Homoptera, particularly Membracidae, seem to be most frequent on *Larrea* in the spring. Few were encountered later in the season. Two that were could be of interest. *Tachardiella larrea* (Comstock). F. Lacciferidae, the lac insect, is present on the Silverbell section of land, but is scarce and local. A mealybug, F. Pseudococcidae, with a query, about 6 mm long and fat, was taken individually several times.

Diptera

Gall flies, probably *Asphondylia auripila* Felt, F. Cecidomyiidae, are conspicuous because of their spherical, cockscomb-like galls. The outer surfaces may be consumed by *Insara* grasshoppers. Flies reared from several fresh galls in the spring were all females. The main period of oviposition and gall formation does appear to be in the spring, but the subject was not pursued very far.

DISCUSSION

At least on Silverbell, *Larrea* makes a very minor contribution to secondary productivity through support of insect populations. The presence of light populations of stridulating grasshoppers might lead one to suppose otherwise, but these maintain themselves at wide spacing through territoriality.

The decision of Mr. Olsen to accept permanent employment elsewhere has forced a reconsideration of the project, and we have decided to terminate it at this point in favor of one that appears to deal with insects that have a greater impact on the ecosystem.

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1972 PROGRESS REPORT

DEMOGRAPHIC AND BIOENERGETIC STUDIES OF CUTWORMS IN
CURLEW VALLEY

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Research Memorandum, RM 73-33

MAY 1973

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It is subject to revision and reinterpretation. The authors
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A B S T R A C T

A survey of all stages of the cutworms of Curlew Valley was carried out in 1972. While the bulk of the material remains unidentified, many species were evident. The most abundant species taken as larvae on the study area were several unidentified species of *Eruxoa*, in addition to *Feltia ducens*, and *Pseudorthosia variabilis*. Numbers recovered at random sample plots were too low to make an estimate of overall abundance in the area. Attempts were made to establish laboratory colonies of two of the more common species for future demographic and bioenergetic studies. Larval rearings have thus far proved successful on a diet of alfalfa leaves and on an artificial diet.

INTRODUCTION

Many species of cutworms occur in the Great Basin, and the large genus Euxoa, which includes many of the cutworm species, perhaps has reached its greatest development in number of species in that region (Hardwick, 1970). During some years high infestations of larvae have been observed to nearly denude large areas of desert rangeland and, as most species have a rather wide host range (Crumb, 1929), the great impact on the desert ecosystem by these insects seems obvious. However, most species have been studied very little, especially those not occurring in areas of cultivation, and demographic and bioenergetic studies of the dominant species should provide valuable information in assessing this impact.

OBJECTIVES

The objectives for 1972 were to determine the species of cutworms present in Curlew Valley, to determine their population density based upon larvae recovered from the soil, and to establish laboratory colonies of the dominant species for future demographic and bioenergetic studies.

METHODS

Surveys were begun in March and continued until November at several sites in Curlew Valley, but with concentrated efforts at the northern validation site, 5 miles northwest of Holbrook, Idaho. Litter samples were processed in Berlese funnels, and soil was carefully examined for the immature stages. Sifting soil through a one-fourth inch mesh screen was at first attempted in recovering larvae but proved too time-consuming and laborious, and the soil was thereafter examined by hand. For the collecting of adults, a Malaise trap was maintained on the study area from March to October and the insects removed at least weekly. Light-trapping was carried out also at least weekly from June to September. During late summer and fall moths were collected from flowers, especially those of Chrysothamnus spp.

Random sampling was begun in a designated area near the north validation site

but, as too few cutworms were recovered for an adequate estimation of overall abundance, this was not continued. The sample plots consisted of one cubic foot of soil. Thereafter searches for larvae were concentrated around the bases of various species of plants to obtain as many larvae as possible and to get an indication of preferred host plants. All immature stages recovered were returned to the laboratory for rearing to the adult stage.

Adults from which laboratory colonies were begun were collected at night and placed in oviposition cages containing soil, a method modified from that of Jacobson and Blakeley (1957). Efforts were made to obtain the same species as those recovered as larvae. Eggs which did not hatch in a few weeks were exposed to a two-month cold period (Berube, 1957). As soon as the larvae appeared they were placed in petri dishes, in which alfalfa leaves or various other food, such as lettuce, bean leaves and wheat sprouts, were provided. An artificial diet, described by Patana (1969) was begun for some of the larvae.

RESULTS

Samples of litter processed in March, April and May contained several Noctuidae larvae, primarily early instars, while no larvae were recovered from the soil, which at that time was quite moist. By late June the litter had dried and contained no larvae, while larvae were then being recovered from the soil. The larvae were found to be deeper as the soil dried, and were most abundant around the bases of certain plants, especially *Lupinus caudatus* Kell. From a total of 137 larvae recovered alive from the soil, 79 emerged as adults. Several species of *Euxoa* appeared to be represented, along with *Feltia ducens* Walker and *Pseudorthosia variabilis* Grote. Twelve of those which did not emerge were parasitized (four by Braconidae, five by Ichneumonidae, one by Chalcidoidea, and two by Tachinidae).

Preliminary identification of the adults collected at the study area indicates a large number of species present. However, much of the material has not been identified. Those which were most abundant were *Euxoa auxiliaris* Grote, *Euxoa declarata* Walker, *Euxoa obeliscoides* Guenee, *Euxoa ridingsiana* Grote, *Feltia ducens* Walker, *Feltia venerabilis* Grote, *Pseudorthosia variabilis* Grote, *Sidemia devastator* Brace and *Spodoptera praefica* Grote. Some of these may have come in from nearby cultivated farms, and therefore only those which were reared from recovered larvae would give the

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true picture of the species occurring in the desert habitat.

It is not known if the small number of larvae recovered from the soil during random sampling presents a true picture of their abundance, or if the method used was adequate. There was no evidence of excessive plant damage due to cutworm activity. On the basis of previous work on the life history of various species, feeding is usually completed in late spring, and a period of arrested development during a prepupal stage lasts through the hot summer months. This coincides with the findings of the present study, as nearly all of the larvae recovered after late June were in a prepupal state and within an earthen case. By early August all had pupated and began to emerge 2 weeks later. Eggs collected from confined adults embryonated in a few weeks. At this time those of two species hatched and the remainder entered diapause.

The rearing of larvae on alfalfa leaves and on the artificial diet is proceeding satisfactorily.

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1972 PROGRESS REPORT

DEMOGRAPHIC STUDIES OF SAGEBRUSH INSECTS AS FUNCTIONS
OF VARIOUS ENVIRONMENTAL FACTORS

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Research Memorandum, RM 73-34

MAY 1973

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It is subject to revision and reinterpretation. The authors
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A B S T R A C T

Seasonal history, population dynamics and biology of the sagebrush defoliator, *Aroga websteri* Clarke, were studied at the Curlew Valley site and in the laboratory. The defoliator had one generation a year at the study site. It overwintered in the egg stage. Eggs hatched in the early part of April and larvae passed through five instars between April and June. Pupation occurred from the beginning of June to the middle of July. Adult emergence began in early July and continued until the end of the month. Malaise trap data indicated that adult activity lasted for a period of 2 to 2½ months. Eggs were collected in field samples as early as July 28. Field development of the defoliator was more rapid in 1972 than in 1971. This was due to the warmer weather conditions of April, May, June and July, 1972.

Ten species of parasites were found to attack the defoliator in 1972. Four major species, *Orgilus ferox*, *Phaeogenes* sp., *Spilochalcis leptis*, and *Apanteles cacoeciae*, accounted for over 75% of the total parasitism on the defoliator. Parasitism was rather low in 1972, and increased only from 12 to 24% during the season. As a result, a five-fold increase in the defoliator population was recorded in 1972 over 1971.

Investigations were conducted in the laboratory on reproduction, food consumption and utilization, and effect of temperature on the development of the defoliator. A preliminary version of life tables was constructed from findings of 1971 and 1972 to assess the roles of various mortality factors in the regulation of defoliator population.

A study was conducted to determine the effects of temperature and photoperiod on the development of overwintering first instar larvae of the garden casebearer, *Apterona crenulella*.

INTRODUCTION

Two major sagebrush insects, the sagebrush defoliator, *Aroga websteri*, and the garden casebearer, *Apterona crenulella*, were included in the investigation of 1972. The sagebrush defoliator was the dominant species on the big sagebrush at the northern Curlew Valley site. Therefore, a large share of the research effort was devoted to the study of this species. Field population of the defoliator was unusually high in 1972 as compared to the previous year. This outbreak provided an opportunity to evaluate the impact of several biotic factors, such as predation, competition and adult flight, more effectively than in 1971. Preliminary studies conducted in 1971 provided an understanding of the biology of the defoliator and enabled the development of techniques for rearing and handling this species. Consequently, it was possible in 1972 to conduct several laboratory experiments to obtain biological information that is essential input for demographic studies of the defoliator. Field sampling methods were also improved to allow more efficient collection of samples and a higher degree of accuracy among samples.

The garden casebearer was investigated with a population found in Green Canyon near Logan, Utah. Several experiments have been conducted with overwintering larvae of this species. Data obtained from laboratory studies have provided the basis for prediction of the spring emergence of the larvae and an understanding of the behavior of the species. Results obtained from these studies are discussed in this report.

OBJECTIVES

Most of the objectives outlined in the 1971 report were accomplished in 1972. The lack of sufficient manpower necessitated a delay in the field study of the garden casebearer.

The following objectives have been pursued in 1972:

1. To determine seasonal history and natural mortality of the sagebrush defoliator.
2. To conduct laboratory studies to determine the effects of environmental factors on development of the two sagebrush insects.
3. To determine the food consumption and utilization by the defoliator.
4. To estimate the quantitative relationships between population size of defoliators and the degree of sagebrush defoliation.

Aroga websteri

METHODS

Sampling procedures

Samples of the immature stages of the defoliator were collected weekly to determine the seasonal history and population density of this insect. The data were also used for analysis of the dynamics of the defoliator population.

Statistical analysis of the sampling procedure conducted in 1971 revealed that a smaller sample unit could be used and a higher level of reproducibility obtained for the same cost effort. Therefore, two alterations were made in the sampling procedure in 1972. The study plot of 100 m² was divided into quadrant blocks, and ten plants were selected randomly within each designated block. A representative branch that extended from the ground level to the height of the plant was selected. The branch was then cut off at ground level, weighed, labeled, and placed in a plastic bag. In the laboratory the samples were examined by shaking the foliage and picking through it with forceps. The numbers and stages of the defoliator were determined. The population density was then expressed in terms of the number of defoliators per kg of fresh sagebrush.

Rearing techniques

Defoliators obtained from field samples were reared in the laboratory. First and second instar larvae were transferred to small plastic cages 2 cm high and 3 cm in diameter with moist filter paper at the bottom. Moisture apparently was important for the establishment of the young larvae, as those placed in containers lacking moist filter paper soon became desiccated. Ten of these cages were mounted on a 7 x 19 cm plexiglas sheet and the tops of the cages covered with tight-fitting plastic lids. Ten larvae were placed in each cage along with 3 or 4 small, tender leaves from the tips of sagebrush plants. The leaves were changed approximately every 3 days to prevent growth of mold.

Third instar larvae were transferred to larger plastic containers, 6 cm high and 5 cm in diameter, for the remainder of larval development. These cages were fitted with nylon cloth tops which were secured with elastic bands. Ten to twenty larvae were placed in each container and supplied with fresh leaves as needed. All cages were placed in a Percival environmental growth chamber maintained at 30 C, a relative humidity of approximately 50 to 60%, and a photophase of 16 hr.

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Pupae were separated from the larvae and held in a large container inside the growth chamber. Upon emergence the moths were transferred to oviposition cages for further study.

Effects of temperature on development of immature stages were investigated with a group of 300 first instar larvae collected from the study site on 22 April, 1972. These were transferred to the small plastic cages previously described. Originally ten larvae were placed in each cage. As they became larger, they were divided into smaller groups to minimize the effects of crowding. The larvae were separated into three groups of one hundred larvae each, and each group was reared in a different growth chamber. The temperatures of the growth chambers were set at 21, 26.5 and 30 C; the relative humidity ranged from 50 to 60%. All growth chambers were set at a photophase of 16 hr.

Larval mortality usually increased if the insects were removed from their feeding sites frequently, so only ten insects in each growth chamber were examined each day. Records were kept of the daily development of the sampled larvae at each of the given temperatures.

Measurement of adult activity

Two methods were used in studying adult activity in the field. A Malaise trap was erected in late June near the study plot and weekly records were kept of the number and sex ratio of moths collected. The height of moth flight was determined by placing sticky traps at the study site from 14 to 28 July, 1972. Three boards 2 m in length and 20 cm in width were painted with Stickem^R. These boards were secured in an erect position by metal stakes and placed in the study site. Weekly counts were made of the number of moths captured on the board at 5 cm intervals.

Oviposition studies

In 1971, attempts were made to sample defoliator eggs in the field. This approach proved unsuccessful because eggs are deposited under sagebrush bark and are quite obscure. The sampling was also very tedious and quite inadequate. In 1972, two methods were used to calculate the fecundity of the females. The first method involved a direct count of the total number of eggs laid by individually-caged females.

An indirect method was also used to determine fecundity. Weekly records were kept of the ovarian development of females captured in the Malaise trap used for adult activity studies. Generally, ten females were dissected weekly and the number of differentiated oöcytes was recorded, thereby allowing an estimation of the number of eggs laid per female.

Food consumption and utilization

Food consumption and utilization of fourth and fifth instar larvae were determined by the use of a gravimetric method (Waldbauer, 1966). Twenty five newly-molted fourth instar larvae were individually weighed and placed in small plastic cages. The cages were then transferred to a growth chamber where a temperature of 30 C and a relative humidity of about 50 to 60% were maintained. The larvae were fed with 3 or 4 pre-weighed leaves obtained from the same leaf cluster. Leaves were changed at two-day intervals. Since the dry weight of the leaves could not be determined before feeding, an estimation of the percent dry matter of leaves was determined from an aliquot. Each time fresh leaves were provided, the weights of uneaten food, fecal matter, and larval weight gain were recorded. On the basis of the results obtained, approximate digestibility (A.D.), efficiency of conversion of ingested food (E.C.I.), efficiency of conversion of digested food (E.C.D.) and consumption index (C.I.), were calculated for the two larval instars.

Defoliation studies

Defoliation studies were conducted in early July, 1972. At this time the damage caused by the sagebrush defoliator had reached a maximum for the season. Twenty-six plants were selected within the study area that represented a range from slight to complete defoliation. These plants were cut off at ground level, weighed, labeled and placed in plastic bags. In the laboratory, the number of defoliators found on each plant was recorded. The damaged leaves were separated from the undamaged leaves and both were dried to constant weight. The ratio of damaged to undamaged leaves was used to calculate the percent defoliation.

The effects of defoliator density on the sagebrush plant were also studied in the field using caged plants. Four defoliator-free plants were selected near the study site and individually enclosed in nylon cages, 1 x 1.5 x 2 m. Third and fourth instar larvae collected from the study site were divided into groups of 100, 200, 300 and 400, and placed on the caged plants of 5 May, 1972. On 1 July, the plants were removed from the cages. The numbers of pupae and pupal cases were counted and the percentage of defoliation was determined by the method described previously.

RESULTS AND DISCUSSION

Seasonal history

The sagebrush defoliator had one generation at the study site in 1972. Table 1 summarizes the data from field sampling of different age groups of the defoliator and

2.3.3.7.-6

the population density throughout the season. These data are graphically represented in Figure 1, to illustrate in relative percentages the progression of development of these age groups. Data collected in 1971 are presented in Figure 2 to provide direct comparison.

Table 1. Age structure and population density of *A. websteri* at Curlew Valley site, 1972 (DSCODE A3UHL01)

Date of sampling	Egg	Larval instar					Pupa	Pupal case	Total	Total defoliators per kg fresh sagebrush
		1st	2nd	3rd	4th	5th				
April 22		758	487	76	7				1328	108.8
May 6		255	504	171	7				937	115.3
May 11		156	516	143	4				819	135.9
May 20		6	172	726	428	13			1345	164.6
May 25			62	455	430	32			979	173.0
June 2				116	653	408			1177	170.7
June 9					238	716	1		955	152.0
June 15					59	689	24		772	150.1
June 22					2	543	98		643	148.3
July 1					4	308	276	9	597	129.8
July 7						50	463	37	550	113.2
July 14						1	293	128	422	100.5
July 16							16	99	115	97.4
July 28	87						4	116	207	-
Sept. 6	92								92	-
Oct. 5	21								21	-

Field sampling conducted in the spring and fall of 1972 revealed that the defoliator overwinters in the egg stage at the study site. The embryos are fully developed, but apparently remain within the chorion until early spring. The study site was inaccessible for sampling until late April due to early spring rains. The first field samples were collected on 22 April. At this time, over 50% of the defoliators were first instar larvae. The increase in the larval population during the subsequent samplings indicated that egg hatching might have continued until the latter part of May. Larval development in the field was earlier and faster in 1972 (Figure 1) than in 1971 (Figure 2). These differences in development rate were due

to the higher mean temperature during the months of May, June and July, in 1972. An analysis of the long-term mean temperature for these three months revealed that a -0.8°C below mean was recorded in 1972 as compared to a -1.1°C below mean in 1971. These measurements were taken at Snowville, Utah, the closest weather station to the site.

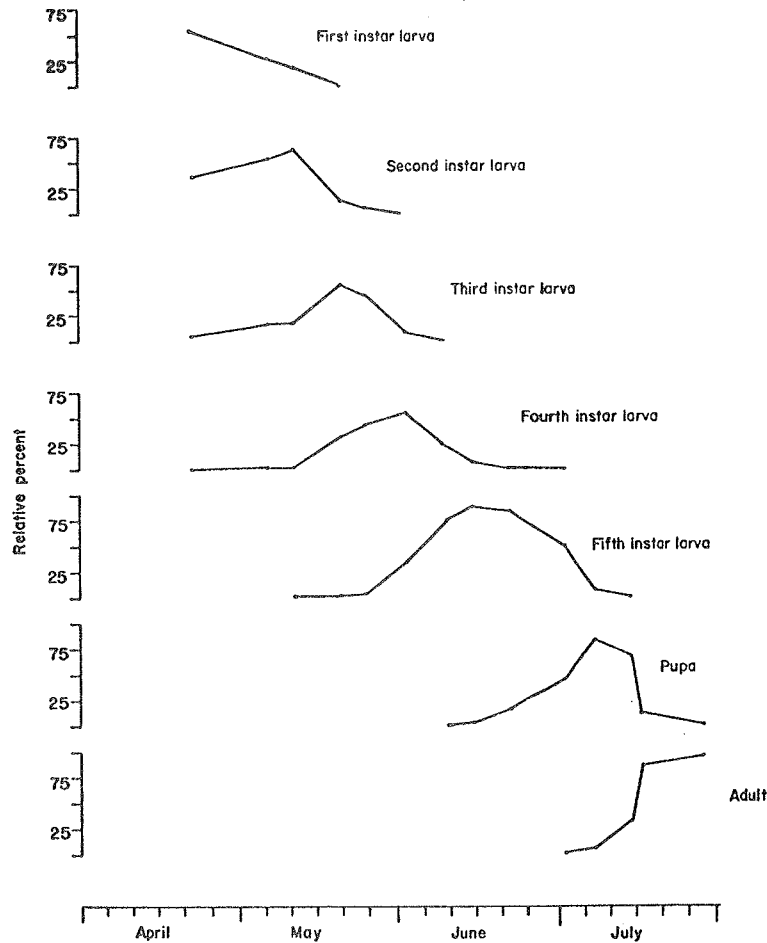


Figure 1. Age structure of *A. websteri* population at Curlew Valley site, 1972. Data obtained from successive sampling dates were calculated as relative percentages of each age class. (DSCODE A3UHL01)

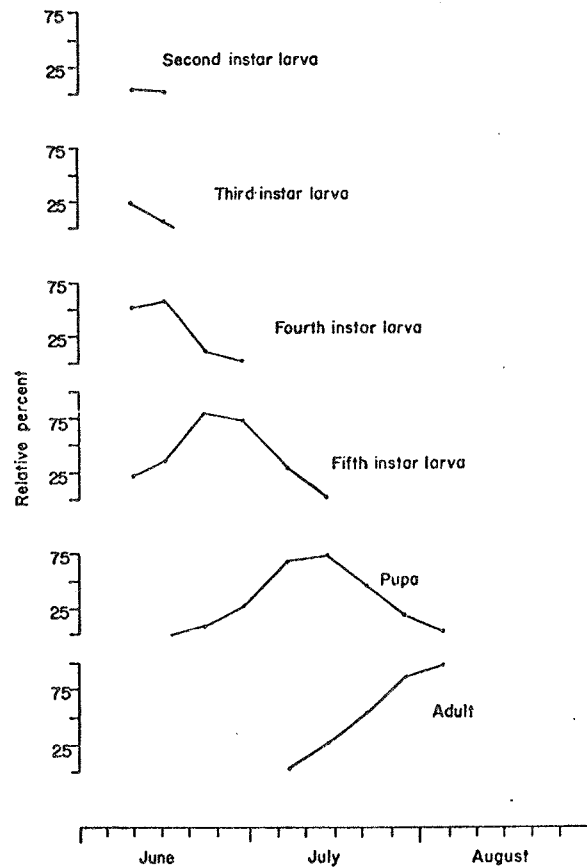


Figure 2. Age structure of *A. websteri* population at Curlew Valley site, 1971. Data obtained from successive sampling dates were calculated as relative percentages of each age class (DSCODE A3UHL01)

The population density of the defoliator, based on the number of individuals per kg of sagebrush, was also found to be about 5 times greater in 1972 than the previous year. As a result of high defoliator population, a general occurrence of sagebrush defoliation was noticeable at the study site.

Biology

Egg: Eggs are generally laid under the light gray bark immediately below the sagebrush foliage, and are occasionally found on outer bark surfaces. Stems of less than one-fourth inch in diameter are preferred for egg laying. Eggs are attached to the plant tissue by a viscous and transparent substance, and are difficult to remove. Although the eggs are laid singly, often small groups of 2 or 3 eggs were found under field conditions. Newly-deposited eggs are clear white in color and later change to a creamy yellow. Embryonic development apparently begins immediately when the eggs are laid. The U-shaped embryo was observed within the egg shell after a two-week incubation at 30 C. Chilling of 100 of these embryonated eggs at 2 C for a 3-week period and then subjecting them to several weeks of incubation at 30 C and a photoperiod of 12 hr of light did not initiate hatching. It can be assumed that the eggs had entered a true diapause. The egg diapause could be broken by rupturing the chorion. Once disturbed, the larva crawled out of the chorion and soon searched actively for feeding sites. The larvae obtained in this manner were unable to establish themselves on sagebrush clippings and eventually died.

Larva: Newly-hatched larvae collected from the field are pale yellow with a dark brown head capsule and cervical shield. The thoracic legs are strong, enabling the larvae to cling to surfaces readily. When placed on caged plants the young larvae were observed to move briskly about the sagebrush leaves until a feeding site was secured. Fifty young larvae placed on a grid travelled an average distance of 5 cm in 5 minutes. It was also noted that they were attracted toward light, and moved upward when placed on an inclined surface. These three factors probably contribute to rapid larval establishment on foliage tips. Under laboratory conditions, however, the newly-emerged larvae had some difficulty in establishing a feeding site. Generally, 1 to 1½ days were required for healthy larvae to begin feeding on sagebrush clippings.

The larvae first attacked the young leaves near the terminal tips of the plants. Initially they produced webbing encompassing 2 or 3 leaves, but the feeding site gradually enlarged during the season.

Whether the larvae completed development and pupated near the original feeding site, or migrated to other branches, largely depended upon the amount of foliage available. Larvae placed on caged plants were observed to migrate to surrounding branches as defoliation increased. In the field, mature larvae were also observed to move to neighboring plants during extensive defoliation.

2.3.3.7.-10

Larvae generally formed web tubes which extended from the main webbing site to the terminal ends of several branches. This enabled them to feed on the surrounding leaves and remain within the protective webbing. When disturbed, the larvae moved rapidly back into the tube or dropped to lower branches by a single silk thread.

As the larvae developed, the webbing extended in length to encompass new plant growth. The web tubes of the mature larvae were 5 to 8 cm in length, but occasionally extended to 10 cm. As the season advanced, larvae tended to congregate among the remaining foliage. Prior to pupation the larvae formed a loosely-webbed cocoon and were quiescent. First instar larvae collected from the study site were reared at constant temperatures of 30, 26.5 and 21 C. The time required to reach the adult stage was 27-34, 30-35 and 40-50 days, respectively.

Pupa: The pupae were initially a light brown in color, but gradually became darker prior to adult emergence. The pupal sizes and weights varied considerably with the food intake of the larvae. Measurements of 25 pupae collected in the field produced the following means: length, 6.6 ± 0.9 mm; width, 2.1 ± 0.3 mm; fresh weight, 7.8 ± 1.2 mg.

Adult: The adult wing span ranges from 13 to 16 mm. The front pair of wings is stippled with black markings and fringed about the outer margins. The hind wings are a lighter gray color and more heavily fringed than the front pair. The male and female are similar in appearance, although the female abdomen is generally larger than that of the male. Claspers also characterize the distal end of the male abdomen.

A total of 2761 moths was captured during the 1972 season. These data are summarized in Figures 3 and 4. Adults were first found in the Malaise trap at the beginning of July, which was about the time that pupal cases were recorded in field samples (Table 1). The number of moths captured gradually increased until it reached a peak in the last week of July, which also coincided with the largest number of pupal cases collected in the field samples. Since this peak number of adults found in the Malaise trap continued at about the same level for approximately 3 weeks, it can be assumed that the adults live for at least this period.

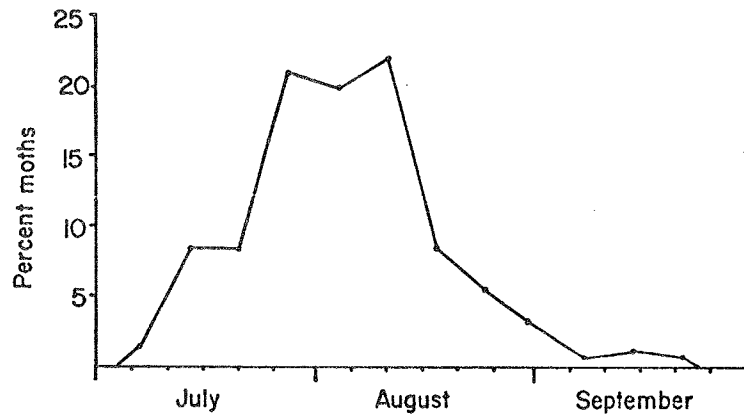


Figure 3. Weekly record of *A. websteri* moths captured in Malaise trap at Curlew Valley site, 1972.

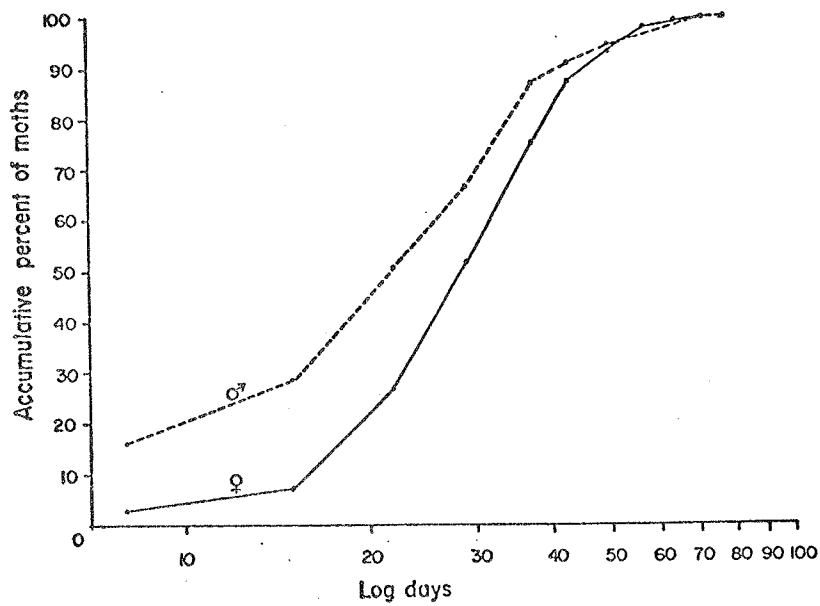


Figure 4. Weekly record of male and female *A. websteri* moths captured in Malaise trap at the Curlew Valley site, 1972.

2.3.3.7.-12

Data from laboratory rearing of 345 pupae and the Malaise trap data (Figure 4) show a tendency toward a higher ratio of males to females (5 to 1) at the early part of adult emergence. This difference gradually diminished until a sex ratio of 1:1 was reached. On the basis of these data, it can be inferred that the Malaise trap data provide an accurate estimation of adult activity in the field.

Adult moths have functional mouthparts and a complete digestive tract. A 10% solution of equal amounts of honey and sucrose was made available to caged moths, and they were frequently observed to feed on this solution. It is not known whether feeding enhances copulation, oviposition or embryonic development in the eggs, but adults provided with the honey-sucrose solution lived for an average of 2 to 3 weeks longer than unfed moths. Caged females lived for as long as one month. In the field, a plant that possibly may have provided nectar as food for the moths was rabbitbrush. This plant was observed to flower during the time of moth flight, and sticky traps placed among rabbitbrush blooms captured as many adults as those placed among sagebrush branches.

The moths spend the day quietly hidden under bark or in debris beneath the plants. Adults placed on caged plants became active 2 to 3 hr following dusk, and reached maximum activity between 2300 and 0500 hours. The moths were observed to move erratically over the bark and leaves of the plants. When released from the cage they flew rapidly in a zig-zag course and landed nearby. Flight activity decreased at sunrise, and the moths gradually dispersed to various hiding places and remained there for the duration of the diurnal period.

Figure 5 compares the height of sagebrush plants at the study site and the number of defoliator adults captured on sticky traps at various heights. The results show that the height of moth flight closely follows the height of the sagebrush. The majority of the moths were captured between 30 and 80 cm above the ground surface, and only a few individuals were found at a height of 120 cm. It can be concluded that moth activity in the field was generally concentrated about the periphery of the sagebrush crown.

Reproduction: Female moths have two ovaries, each with four ovarioles. Upon adult emergence, none of the 7-12 visible oöcytes is fully-grown. The largest oöcyte is approximately 0.120 mm in width, and the ovarioles become gradually narrower towards the anterior. An additional number of undifferentiated cells is present in the suspensorial apparatus of the ovary. During the oviposition period the last egg of each tube is abruptly larger than any of those preceding it (usually 0.360 mm wide by 0.601 mm long).

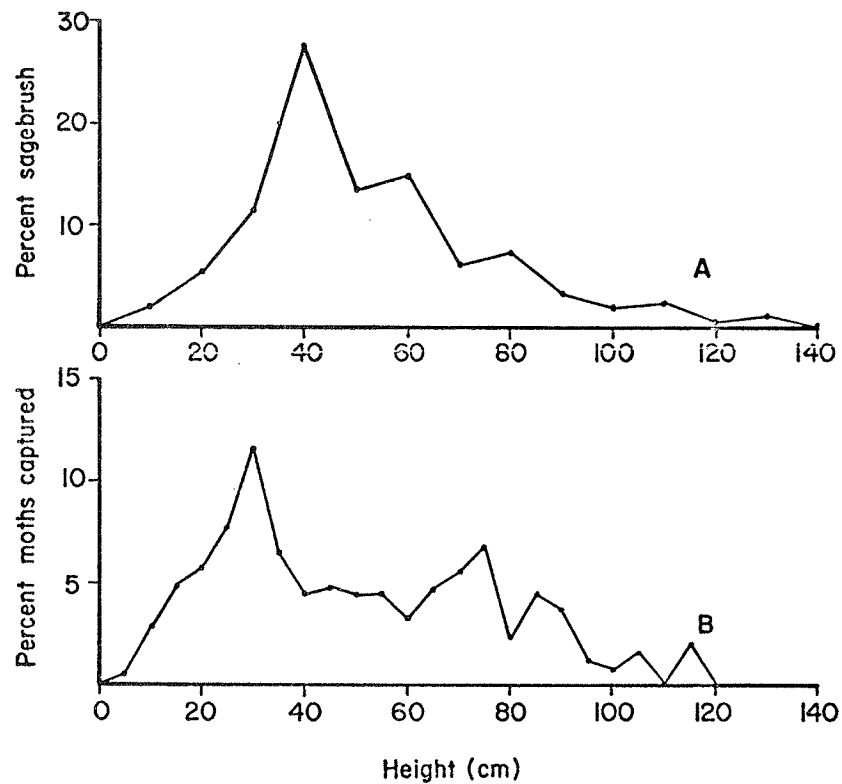


Figure 5. Comparison of the height of sagebrush to *A. websteri* moths captured at various heights. A. Percentage of sagebrush at given heights. B. Moths captured as determined by sticky trap collections. Curlew Valley site, 1972. (DSCODE A3UHL03)

All females captured in the Malaise trap were gravid. Therefore, egg production is assumed to be continuous during the active part of adult life. Examination of 50 females produced 2-16 fully-grown oöcytes per ovary, with a mean of 9.8. The maximum number of differentiated oöcytes found within a single ovariole was 15; therefore the potential production would be 120 eggs. However, this is only an estimation because oöcyte production in the female was continuous.

2.3.3.7.-14

A direct count of the number of eggs laid by caged females was also taken to estimate fecundity. Eighteen females were individually confined in 1.9 liter cylindrical cages containing sagebrush plants. Only 8 of the females thus caged deposited eggs. Two females that were kept in larger cages (30 and 45 cm³) deposited 81 and 84 eggs, respectively. These preliminary data indicate that cage size is an important factor in reproductive success of the female.

A variety of surfaces such as filter paper, debarked stems, paper towels, and tree bark were provided to caged moths for egg laying, but none was observed on these substrates. Apparently, physical texture or chemical stimulation are required to initiate egg laying. Moths were found to lay eggs readily on dead sagebrush branches in the laboratory and under field conditions. However, the proportion of eggs deposited on dead vs. growing plants is not known.

Natural enemies

Ten parasites were found to attack the sagebrush defoliator at the study site. These were *Apanteles cacoeciae* Riley, *Orgilus ferox* Mues., *Meteorus* sp., and *Microtypus* sp. (Braconidae); *Phaeogenes* sp., *Diadegma* sp., and *Temelucha* sp. (Ichneumonidae); *Copidosoma bakeri* (Howard) (Encyrtidae); *Microdontomerus* sp. (Torymidae); and *Spilochalcis leptis* Burks (Chalcididae).

Detailed data on the percentage of parasitism due to these parasites are summarized in Table 2. As a whole, percent parasitism was lower in 1972 than in 1971. *O. ferox* was the most common parasite in 1971 and caused mortality of approximately one-third of all fifth instar larvae. However, in 1972 the incidence of parasitism by this species was much lower. Muesebeck and Walkley (1951) reported that parasites of the genus *Orgilus* have been reared from species of five lepidopteran families. Therefore it is likely that the defoliator is not the only host for this parasite.

Phaeogenes sp. and *S. leptis* both oviposited in young host pupae. These parasites fed internally until they emerged as adults in early to mid-July. Both species are considered to be important parasites of the defoliator.

Apanteles sp. attacks either the egg or the young larvae of the defoliator. The parasites emerged from fourth instar larvae in mid-June and spun a white silken cocoon within the defoliator feeding site. Prior to this time they were not visible within the host.

Copidosoma bakeri was believed to attack the egg stage, although some early rearings in 1972 did not contain this parasite. King and Atkinson (1928) reported that this species oviposited in the eggs of *Euxoa ochrogaster*, but that the parasite did not begin development until the host larvae were in the last instar. This is also assumed to be the case with the defoliator.

Table 2. Parasites of *A. websteri* reared from field samples

	No. hosts reared	No. non-para- sitized hosts	No. parasitized hosts	<i>Apanteles</i> <i>cacoeiae</i>	<i>Temelucha</i> sp.	<i>Orgilus</i> <i>ferus</i>	<i>Copidosoma</i> <i>bakeri</i>	<i>Phaeogenes</i> sp.	<i>Spilochaleis</i> <i>leptis</i>	Other*	Total % Parasitism
<u>1971</u>											
June 10	73	40	10	4.0	10.0	4.0	2.0	0	0	0	20.0
16	98	52	23	1.3	9.3	17.3	1.3	0	0	1.3	30.5
23	205	120	111	1.3	10.0	32.9	2.2	0.9	0	0.9	48.2
30	201	87	123	0	0	29.5	1.9	15.7	8.7	2.8	58.6
July 7	327	68	211	0	0	55.6	0.7	11.8	7.2	0.4	75.7
14	296	138	153	0	0	0	0	34.7	16.8	1.0	52.5
21	45	26	10	0	0	0	0	16.7	11.1	0	27.8
<u>1972</u>											
Apr. 22	605	145	21	9.6	3.0	0	0	0	0	0	12.6
May 6	510	130	52	17.6	0	5.5	5.5	0	0	0	28.6
11	553	158	25	9.8	2.2	0.5	1.1	0	0	0	13.6
20	971	377	119	18.3	2.0	2.2	1.0	0	0	0.4	23.9
25	950	372	118	15.1	2.4	1.6	2.4	0	0	2.4	23.9
June 2	1107	565	103	8.5	2.2	1.3	1.8	0	0	1.5	15.3
9	873	667	45	2.0	0.6	1.0	2.0	0	0	0.8	6.4
15	707	493	46	0.9	0.4	1.7	3.3	0.7	0.6	0.9	8.5
22	521	304	49	0	0	0	5.4	2.0	4.2	2.2	13.8
July 1	580	309	77	0	0	0	4.4	6.5	9.1	0	20.0
7	570	401	82	0	0	0	5.1	11.1	0.6	0.1	16.9
14	200	160	21	0	0	0	0	4.4	7.2	0	11.6
16	16	3	1	0	0	0	0	0	2.5	0	2.5

* *Diadegma* sp., *Microdontomerus* sp., *Meteorus* sp., *Microtypus* sp.

Two species of hyperparasites were encountered during both 1971 and 1972; they were *Catolaccus aeneoviridis* and *Gelis* sp. *C. aeneoviridis* was found to attack *O. ferus*, *Diadegma* sp., *Temelucha* sp., *S. leptis*, and *Phaeogenes* sp. Between 20 and 28% of these primary parasites were destroyed by this species. The incidence of hyperparasitism by *Gelis* was not high enough to be recorded.

Fillmore (1965) recorded 18 species of Hymenoptera and one species of Diptera as parasites of the defoliator in southern Idaho. Of these parasites, seven species were recorded in the rearing of defoliators collected from northern Curlew Valley. The other three hymenopterous species, *Microdontomerus* sp., *Meteorus* sp. and *Microtypus* sp., are new records of parasites of the defoliator.

Larvae of a chrysomelid beetle, *Phyllobaenus* sp., were occasionally found feeding on the larvae or pupae of the defoliator. The adult stage was never found to attack the defoliator. The actual impact of this predator on the population dynamics of the moth is assumed to be minimal. Field samples showed an average of 1 beetle larva per 26 defoliators in 1971 and 1 per 125 in 1972.

A microsporidian was found to attack the larval and pupal stages in the field and in the laboratory. Infected larvae became sluggish and stopped feeding after they were infected. The integument became soft-textured and the larvae turned a characteristic dark color. The integument did not rupture following death, but hardened and became distinctly brittle. When diseased larvae were dissected and examined under the microscope, the gonads and fat bodies were found to be teeming with the protozoan. Often the fifth instar larvae were able to pupate, but the adults failed to emerge.

The egg tubes of infected females became sac-like chambers which were filled with protozoa. Usually only one or two oöcytes remained intact. The crowded condition of the host during 1972 probably promoted wide dissemination of spores, although the microsporidian was able to manifest itself also during the low population level of 1971. Under laboratory conditions, a high mortality rate of 4th and 5th instar larvae was due to parasitism by the microsporidian. However, mortality due to this cause rarely exceeded 5% in the field.

Life tables

On the basis of field and laboratory data collected in 1971 and 1972, preliminary life tables were constructed to define the various mortality factors within specific age intervals (Harcourt, 1969).

The sampling period of the defoliator was divided into five intervals. This was based on the similarity of the "crucial trials" through which the insects must pass if they are to survive. The five intervals are: larvae, period 1; larvae,

period 2; larvae, period 3; pupae; and adult (at emergence). Table 3 and 4 show the values for two generations of the defoliator. The column headings are those proposed by Morris (1963).

Larvae, period 1 (Instar 1, 2 and 3): The l_x was obtained by population sampling in early June, 1971, and mid-April, 1972. The actual number of larvae entering this period was not determined, but the l_x was calculated by graphic summation as outlined by Southwood and Jepson (1962). The principal mortality factor during this interval was assumed to be the failure of larvae to become established on the sagebrush foliage. The exact environmental factors responsible for the mortality were not determined. Mortality was not caused by parasite emergence during this period. The young larvae rarely encountered diseases and predation was minimal.

Larvae, period 2 (Instar 4): The larvae were well established on the sagebrush plants. Collections were made at the beginning, middle, and end of the fourth instar and the larvae were reared to establish the incidence of parasitism. The effect of the factors of competition and overpopulation varied with the amount of foliage available to the defoliator.

Larvae, period 3 (Instar 5): The l_x was determined by a series of population samples prior to and during the fifth instar development. Parasites, pathogens and food shortage accounted for a significant population reduction during this period. Starvation became significant with the increase in defoliators during this age interval.

Bird predation was not an important mortality factor as indicated by lack of defoliator head capsules in 150 bird droppings collected in the study site.

Pupae: The l_x for the pupal stage was determined by direct field counts prior to and during moth emergence. Pupae were transferred to the laboratory where the incidence of parasitism was determined. Predation by beetle larvae was detected by examination of the pupae for beetle feeding marks.

Adults (at emergence): The adult l_x was determined by examination of pupal cases in the field for evidence of normal ecdysis. Infertility caused by microsporidia was determined by dissection of 50 moths which were captured at the study site. The mortality factors listed for the adults are not complete (Tables 3 and 4). Other factors which may affect adult survival before oviposition were not determined because of the mobility of this stage.

Table 3. Life table of one generation of *A. websteri* at Curlew Valley study site, 1971

x	l_x	$d_x F$	d_x	100 q_x
Age interval	No.* alive at beginning of x	Factor responsible for d_x	No.* dying during x	d_x as percentage of l_x
Larvae				
Period 1	37	Failure to establish and other **	7	18.92
Period 2	30	<i>Apanteles cacoeeciae</i> <i>Phyllobaenus</i> sp. <i>Temelucha</i> sp. Unknown Total	<1 <1 1 2 4	13.33
Period 3	26	<i>Orgilus fexus</i> <i>Diadegma</i> sp. <i>Copidosoma bakeri</i> <i>Phyllobaenus</i> sp. Microsporidia Unknown Total	10 <1 <1 1 2 3 16	55.17
Pupae	10	<i>Phaeogenes</i> sp. <i>Spilochalcis leptis</i> <i>Microdontomerus</i> sp. <i>Phyllobaenus</i> sp. Microsporidia Unknown Total	2 1 <1 1 <1 1 5	50.00
Adults	5	Physiological causes Microsporidia Sex Ratio = 1:1 Total	1 <1 1	20.00
Generation totals			33	89.19
Generation survival (S_G) = 0.11				

* Number per kg fresh sagebrush

** Miscellaneous factors such as predation, misadventure and physiological causes

Explanation of symbols:

- x - Age interval at which the sample was taken.
 l_x - The number surviving at the beginning of the stage noted in the x column.
 d_x - The number dying within the age interval stated in the x column.
 $d_x F$ - The mortality factor responsible for d_x .
 100 q_x - Percentage mortality.

Table 4. Life table of one generation of *A. websteri* at Curlew Valley study site, 1972

x	l_x	d_x^F	d_x	$100 q_x$
Age interval	No.* alive at begin- ning of x	Factor responsible for d_x	No. ** dying during x	d_x as percentages of l_x
Larvae				
Period 1	209	Failure to establish and other **	34	16.27
Period 2	175	<i>Apanteles cacoeeciae</i> <i>Phyllobaenus</i> sp. <i>Temelucha</i> sp. Competition and over- population factors Total	18 2 1 5 26	14.86
Period 3	149	<i>Copidosoma bakeri</i> <i>Orgilus ferox</i> <i>Diadegma</i> sp. <i>Phyllobaenus</i> sp. Microsporidia Competition and over- population factors Total	4 2 <1 1 8 21 36	24.16
Pupae	113	<i>Spilochalcis leptis</i> <i>Phaeogenes</i> sp. <i>Microdontomerus</i> sp. <i>Phyllobaenus</i> sp. Total	9 6 <1 1 16	14.16
Adults	97	Physiological causes Microsporidia Sex Ratio $\approx 1:1$ Total	7 5 12	12.37
Generation totals			33	59.33
Generation survival (S_G) = 0.41				

* Number per kg fresh sagebrush.

** Miscellaneous factors such as predation, misadventure and physiological causes.

See Table 3 for explanation of symbols.

Major mortality factors

Certain trends were apparent in the data compiled from 1971 to 1972. They show that moderate to heavy mortality occurred during the larval and pupal stages. Figure 6 compares the mortality of different age groups during the two field seasons. These data show that the fifth larval instar was the "crucial trial" period for the defoliator. High mortality during this period was brought about by the sequential action of parasites, disease and food shortage.

Parasites: Parasitism increased from 20 to 75% at the study site during 1971, but only from 12 to 24% in 1972 (Table 2). This reduction of parasitism resulted in a 500% increase in defoliator population. It would appear from these data that the parasite complex plays a major role in regulating defoliator density.

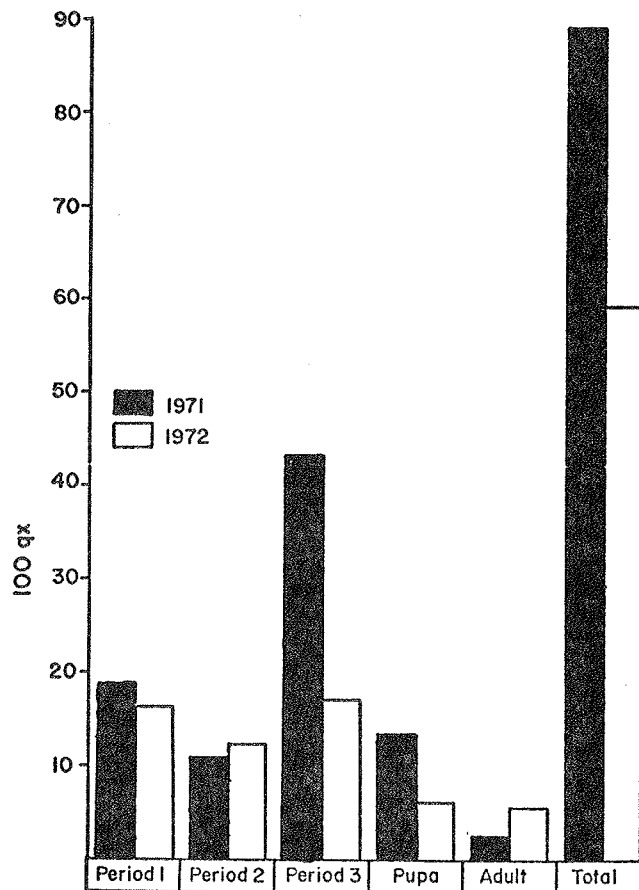


Figure 6. Mortality of *A. websteri* during five age intervals, Curlew Valley site, 1971 and 1972. For each year, 100 q_x values are based on the initial population.

Parasitism may also have caused indirect mortality by making the host more sensitive to catastrophic factors, thus increasing the host mortality prior to the emergence of the parasite.

Fillmore (1965) found some evidence that the ratio of hosts parasitized increased as the host density increased. This also appeared to be the case with the defoliator population at the study site, although the incidence of parasitism definitely lagged behind the host density in 1972. Functional responses of this type have also been observed for parasites of the spruce budworm (Miller, 1960) and the diamondback moth (Harcourt, 1969).

Disease: The microsporidian which infested the defoliator showed no indication of causing a significant population decline. The incidence of the protozoan was high enough in 1972, however, to cause 5% mortality of fifth instar larvae (Table 4). The occurrence of the protozoan was probably a result of defoliator overpopulation, although throughout the course of 1972 the disease remained at an enzootic level.

Competition and overpopulation factors: Several species of insects were found on sagebrush at the study site, such as: a lepidopteran leaf miner, *Bucculatrix tridenticola*; the garden case bearer, *Apterona crenulella*; the harvester ant, *Pogonomyrmex owyheei*; grasshoppers, and many unidentified moths. There is no evidence at present to suggest that these organisms compete directly with the defoliator for food.

Food shortage was evidently an important factor in the reduction of the defoliator population during the 1972 season. When sagebrush plants were completely stripped of foliage, larvae were frequently seen wandering about at the base of the plants. Defoliator mortality from the effects of food shortage was not directly determined, but represents the number missing which could not be accounted for by known mortality factors. Starvation was evidenced by the small size of many mature larvae and the frequent failure of larvae to pupate.

Food consumption and utilization

Figure 7 shows the mean food consumption and weight gain of 25 larvae during the 4th and 5th instars. These data indicate that the larvae ingested, on a dry weight basis, about 37 mg of sagebrush foliage. The mean fresh weight gain of larvae during the same period increased from 0.81 mg to 12.5 mg. The amount of food consumption was not determined for the first to third larval instars. However, an estimate from the body weight of newly-molted 4th instar larvae suggested that food consumption of these earlier instars would not exceed 3 mg. On this basis, the total food consumption for the entire duration of larval development would be about 40 mg of dry foliage or 80 mg of fresh foliage (based on a 50% dry weight).

The results of the utilization experiment involving fourth and fifth instar larvae are summarized in Table 5. The A.D., E.C.I. and E.C.D. indices indicate the insect's ability to gain weight with increased food consumption. These indices are relatively low when compared with other lepidopteran species (e.g., Waldbauer, 1968). Soo Hoo and Fraenkel (1966) suggested that plants with low water content tend to be inferior food and that this results in digestibility indices ranging between 25 and 35%. The high dry matter content of sagebrush leaves, ranging from 42 to 53%, and low digestibility indices of the defoliator, support this conclusion.

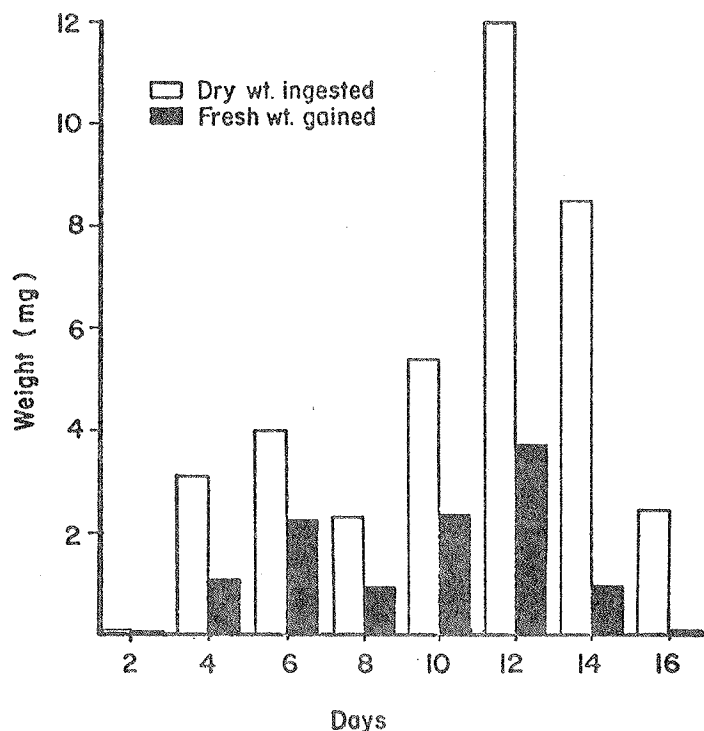


Figure 7. Mean food consumption and weight gain of *A. websteri* during the 4th and 5th larval instars. (DSCODE A3UHL04)

Table 5. Food utilization of 25 fourth and fifth instar larvae of *A. websteri* fed on sagebrush leaves (DSCODE A3UHL04)

	Duration of feeding period (days)	Dry weight consumed (mg)	Dry wt. gained (mg)	Fecal wt. (mg)	A.D. (%)	E.C.I. (%)	E.C.D. (%)	C.I.
Mean	16	37.0	3.1	24.1	34.9	8.4	24.0	0.4
Standard Error	1.1	3.3	0.8	1.2	1.8	0.8	1.6	0.1

A.D. = approximate digestibility.
 E.C.I. = efficiency of conversion of ingested food.
 E.C.D. = efficiency of conversion of digested food.
 C.I. = consumption index.

Defoliation studies

In 1972 the defoliator population was more than five times larger than the previous year. As a result many plants were completely defoliated, and the overall damage was up to 80% in the study area. Most plants recovered from defoliation in the fall. Only 20 to 30% of the plants which were completely defoliated failed to produce new leaf buds.

Data obtained from sampling of defoliation of 26 randomly selected sagebrush plants are summarized in Table 6. Regression analysis of the relationship between percent defoliation and the sagebrush defoliator density revealed only a 5% correlation. It is likely that the lack of correlation was a result of sampling too late in the season for accurate estimation of the larval population which caused the damage. In the previous year the defoliator was rarely affected by factors such as food shortage and crowding, but in 1972 these factors caused high mortality. As a consequence, plants which were highly defoliated during June probably retained fewer larvae than plants that had sustained moderate to low defoliation. The presence of fewer larvae on the defoliated plants would have resulted in an underestimation of larval density.

Table 7 summarizes the findings on the effect of artificial introduction of defoliator larvae to caged plants. The results indicate that all caged plants suffered almost complete defoliation, regardless of the number of defoliators introduced. Introduction of 100 larvae to a caged plant resulted in a 91% recovery of defoliators. However, the addition of a higher number of defoliators to caged plants invariably reduced the defoliator recovery to a level between 28 and 39%. This fact emphasizes the importance of the role of food shortage in the defoliator ecology. On the basis of the results obtained from cage 1, it appears that each kg of sagebrush can support the development of not more than 240 defoliators.

Apterona crenulella

METHODS AND RESULTS

The number of degree-days required to initiate the spring emergence of overwintering first instar larvae of *A. crenulella* has been investigated in our laboratory. Overwintering old larval cases containing eggs were collected from the Green Canyon site near Logan on 29 January, 1972. Three constant temperature

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incubators of 15.5, 21 and 26.5 C with a 16-hr photophase were used for this experiment. One hundred larval cases were placed in each incubator and the number of larvae that emerged each day was recorded. The temperature recorded for development was based on the time necessary to reach 50% larval emergence in the samples. Daily weather data were obtained from a weather station located near the study site. The results are graphically presented in Figure 8. The theoretical base temperature for larval emergence was calculated to be 10 C. The number of degree-days required for the larvae to emerge was calculated by subtracting the minimum development temperature from the incubation temperature, and multiplying this result by the number of days required for 50% larval emergence. The results indicate that 111 degree-days are required for initiation of larval emergence. A calculation of field temperature data showed that this degree-day was reached by late April. This is approximately the time when emergence of overwintering larvae was first observed in the field.

Table 6. Comparison of population density of *A. websteri* and percent defoliation of selected sagebrush plants at Curlew Valley site, July 1, 1972 (DSCODE A3UHL03).

Plant Number	Plant fresh wt. (kg)	No. of defoliators	Defoliators per kg sagebrush	Percent Defoliation
1	0.0845	59	70	71
2	0.1061	13	123	54
3	0.1760	42	239	47
4	0.1943	18	93	40
5	0.0455	28	615	96
6	0.0816	9	110	38
7	0.0726	34	468	93
8	0.1937	26	134	93
9	0.1002	16	159	80
10	0.1125	13	116	40
11	0.0895	9	101	98
12	0.1340	8	60	59
13	0.2246	17	76	78
14	0.1030	16	155	28
15	0.1287	32	249	91
16	0.1264	11	87	91
17	0.1626	22	135	23
18	0.0983	43	437	79
19	0.1138	11	97	73
20	0.0961	12	125	85
21	0.1007	14	139	82
22	0.0940	4	43	74
23	0.0990	10	101	21
24	0.1929	11	57	37
25	0.1158	41	354	98
26	0.1199	38	317	67

Table 7. Defoliation of caged sagebrush plants by four levels of introduced population of *A. websteri* larvae: Curlew Valley site, May 5 - July 1, 1972.

Cage No.	Plant fresh wt. (kg)	No. defoliators introduced	No. defoliators recovered	% defoliators recovered	% defoliation
1	0.4205	100	91	91	96.9
2	0.5025	200	56	28	98.5
3	0.4607	300	117	39	100.0
4	0.5260	400	118	30	100.0

Table 8. Effects of photoperiods on larval emergence of *Apterona crenulella*.

Photophase Duration (hr.)	Photophase		Scotophase		Total no. larvae emerged
	Mean no./hr photophase	%	Mean no./hr scotophase	%	
6	14.31	68.47	6.59	31.53	1227
8	8.14	72.74	3.05	27.26	1140
12	11.81	86.65	1.82	13.35	1307
14	12.82	86.98	1.92	13.03	1192

The effect of different day lengths on larval emergence was investigated by subjecting overwintering larval cases to photophases of 6, 8, 12 and 14 hr in incubators. The experiments were carried out at a temperature of 23.5 ± 1.5 C. Larval emergence was recorded at the beginning and the end of the photophases each day. The results are summarized in Table 8. The data show a direct correlation between the photophase duration and the mean number of larvae that emerged per hour of photophase. At a photophase of 14 hr, 87% of the larvae emerged during the day and 13% during the night. Even at a photophase of 6 hr, approximately 70% of the larvae emerged during the day. These data demonstrate that *A. crenulella* is a day-active species and that larval emergence occurs during the light period of the day. In order to determine the peak of larval emergence during a single day, larval cases were incubated at a 14 hr photophase and larval emergence was recorded at 2 hr intervals. Figure 9 summarizes the results of this experiment. The peak of larval emergence occurred within 2 hr after the initiation of the photophase. More than 90% of emergence was completed during the first 8-hr period. The remainder emerged before the end of the photophase.

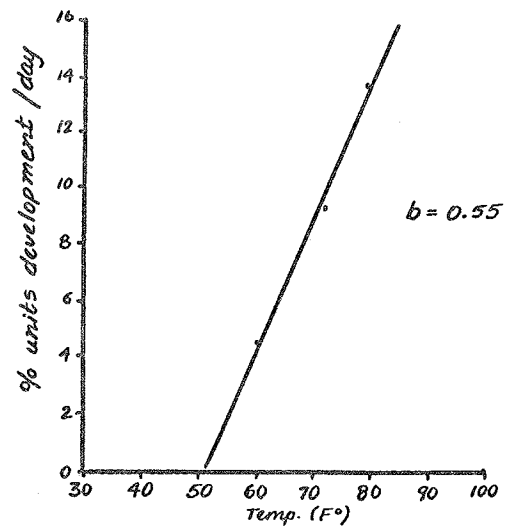


Figure 8. Percentage units of development/day of *A. crenulella* overwintering larvae.

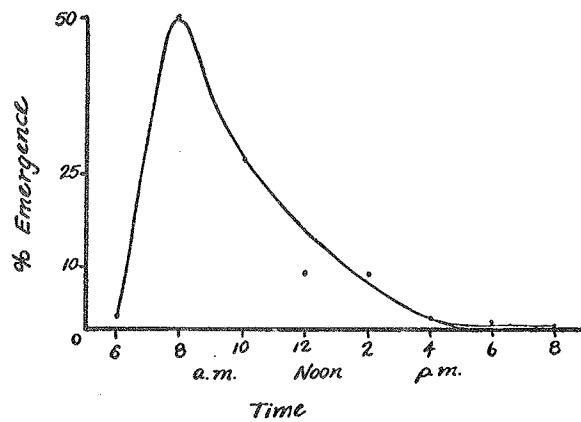


Figure 9. Time of larval emergence when kept in a 14 hr photoperiod.

Examination of a large number of larval cases collected in the field revealed an average of 16.3 eggs per case. An average of 15.3 larvae emerged from these cases, and infertility of 6.1% was indicated. Overwintering mortality was found to be very low in this species. Natural enemies include a clerid predator (*Phyllobaenus* sp.) and an unidentified hymenopterous parasite.

EXPECTATIONS

The population trend of the defoliator will be predictable when additional field data are compiled and analyzed. Two mortality factors, natural enemies and food shortage, exert major influences on the defoliator population. Detailed measurements of these mortality factors will provide accurate assessment of their relative importance in the regulation of population. Information on host range and degree of defoliation under field conditions will be available to assess the extent of sagebrush infestations. Laboratory studies will provide biological data that are essential inputs for the construction and improvement of life tables for this species.

Investigations on seasonal history and mortality factors of the garden casebearer will provide preliminary data on the ecology and population dynamics of this insect. Data on host range and feeding habits of the garden casebearer will be available to estimate the extent of defoliation of the big sagebrush as well as on other plants by this polyphagous insect. Biological data necessary for the construction of life tables will be supplied in the course of the study.

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1972 PROGRESS REPORT

NITROGEN DYNAMICS IN STANDS DOMINATED BY SOME
MAJOR COLD DESERT SHRUBS

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Utah State University

Research Memorandum, RM 73-35

MAY 1973

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Report Volume 3

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PART I

2.3.4.1.-1

A B S T R A C T

Effects of various environmental factors on several nitrogen fluxes in Curlew Valley, Utah, were examined. The activities of interest were nitrogen influx from precipitation, ammonium volatilization, leaching from plants, N-fixation (autotrophic and heterotrophic), nitrification, ammonification, proteolysis and denitrification.

The studies were conducted with soils collected from 3 sites west of the Wildcat Hills, site #5 is a sagebrush (*Artemisia tridentata*) dominated area; site #6 is a winterfat (*Eurotia lanata*) dominated area; and site #7 is dominated by shadscale (*Atriplex confertifolia*).

It appears that a considerable amount of nitrogen, as nitrate, is added to soils by way of precipitation. The amount of NO_3^- , however, is proportional to weight of dust present in the precipitation.

NH_3 volatilization from soils was verified. There seems to be some effect of the canopy on NH_3 volatilization but this has not yet been fully elucidated. More replications and applications of ^{15}N methodology should help clarify this phenomenon.

Denitrification experiments showed evidence of the "priming effect" upon addition of KNO_3 and incubation. Further studies in progress and ^{15}N data will clarify the rate of denitrification when the "priming effect" is evident.

Nitrification and ammonification experiments at lower soil humidities showed that considerable biological activity in desert soils may take place at water tensions as high as -45 atmospheres.

The ammonia electrode was introduced as a rapid method of determining soil ammonium ion concentration.

It was thought that due to the high pH of soils, NO_2^- may accumulate; however, nitrite has not been found to accumulate significantly.

Ammonium ion does inhibit N-fixation, but due to the low NH_4^+ values for Curlew soils, it may not be significant here.

N-fixation beneath the surface crust may be potentiated if a readily available carbohydrate supply is present; otherwise, subsurface (heterotrophic) N-fixation is negligible. Dark or endogenous N-fixation is 10-13% of light fixation. N-fixation

on the winterfat site is only a fraction of the same in the sagebrush or shadscale sites. N-fixation and also nitrification rates are greatly inhibited by the shrub litter.

N-fixation occurs optimally at 30 C, and is greatly reduced below 20% moisture.

It is expected that these results will be expanded and verified by ^{15}N methods in 1973.

Preceding studies are described in: J. Skujins, IBP Process Study, Progress Report (RM 72-40).

INTRODUCTION

The exploratory studies (1969-1970) and the process studies on nitrogen turnover in Curlew Valley soils in 1971 were performed on the IBP Desert Biome validation study area. Starting in 1972, however, the project was revamped to be a collective effort by J. Skujins and N. West and the study sites were chosen on the west side of Curlew Valley at the contour of the Stansbury Water Plain. These sites have been extensively studied previously with respect to soil chemical and physical characteristics and plant phenology and plant growth.

The intent of the study is to look at the several and varied nitrogen input, transformation and loss fluxes, to determine the importance of these in a representative cool desert ecosystem and to obtain quantitative values for the most significant ones.

OBJECTIVES

The objectives for 1972 were to determine:

1. Nitrogen fixation by the surface crust and in the soil profile (acetylene reduction method),
2. Ammonification at various moisture availability levels,
3. Characteristics of denitrification,
4. Nitrification at various moisture availability levels,
5. Kinds and respective amounts of nitrogen entering the ecosystem through precipitation,
6. Kinds and respective amounts of nitrogen leaching from above-ground vegetal surfaces,
7. Amounts of ammonia released from soil profiles in the systems of interest.

METHODS

Because of the lack of existing methodology appropriate to deserts, much of the period was devoted to working out procedures by which longer and more detailed runs of data will be forthcoming in 1973.

Sampling sites

Three sites were chosen on the west side of Curlew Valley. These locations make about a 1.75 km bisect of the valley bottom at the Stansbury Water Plain contour. The precise locations (Figure 1) were chosen because of their relation to prior study sites where data were available on soil physical and chemical characteristics (Gates, et al., 1956; Mitchell et al., 1966; Bjerregaard, 1971), climate, soil moisture, plant phenology (Gasto, 1969) and plant growth (Love and West, 1972; West, 1972). Sites dominated by nearly pure stands of *Artemisia tridentata* ssp. *wyomingensis* (big sagebrush), *Atriplex confertifolia* (shadscale), and *Eurotia lanata* (winterfat) were selected. Detailed soil descriptions appear in Tables 1-3.

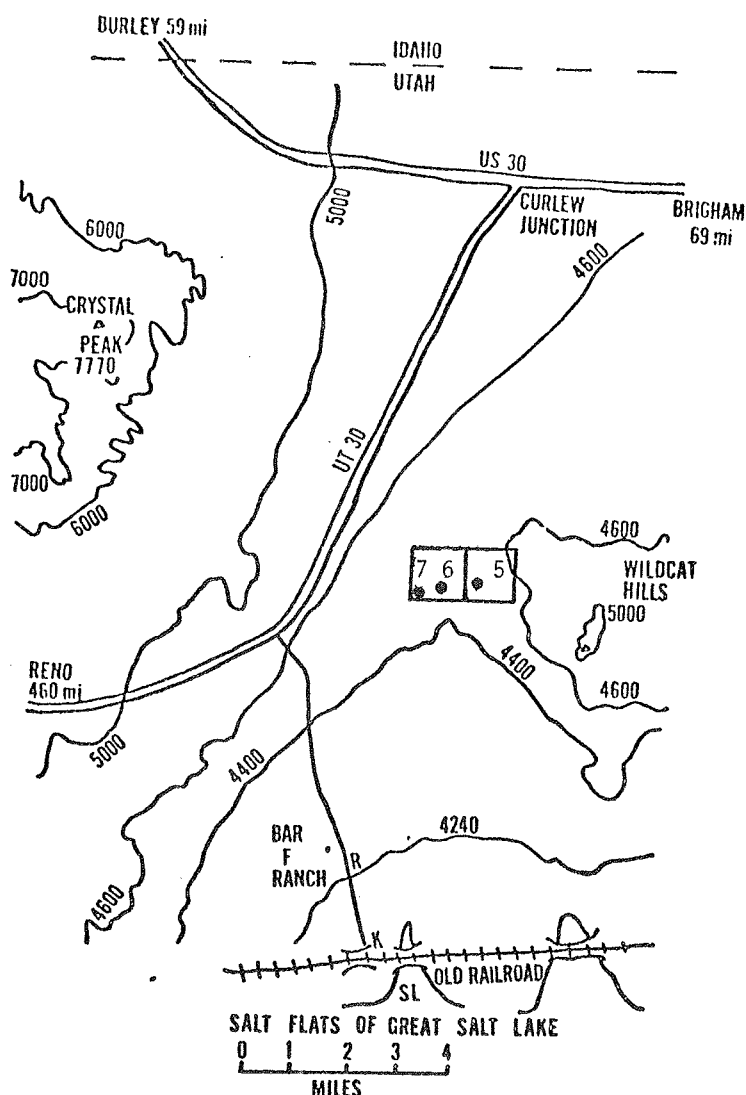


Figure 1. Sketch map of Curlew Valley sampling points.

Site 7 *Atriplex confertifolia*

Site 6 *Eurotia lanata*

Site 5 *Artemisia tridentata*

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Table 1. Profile description of soil at big sagebrush site No. 5 Curlew Valley -- Sect 14, T. 13 N., R. 11 W.

A1	0 - 10 cm	Dark Grayish Brown (2.5Y 4/2 moist 7/2 dry) loam; strong very fine platy separating to fine granular; a few vesicles in the upper 2.5 cm; clear wavy boundary.
B	10 - 26 cm	Light brownish gray (2.5Y 6/2 moist 8/2 dry) silt loam: weak prismatic separating to moderate fine granular; clear wavy boundary.
C _{ca}	26 - 62 cm	Light brownish gray (2.5Y 6/2 moist 8/2 dry) silt loam; moderate fine granular; firm; gradual boundary.
C1	62 -105 cm	Gray Brown (10YR 5/2 moist 6/3 dry) silt loam; weak fine granular; friable; gradual boundary.
C	105 -115 cm	Light Brownish Gray (2.5Y 6/2 moist 7/2 dry) silt loam; strongly mottled with large contrasting 2/5Y 4/6 and 10YR 5/6 mottles gypsum concentrated in this zone.

Varved sediments in alternating layers as follows:

115-123 cm, silt; 123-128 cm, sand; 128-133 cm, silt; 133-145 cm, sand; 145-140 cm, silt; 150-160 cm, sand; 160-165 cm, silt; 165-180 cm, sand.

Silt layers are mottled and firm in place, sand layers are loose.

This pedon is calcareous throughout.

Table 2. Profile description of soil at winterfat site No. 6 Curlew Valley -- Sect. 15, T. 13 N., R 11 W.

A1	0 - 8 cm	Gray Brown (2.5Y 5/2 moist 7/2 dry) loam; strong medium platy, clear wavy boundary.
B1	8 -20 cm	Gray Brown (2.5Y 5/2 moist, 7/2 dry) silt loam; weak fine granular; loose, friable; clear wavy boundary.
B2	20- 43 cm	Gray Brown (2.5Y 5/2 moist, 7/2 dry) silt loam; weak fine granular; loose, friable; clear smooth boundary.
C ₁ Ca	43- 74 cm	Gray Brown (2.5Y 5/2 moist, 7/2 dry) very fine sandy loam; weak fine granular; loose, friable; gradual boundary.
C ₂	74- 99 cm	Gray Brown (2.5Y 5/2 moist, 7/2 dry) sandy loam; very firm in place, slightly hard; clear wavy boundary. Much volcanic glass.
IIC ₃	99-125 cm	Gray Brown (2.5Y 5/2 moist, 7/2 dry) fine sandy loam; massive; very firm in place, few cicada casts and few mottles along bedding planes. Abrupt boundary.
IIC ₄	125-160 cm	Gray Brown (2.5Y 5/2 moist 7/2 dry) interbedded silts and sands many fine prominent 2.5Y 5/6 mottles, sand lenses about 0.5 cm thick silt layers to 5 cm thick.
	160-195 cm	Similar to above. Separated for sampling and analysis.
This pedon is calcareous throughout.		

Table 3. Profile description of soil at shadscale site No. 7 Curlew Valley -- Sect. 15, T. 13 N. R., 11 W.

A1	0 - 13 cm	Gray Brown (10YR 5/2 moist, 7/2 dry) silt loam; vesicular platy vesicles concentrated in surface 2.5 cm. Clear wavy boundary.
B	13 - 32 cm	Brown (10YR 5/3 moist, 6/3 dry) silt loam; moderate fine granular; clear wavy boundary.
C _{ca}	32 - 66	Olive Brown (2.5Y 4/3 moist 7/2 dry) silt loam; moderate fine granular; clear wavy boundary.
	66 - 84 cm	Dark Grayish Brown (2.5Y 4/2 moist, 7/2 dry) silt loam; strong medium platy; cicada activity; clay wavy boundary.
IIC _{ca}	84 -132 cm	Gray Brown (10YR 5/2 moist, 6/2 dry) silt loam; weak medium prismatic separating to weak medium subangular blocky; seams of CaCO ₃ along cicada casts; few mottles, clear wavy boundary.
C	132 -162 cm	Light Brownish Gray (2.5Y 6/2 dry) silt loam; weak, medium subangular blocky; mottles of 5YR 5/6 mottles and gypsum concentrated in 154-157 cm zone.
	162 -175 cm	Gray Brown (2.5Y 5/2 moist, 6/2 dry) silt loam massive, friable seams of gypsum.
	175 -183 cm	White 2.5Y 8/2 with mottles of 10YR 5/6 and seams of gypsum. Fine roots extend to 167 cm.
This pedon is calcareous throughout.		

Supplementary textural and chemical analyses of these soils appear in Table 4. All profiles are members of the Thiokol Series, fine silty mixed mesic family of xerollic calciorthid.

Sites 1, 2, 3 and 4 are described in the Annual Progress Report (Skujins, 1972).

Above-ground nitrogen input and loss

The automatic precipitation collectors were limited to use where line electric power was available. They were first installed on Victor Land and Livestock Co. property about 5 km west of Snowville but later moved to the Ecology Center compound in Snowville when irrigation sprinklers affected the first location.

The nitrogen input in precipitation was analyzed by use of a Wong Mark IV Automatic Precipitation collector. The "wet" was separated from the "dry" precipitation through moisture-sensitive controls on the covers of the nalgene containers. The "wet" gauge opened when precipitation wetted the sensor and closed when the storm ceased and the sensor dried off. The "dry" gauge was open when its sensor was dry. Particulate matter falling in the absence of rain, snow or hail was thus separable from that being "scrubbed" out by precipitation. Materials were collected by Biome personnel living at Snowville.

Table 4. Textural and chemical analyses of soils at Curlew Valley Sites; profiles of which are described in Tables 1-3

Shadscale Site No. 7	Profile depth	Map		Class.	ppm B	(WSS) me/l Na	mmhos EC _e	(Air dry) %CaCO ₃
		% Sand	% Clay					
Shadscale Site No. 7	0 - 13 cm	19.8	16.2	64	1.0	64	6.7	15.2
	13 - 32	34.2	20.9	44.9	14.4	265	34.0	11.5
	32 - 66	15.5	18.2	66.3	10.4	915	89.0	26.6
	66 - 84	15.4	8.6	76.0	2.7	840	91.0	26.1
	84 - 132	2.2	27.4	70.4	1.9	328	42.0	26.1
	132 - 162	3.5	26.8	69.6	3.5	318	42.0	18.9
	162 - 175	6.0	27.1	66.9	4.0	330	45.0	20.0
	175 - 183	5.0	27.2	67.8	3.9	380	52.0	13.1
	183 - 193	4.3	29.8	65.9	3.0	280	35.0	11.5
	(contact)	3.4	28.8	67.8	3.6	329	42.0	19.1
Big Sagebrush Site No. 5	183 (Krotovina)	8.9	25.8	65.3	3.2	308	43.0	17.6
	0 - 10 cm	25.7	15.3	59.0	0	3.0	1.4	14.7
	10.5	29.8	12.5	57.7	0	2.5	.5	19.3
	32	21.5	9.7	68.8	3.6	110	12.0	30.3
	62 - 105	31.4	10.9	57.7	3.9	413	50.0	17.5
	105, 115, 121, 123 Silt varves	15.5	12.0	72.5	3.7	240	32.0	19.0
	173 - 180	15.8	14.4	69.8	2.9	242	34.0	19.4
	Sand varves, composited	81.8	3.9	15.0	2.7	138	19.0	12.8
Winterfat Site No. 6	0 - 8 cm	44.9	9.2	45.9	.2	2.3	1.7	14.0
	8 - 20	47.7	7.6	44.7	.1	1.6	.4	17.7
	20 - 43	47.4	6.7	45.9	.1	3.0	.6	19.1
	43 - 74	35.0	5.2	59.8	1.1	114	17.0	21.7
	74 - 99	41.2	2.9	55.9	3.5	112	14.0	19.0
	99 - 125	63.3	2.9	33.8	3.9	85	9.6	17.6
	125 - 160	2.5	16.6	80.9	4.5	195	27.0	19.3
	160 - 195	5.0	15.7	79.3	4.0	195	26.0	19.8

Exchange time was furnished to make up for this on-site service. A few cm^3 of chloroform was also added to the sample to inhibit microbial activity. The samples were frozen at Snowville and periodically brought to Logan (DSCODE A3USQ20). A recording rain-gauge was operated at the Snowville compound to give storm intensity and timing. A pair of glass funnel type precipitation collectors were also installed for backup on total input should the automatic mechanisms fail.

Leaching techniques were developed after pilot sampling to develop a feasible procedure. A modified sprinkler setup adapted from the Rocky Mountain infiltrometer (Dortignac, 1951) was used to create an artificial rainfall over a 100×100 cm collection pan on which freshly cut plants were secured in an upright position by a Christmas-tree type base support. The water flowing from the pan was divided into aliquots collected over sequential time intervals (DSCODE A3USQ21). The set-up was run in high-ceilinged Utah Highway Department sheds at Snowville to prevent wind effects.

Water samples for both processes were analyzed by the semi-microKjeldahl method for total N (Chapman and Pratt, 1961). Nitrate was determined by using Hack Chemical Company's DR-EL Direct Reading, Portable Engineers Laboratory Kit. This is a patented cadmium reduction method (modified diazotization with 1-naphthylamine-sulfanilic acid). Ammonium from N was analyzed by a indole-phenol chlorometric method (Solorzana, 1969). Height and canopy volume measurements were taken, before leaching. The shrubs used were then oven dried and weighed after treatment. Debris was screened out of the leachate.

Ammonia volatilization

The NH_4^+ ion is the form most likely to come from fixed organic N. Therefore, an experiment was initiated to determine what percent of this NH_4^+ was volatilized over an 8-day period.

Soil samples (160 g) from under the canopy and between the canopy were amended with $(\text{NH}_4)_2\text{SO}_4$ containing 30 At% ^{15}N . One mg N for each 50 g of soil raised the NH_4^+ concentration in the soil to 20 ppm, a concentration that may be found under natural conditions. The N was added as a solution in a 40 ml aliquot. Moisture and temperature remained constant.

The NH_3 volatilized was trapped in 10% H_2SO_4 by sucking the atmosphere above the soil through the acid. An initial acid trap absorbed any NH_3 in the laboratory atmosphere. The acid was removed at each time period of the experiment and replaced with new acid.

2.3.4.1.-10

The acid was neutralized with NaOH and made alkaline for steam distillation. The NH_3 liberated by the Kjeldahl method was collected in H_3BO_3 - indicator solution and titrated with 0.01N KHIO_3 . The mg N was calculated from this determination.

Total gaseous loss of NH_3 escaping from the soil was also studied in climate-controlled gas exchange chambers (Koch et al., 1968) in the laboratory. Plaques of soil (3 cm deep) from the shrub interspaces were lifted out intact and placed in 20 x 30 x 5 cm plastic trays. These were placed in the gas exchange chambers at conditions of 25 C and 6 C dewpoint humidity and allowed to metabolize for 1 day. The NH_3 given off was collected by bubbling the air through dilute H_2SO_4 . The N content was analyzed by the semi-micro-Kjeldahl technique (DSCODE A3USQ22).

Denitrification

Ten-g soil samples from under the sagebrush canopy and between the canopy were amended with 2 mg of N from KNO_3 containing about 2 A% ^{15}N . The samples were incubated at constant 32 C temperature for 1, 4 and 8 days at three different moisture contents (5%, 15% and 30%). Upon completion of the incubation time 30 ml of 2 N KCl was added to extract NH_4^+ , NO_2^- and NO_3^- . Kjeldahl determination done on the remaining soil reveals the amount immobilized. The MgO steam distillation of the KCl extract with Devarda alloy gives the mg ^{15}N left in the soil. Differences between this and the amount added was classified as denitrification. The change in A% ^{15}N with time can be used to determine a rate of mobilization.

The experimental setup for the three moistures (H, M, L), times (1, 4, 8), and replication (a+b) is depicted below:

Between Canopy	L1a,	L4a	L8a
	M1a,	M4a	M8a
	H1a	H4a	H8a
	H1b	H4b	H8a
Under Canopy	H1a	H4a	H8a
	H1b	H4b	H8b

The KNO_3 was added to the soils in solution. Respective aliquot sampling gave results on imposed moisture contents.

Nitrification potential

The potential of soil samples was measured in duplicate and average values were reported (DSCODE A3USQ05).

Ammonification potential (DSCODE A3USQ03)

Soil samples from the shadscale site taken at 0-3 and 5-20 cm depths, and cultivated garden soils, were dried at room temperature for 5 hr. These three soils were sieved and examined for water-holding capacity. Soils were moistened with water to obtain 25, 40, 55, and 75% water-holding capacity. Soils of different water-holding capacity were checked for water potential (bar pressure) by the use of a thermocouple psychrometer at the end of the experiments. The correlation (as determined with a thermocouple psychrometer, WESCO) between water-holding capacity and water potential was established as follows:

Water-holding capacity (%)	Water potential (-bar pressure)		
Air dry soil (5 hr dried at room temp)	115	to	125
25	40	to	45
40	5	to	10
55	1.7	to	1.8
75	0.25	to	0.3

All soil samples tested from the shadscale site fell within these limits.

Fifty g samples of moist soils were placed in 250 ml Erlenmyer flasks. In all the flasks 5 ppm 2-chloro-6 (trichloromethyl) pyridine was added. Keeping one set as a control, in other sets either 0.25 g casein per 50 g soil or 5.8 g plant and peat litter were added. In each flask, the trap-tube containing 5 ml 0.02N H_2SO_4 trapped volatilized ammonia. These flasks were then stoppered with rubber stoppers and incubated at 22 C for four weeks.

NO_2^- and NO_3^- were determined by centrifuging 1 g samples with 5 ml distilled water at 10,000 rpm for fifteen minutes. The supernatant was analyzed for NO_2^- and NO_3^- by the sulfanilic acid (Allen, 1957) and 4-methyl-umbelliferone method (Skujins, 1964), respectively. At the end of the experimental run trap-tubes were analyzed for NH_4^+ by Nessler's method. Also, at the beginning and at the end of an experiment the organic-N contents of each soil and of incubated samples were determined with the Kjeldahl method as described below. All experiments for ammonification were performed in duplicate and average values were reported.

Analysis of NO_2^- and NH_4^+ , for samples collected after 15 April, 1972 (DSCODE A3USQ01)

Soil sampling. Samples were taken at 0-3 cm, 5-20, 40-50 cm, and 70-80 cm depths. The samples were placed in sterile whirl-a-pak bags and stored at 3 C. The entire sample was mixed well with a mortar and pestle just prior to use.

Intact soil crusts (0-3 cm depth) were collected in whirl-a-pak bags and stored at 3 C until use.

2.3.4.1.-12

Soil cores (0-3 cm), with intact crusts, were collected using 16 x 500 mm glass tubes. The upper end is fire polished and capped with an injectable serum bottle rubber stopper. The lower end is not fire polished so as to facilitate penetration into the soil to the 3 cm depth. After collection of the core, the lower end is sealed with a rubber stopper. Cores were stored at 3 C until use.

Soil extraction: Soil samples were weighed and extracted with 2N KCl (5 ml KCl/g of soil) by shaking for 1/2 hr. The soil was then permitted to settle for approximately 1/2 hr. The supernatant is used for subsequent nitrite-N and ammonium-N analysis.

Ammonium-nitrogen by Kjeldahl method: Twenty-five ml of the KCl soil extract supernatant was introduced into a Kjeldahl flask; approximately 1 g of MgO was added, and the mixture boiled by steam. Approximately 40 ml of the distillate was collected in a receiver flask containing 5 ml of 2% boric acid and a few drops of indicator. The collected solution was titrated with standard H_2SO_4 .

$$\mu g \text{ NH}_4^+-N/g \text{ soil} = \frac{\text{ml } H_2SO_4 \text{ used for titration}^* \times \text{Normality } H_2SO_4 \times 14}{5 \text{ g}}$$

* corrected for KCl blank

Ammonium-nitrogen by the ammonia electrode method: One hundred ml of the KCl soil extract supernatant was carefully decanted into a 100 ml volumetric flask. One ml of 10N NaOH was added and the solution mixed thoroughly and decanted into a 100 ml beaker for immediate assay. The ammonia electrode (Orion Co.) was used with a Corning pH meter with an expanded scale. The pH was set at zero, and read at 0-1 expand. Selector was set at + or - millivolts depending upon the reading (or concentration of ammonia). The 0-1 reading (red scale) was multiplied by 100 to give the millivolt reading. Millivolts are a linear function of the log of the ammonia concentration. The respective results regarding this method are shown in Table 5 and Figures 2 and 3.

Table 5. Comparison of ammonium-N determination by ammonia electrode and Kjeldahl methods (DSCODE A3USQ01)

$\mu g/ml$ ammonium-N		
By weight (theoretical)	Ammonia Electrode	Kjeldahl
20.20	20.12	21.08
8.06	7.98	7.75
4.03	3.95	4.18

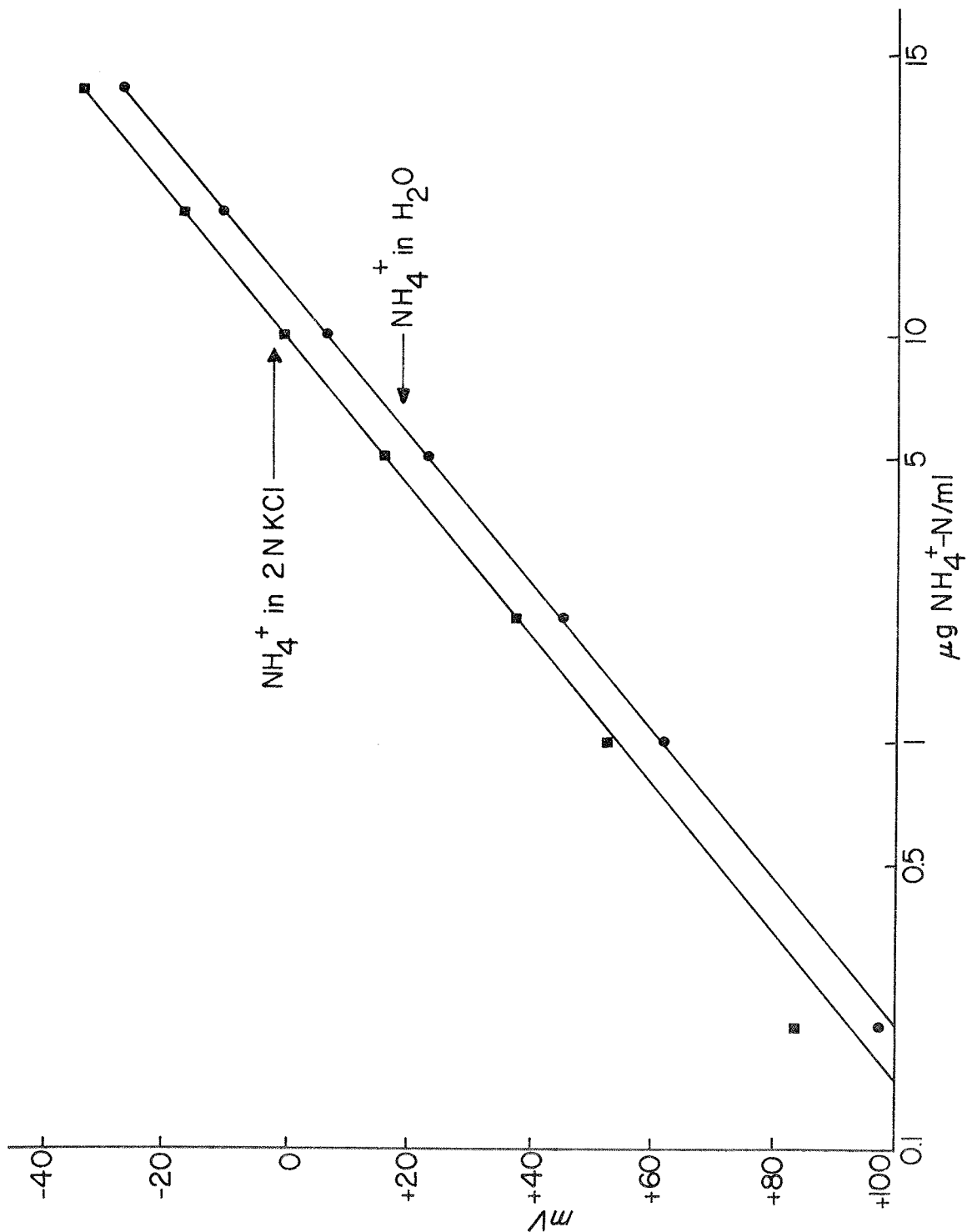


Figure 2. Ammonium-N by ammonia electrode method in 2N KCl and in distilled water. DSCODE A3US001

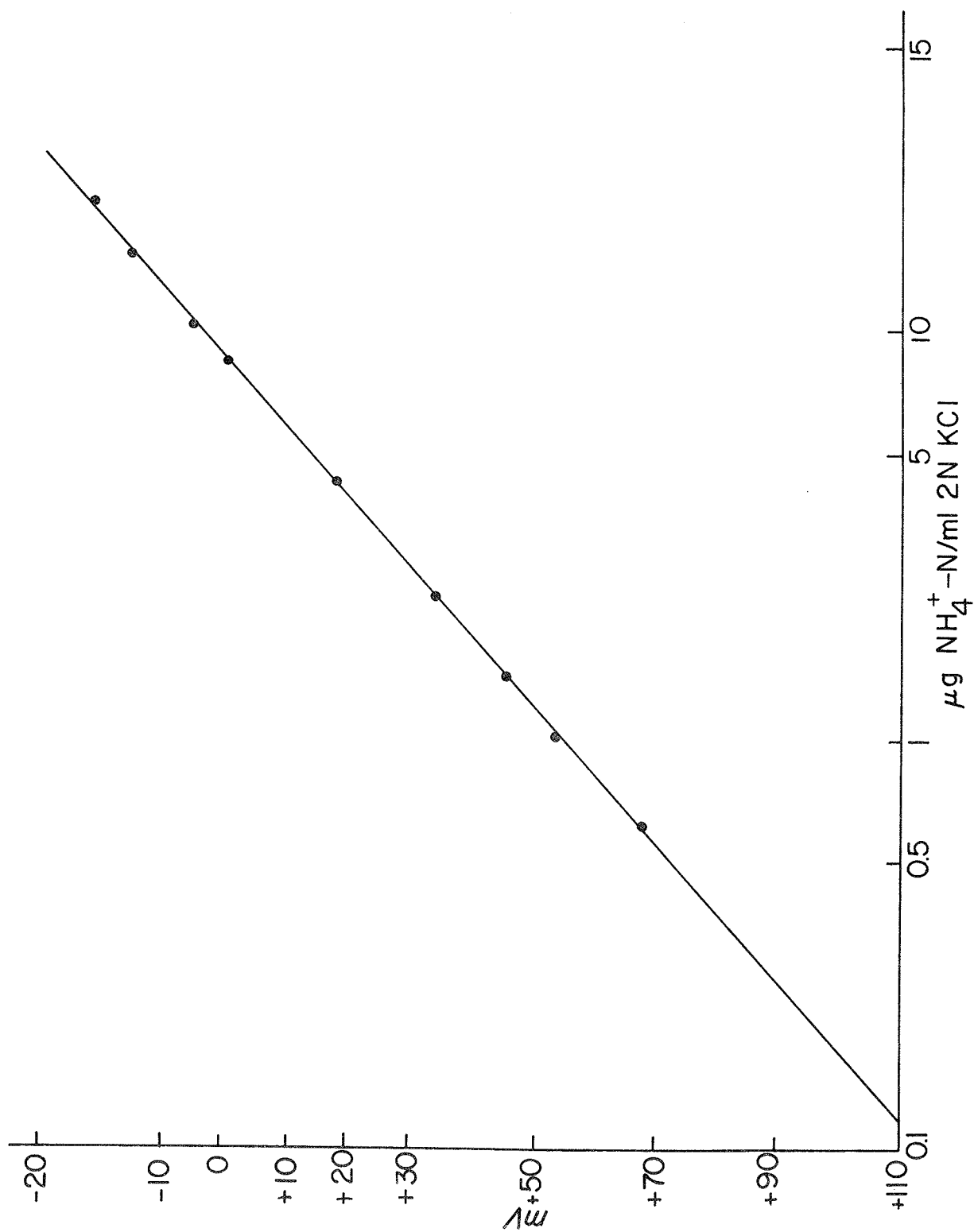


Figure 3. Ammonium-nitrogen standard (ammonia electrode) DSCODE A3USQ01.

Concentrations of ammonia around 1 $\mu\text{g/ml}$ or less require a 4-5 minute equilibration (reading) time. Greater concentrations require 2 minutes or less to read. It is important to run a KCl blank, particularly when working with low concentrations of ammonia. Ammonia (or $\text{NH}_4^+\text{-N}$ concentration) is read from a standard of millivolts vs. $\log \text{NH}_3$).

$$\mu\text{g NH}_4^+\text{-N/ml} \times 5 = \mu\text{g NH}_4^+\text{-N/g soil}$$

Nitrite analysis. The KCl soil extract was filtered through a Watman #5 filter. Two ml of the filtrate (dilute if the nitrite concentration is greater than $2.5 \times 10^{-4}\text{M}$) was withdrawn. Five ml of sulfanilic acid solution was added to the 2 ml followed by addition of 5 ml of the α -naphthylamine solution. The solution was mixed and permitted to stand for 1/2 hour. Absorbance was read on a Spectronic 20 spectrophotometer at 540 nm. $\mu\text{g NO}_2^-\text{-N/2 ml}$ KCl extract was read from a standard curve of absorbance 540 vs. $\text{NO}_2^-\text{-N/2 ml}$.

$$(\mu\text{g NO}_2^-\text{-N/2 ml KCl extract}) \times 2.5 = \mu\text{g NO}_2^-\text{-N/gram soil}$$

Reagents: 1) α -naphthylamine solution: 0.5 g α -naphthylamine is dissolved in 100 ml of glacial acetic acid and the volume made to 500 ml with water. 2) sulfanilic acid solution: 2 g of sulfanilic acid is dissolved in hot water: 100 ml of glacial acetic acid is added and the volume is made to 500 ml with water.

Nitrogen fixation by acetylene reduction (DSCODE A3USQ04)

The acetylene reduction assay is a modification of the method of Stewart et al. (1967).

Two to three mm of soil crust from an intact crust were scraped from the surface into a 6.5 ml serum bottle. The crust was then moistened with 4-5 drops of distilled water, the bottle capped with an injectable rubber stopper, and evacuated. Following evacuation the bottle was flushed with a mixture of Ar , O_2 , CO_2 (80%, 20%, 400 ppm) (Matheson Co.). At zero time acetylene was injected to yield 0.1 atmospheres of C_2H_2 . The glass tubes (approx. 13 ml airspace volume) used to collect the soil cores were treated in a similar fashion.

After the appropriate incubation time, under specified conditions, a 0.2 ml sample was withdrawn for ethylene (C_2H_4) analysis using a Varian series 1700 gas chromatograph. Reactions may be slowed to a negligible rate by placing the reaction vessel at 3 C.

The Varian GC analysis uses helium as a carrier gas with a flow rate of approximately 25 ml/min. at a temperature of 50 C, with a 3 m (10 ft.) Porapak R column. The injection temperature is set at 55 C and the Hydrogen flame detector at 90 C.

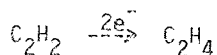
A Varian model 20 strip chart recorder was used for analysis of the ethylene and acetylene peaks. A chart speed of 38 cm (15 inches)/hr. is appropriate. Peak height is not proportional to sample volume injected, so it is important to consistently use a 0.2 ml volume for assay.

The Attenuation was set at 1 and the Range at 10^{-11} for assaying ethylene peaks. Setting Attenuation to 2 and Range to 10^{-9} was used for reading the acetylene peak; acetylene being a useful internal standard.

The retention time for ethylene is 4.5 minutes; and 5.9 minutes for acetylene. Ethylene concentration was read from a standard curve obtained using pure ethylene (Matheson Co.).

Calculations: The surface area of both the serum bottles and the 16 x 500 mm glass tubes is 1.324×10^{-8} hectares.

While there appears to be some dispute about making the following approximation (Bergerson, 1970), the following assumptions will be made in order to obtain an estimation of nitrogen fixed by the acetylene reduction technique:



$$1.0 \text{ nanomole } \text{C}_2\text{H}_4 \text{ produced} = \frac{28 \times 10^{-12}}{3} = 9.33 \times 10^{-12} \text{ kg nitrogen fixed}$$

$$\text{and nanomoles } \text{C}_2\text{H}_4 \text{ produced} \times \frac{9.33 \times 10^{-12}}{1.324 \times 10^{-8}} = \text{kg nitrogen fixed per hectare.}$$

Water potential

Water potential (in negative bar pressure) was determined with a Wescor Psychrometric Microvoltmeter MJ55.

Percent moisture

Soil percent moistures were determined by weight differences. The soils were dried overnight at 110 C.

RESULTS

Due to delays in arrival of equipment, no data on N_2 fixation by ^{15}N methods are presently available. However, some preliminary results are available for NH_3 volatilization and denitrification and are presented herein.

Ammonia volatilization

The mg N volatilized from 160 g soil from three sites and either under the canopy or between the canopies are presented in Table 6. Moisture content of the soils was $25 \pm 2\%$. The temperature was $21 \pm 1^\circ\text{C}$.

Table 6. Ammonia removed from the atmosphere above soils from the Curlew Valley and captured in H_2SO_4 (DSCODE A3USQ22)

Site and Condition		Time in Days							
		1	2	4	8	1	2	4	8
		mg N (cumulative)				% of applied N (cumulative)			
Sagebrush	between canopies	0.05	0.28	0.45	0.53	1.0	5.6	9.0	10.6
	under canopy	.17	.22	.24	.27	3.4	4.4	4.8	5.4
Winterfat	between canopies	.16	.29	.46	.55	3.2	5.8	9.2	11.0
	under canopy	.20	.24	.31	.35	4.0	4.8	6.2	7.0
Shadscale	between canopies	.16	.22	.31	.42	3.2	4.4	6.2	8.4
	under canopy	.50	.78	.95	1.09	10.0	15.6	19.0	21.8

Figure 4 depicts the influence of the canopy covering on NH_3 volatilization.

The gaseous loss of NH_3 from the dry soils run in the environmental chambers was undetectable, however (DSCODE A3USQ22).

Nitrogen input by precipitation

Table 7 summarizes the nitrogen inputs in the storms that were sampled. It excludes those samples which were invalidated by contamination or when opening or closing of the automatic covers was miscued by the temperature sensitivity of the mechanism. The automatic precipitation collection devices were not received until April. After encountering some difficulty in locating a suitable site with line power and getting an electrician to connect it, the equipment was finally running in late May. After collecting a few storms, we discovered that sprinkler irrigation would come too close to our first site. We encountered considerable problems with defecating birds and bugs being attracted to the gauges. The control mechanism for opening and closing the gauges was very temperature-sensitive and gave erratic responses.

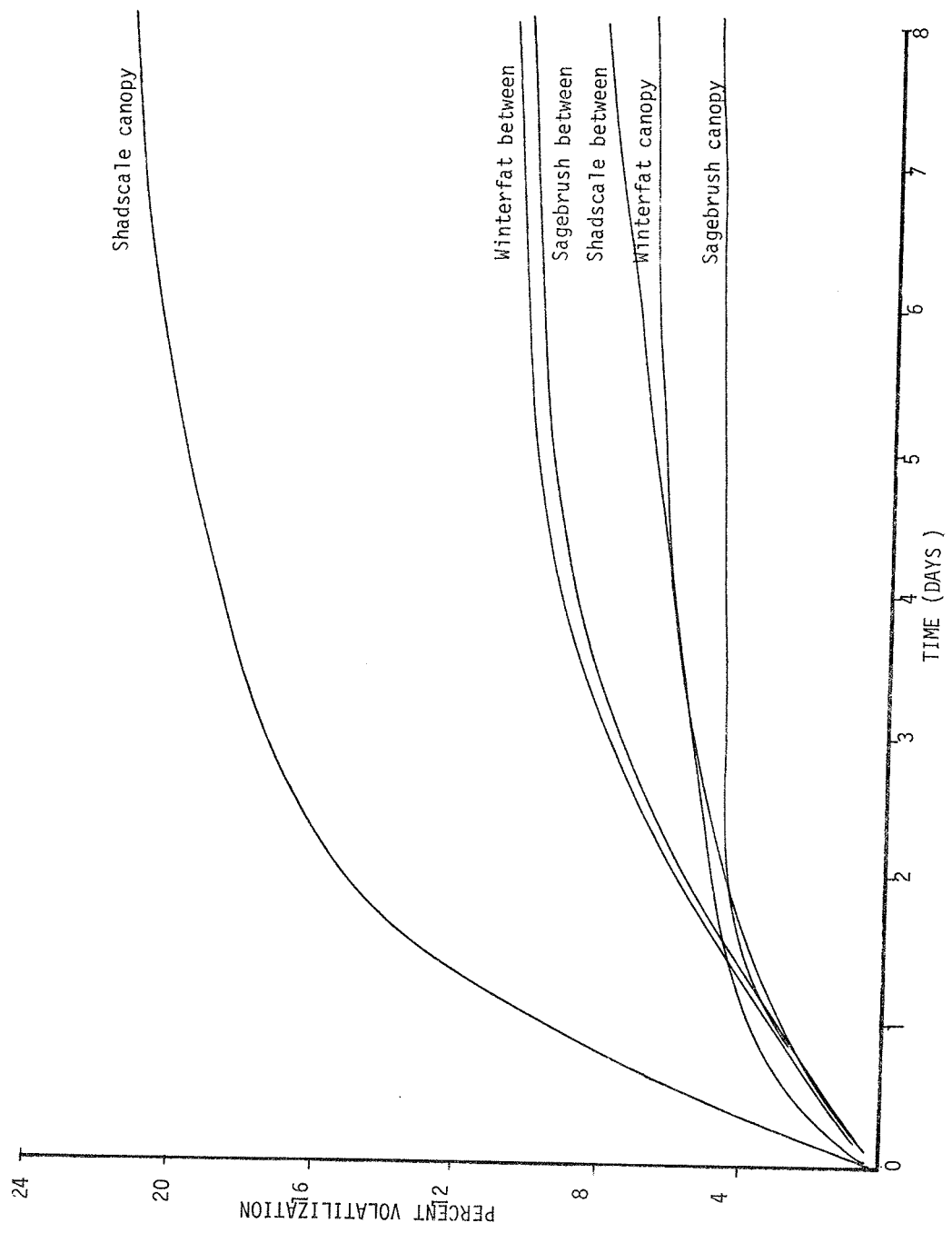


Figure 4. Influence of plant canopy on ammonia volatilization.

Table 7. Intervals, amount, storm type and nitrogen and particulate content of precipitation at and near Snowville, Utah, 1972 (DSCODE A3USQ20)

Date	Storm Type	Amount Collected	Total N	NO ₃ N	NH ₃ N	Particulates
<u>Automatic Collectors</u>						
6/24/72	Rain-Lightning	70 ml	14 µg	4.14 µg	8.2 µg	1.0 mg dust
6/3 to 6/24	Dry ppt		4 µg	3.5 µg		2.5 mg dust
<u>Funnel Type</u>						
10/4/72	Gentle fall rain	250 ml	37 µg	16.7 µg	17 µg	6 mg dust
10/14/72	"	8.5 ml	3 µg	1 µg	2 µg	0.5 mg dust
10/24/72	"	60 ml	193 µg	123 µg	58 µg	23 mg dust
11/20/72	Snow	148 ml	322 µg	288 µg	15 µg	51 mg dust
<u>Automatic Collectors</u>						
10/20/72	Wet	287 ml	510 µg	455 µg	10 µg	72 mg dust
11/2 to 11/20/72	Dry ppt		187 µg	170 µg	2 µg	21 mg dust

The gauges were returned to the manufacturer for modification. They were not received and reinstated at the Snowville compound until November. Instruments are now properly working and procedures are clarified with cooperating personnel. We should be able to obtain a quite complete run for 1973 (DSCODE A3USQ20).

N leaching from plants

Figures 5-13 summarize the results of our leaching experiments (DSCODE A3USQ21).

Denitrification

Table 8 shows the influence of moisture and plant cover on the denitrification of added nitrate.

Changes in ammonium and nitrite concentration

Seasonal changes in ammonium and nitrite concentrations in Curlew Valley soils are shown in Tables 9 and 10 (DSCODE A3USQ01).

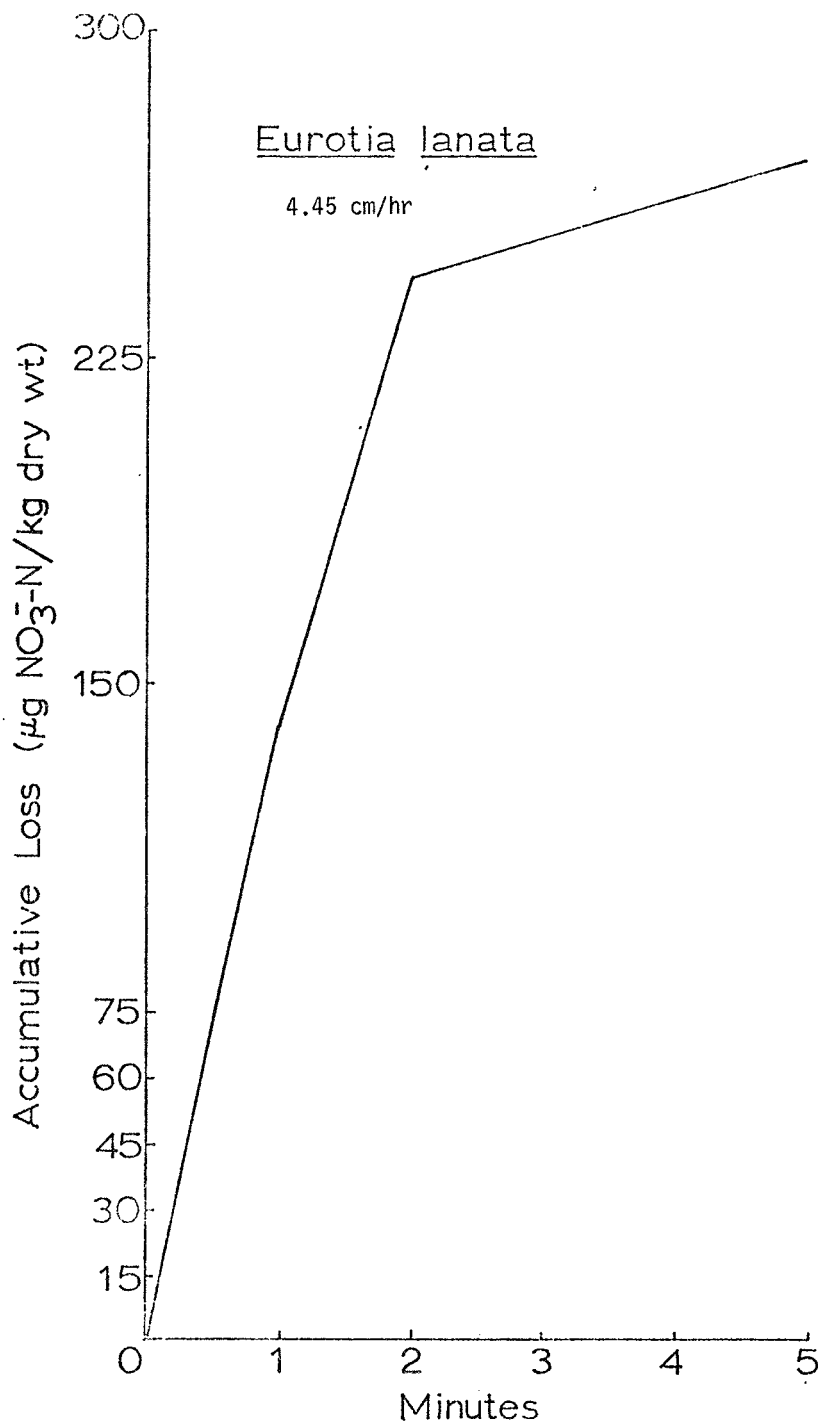


Figure 5. Accumulative loss of $\text{NO}_3\text{-N}$ from foliage of *Eurotia lanata* from simulated rainfall of 4.45 cm/hr, August 23, 1972. Mean of 5 replications. (DSCODE A3USQ21)

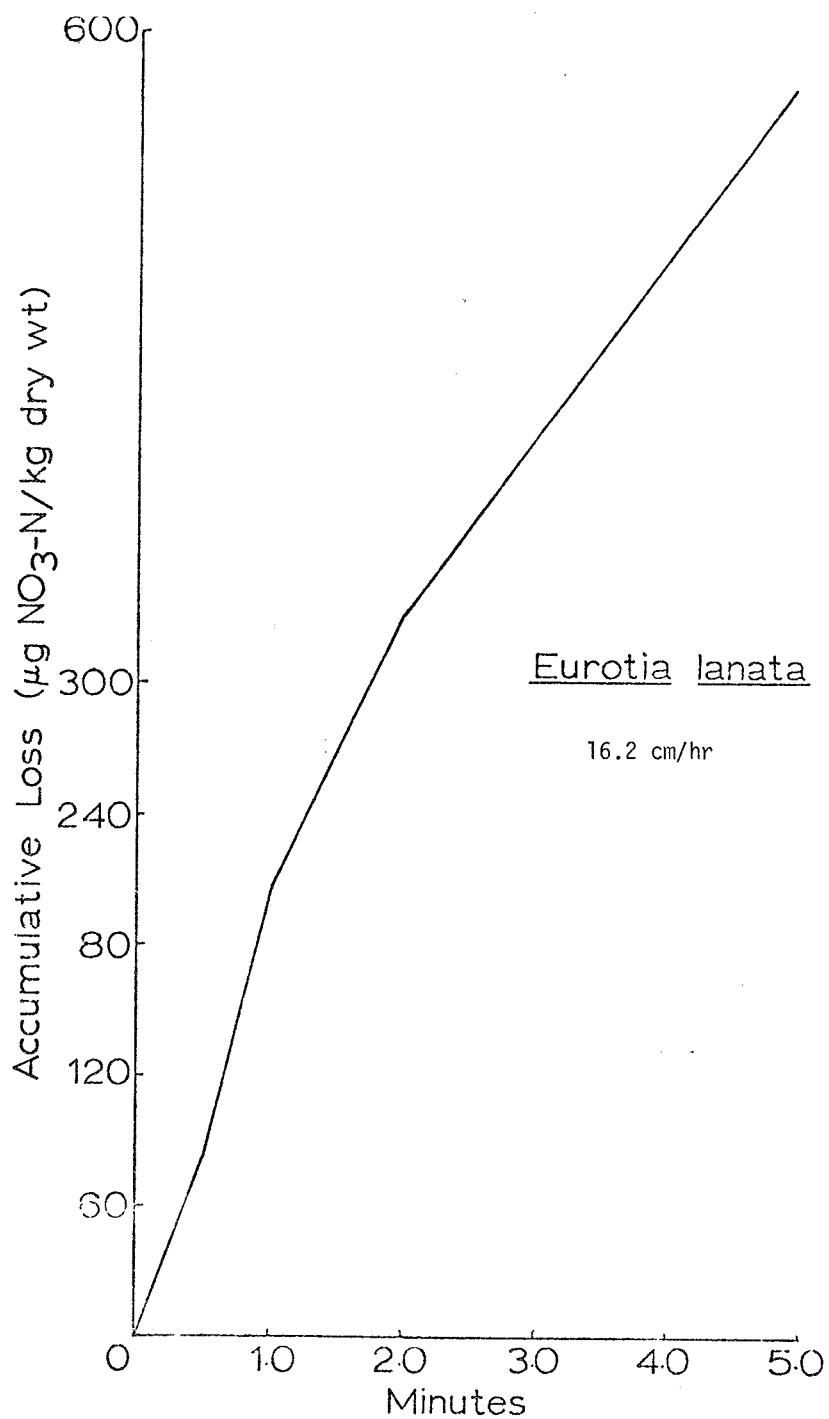


Figure 6. Accumulative loss of NO₃-N from foliage of *Eurotia lanata* from simulated rainfall of 16.2 cm/hr, August 23, 1972. Mean of 5 replications. (DSCODE A3USQ21)

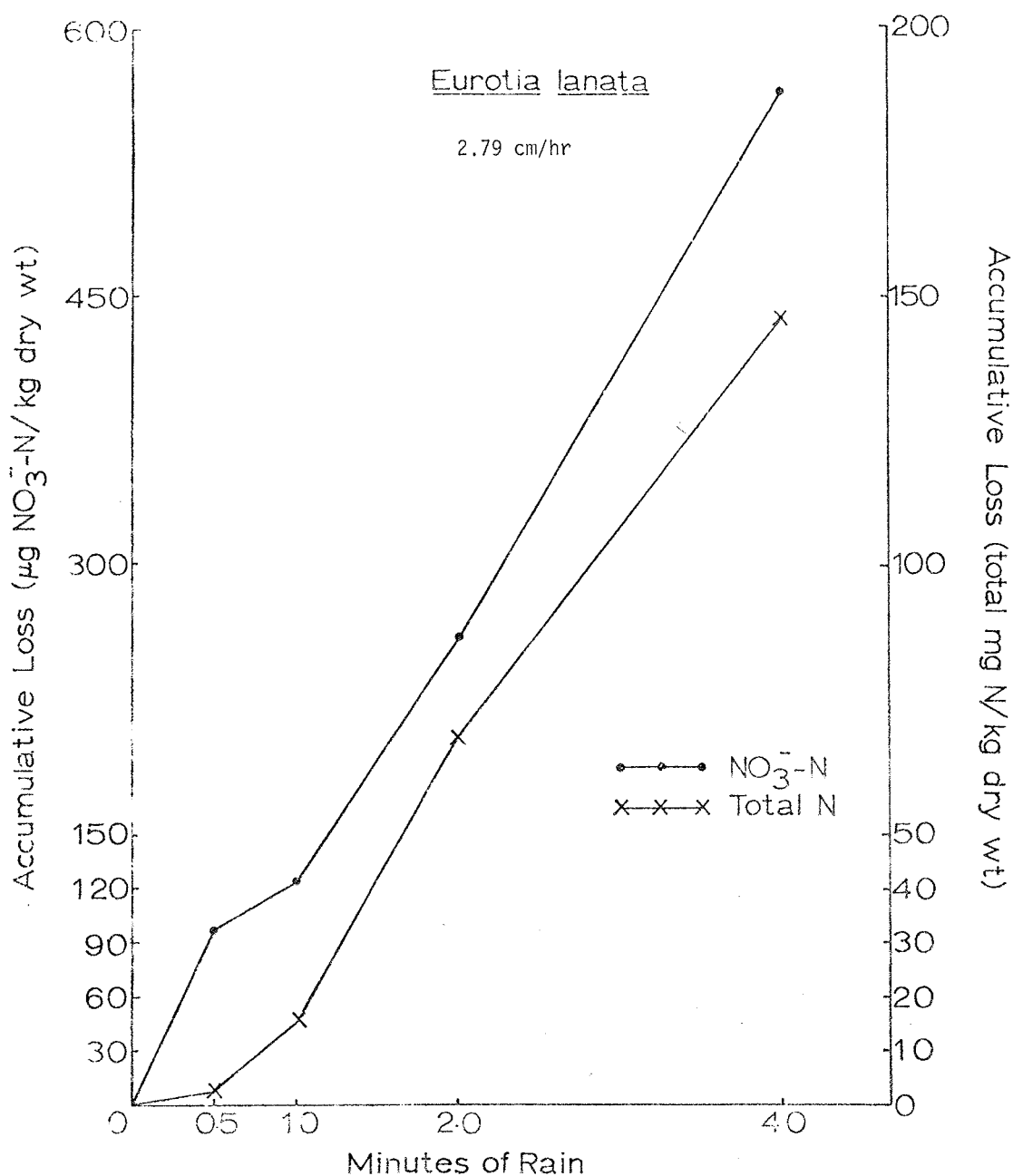


Figure 7. Accumulative loss of $\text{NO}_3^- \text{N}$ and total N from foliage of *Eurotia lanata* from simulated rainfall of 2.79 cm/hr, October 25, 1972. Mean of 10 replications. (DSCODE A3USQ21)

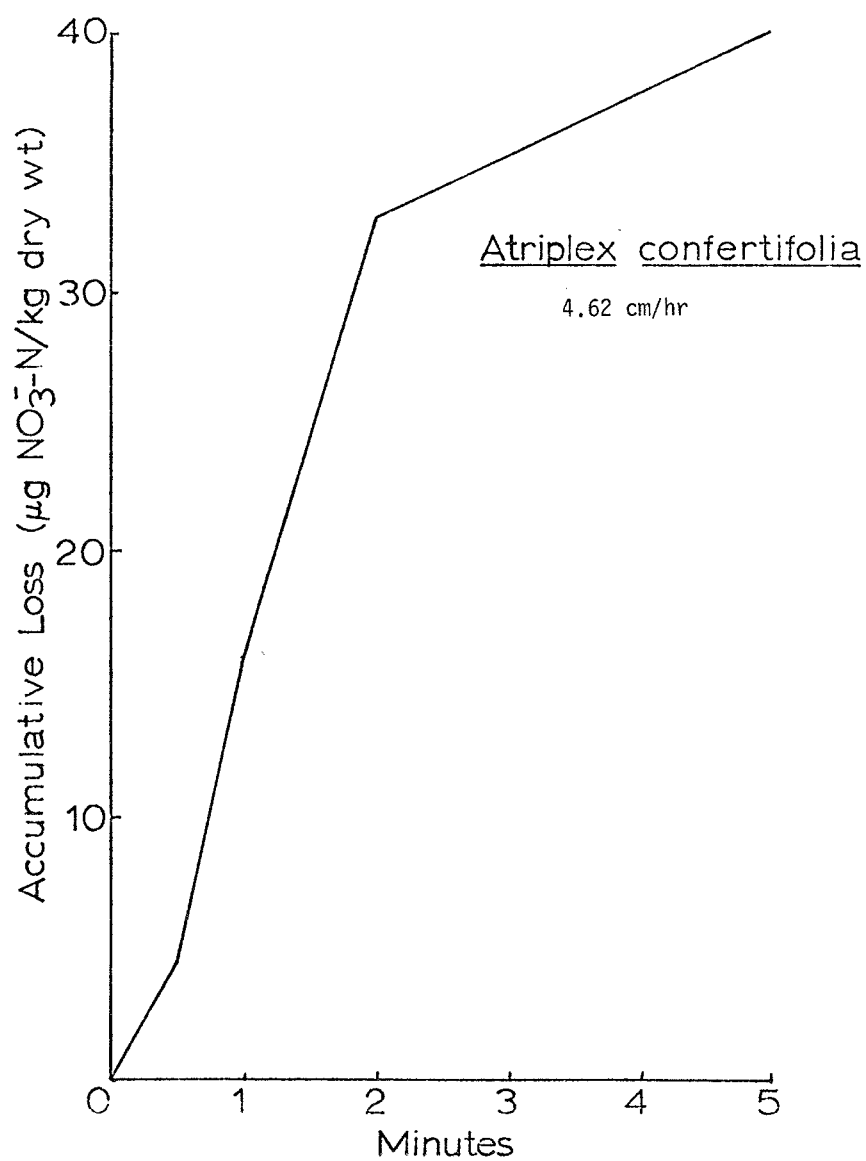


Figure 8. Accumulative loss of $\text{NH}_3\text{-N}$ from foliage of *Atriplex confertifolia* from simulated rainfall of 4.62 cm/hr, August 23, 1972. Mean of 5 replications. (DSCODE A3USQ21)

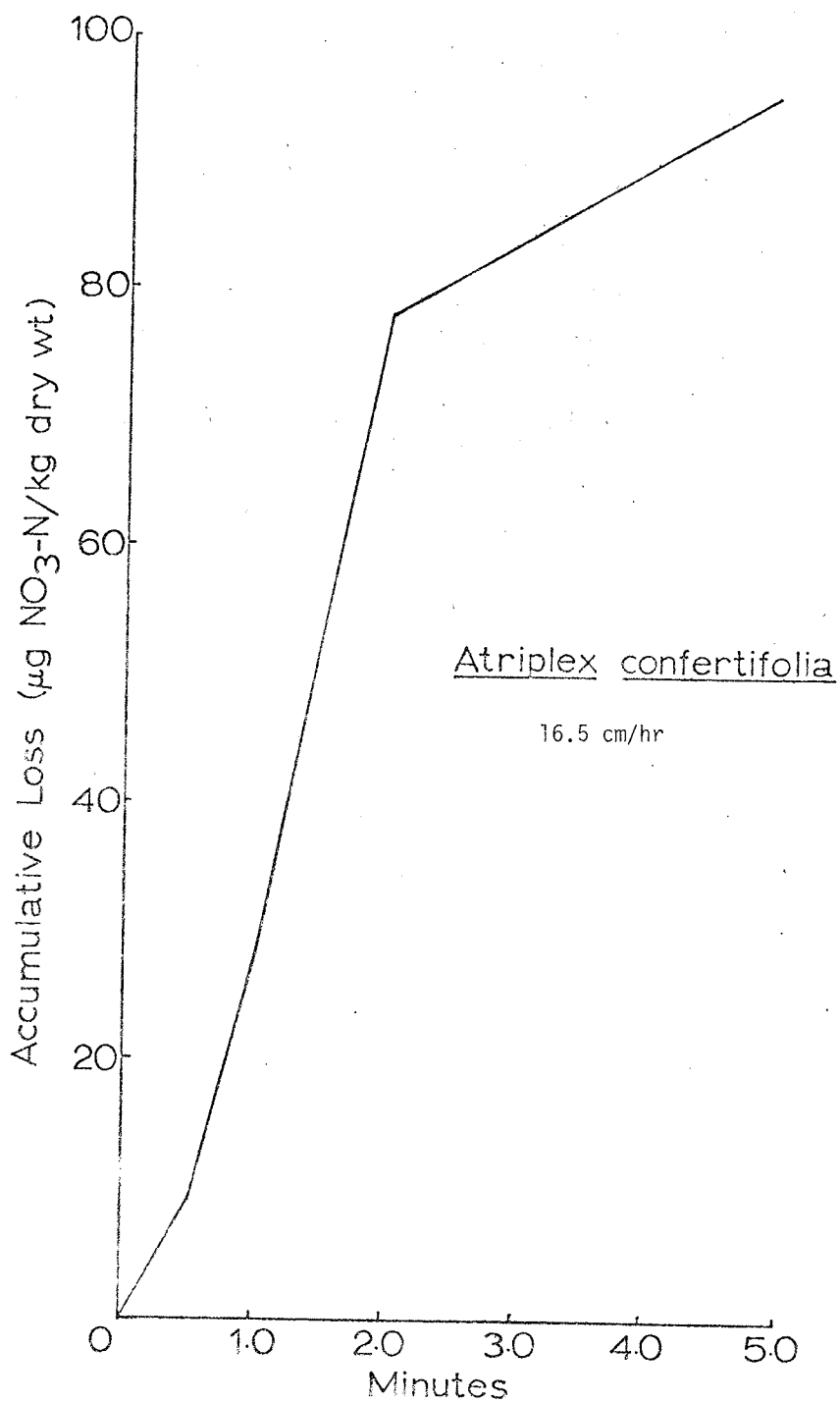


Figure 9. Accumulative loss of $\text{NO}_3\text{-N}$ from foliage of *Atriplex confertifolia* from simulated rainfall of 16.5 cm/hr, August 23, 1972. Mean of 5 replications. (DSCODE A3USQ21)

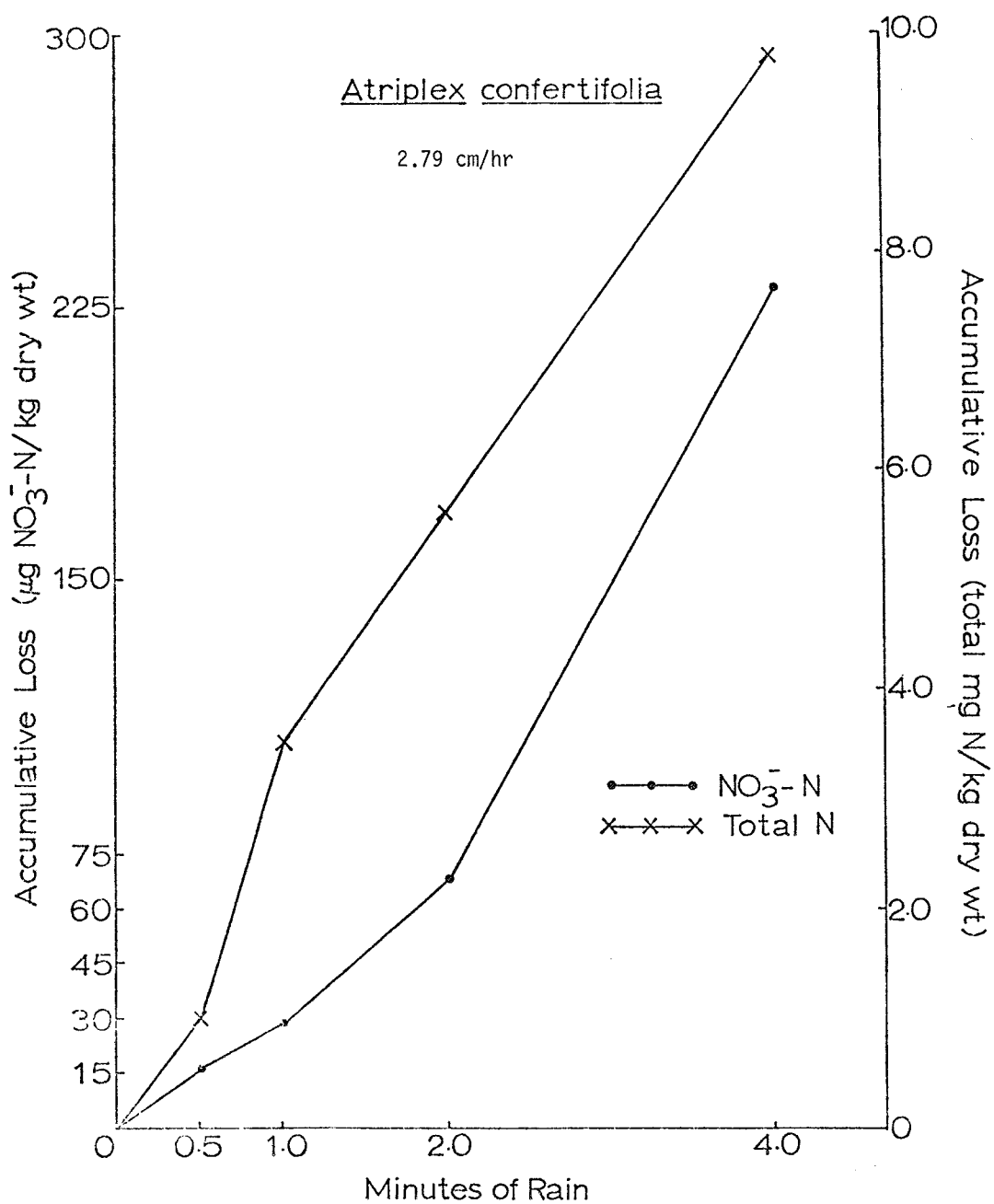


Figure 10. Accumulative loss of $\text{NO}_3^- \text{N}$ and total from foliage of *Atriplex confertifolia* from simulated rainfall of 2.79 cm/hr, October 25, 1972. Mean of 10 replications. (DSCODE A3USQ21)

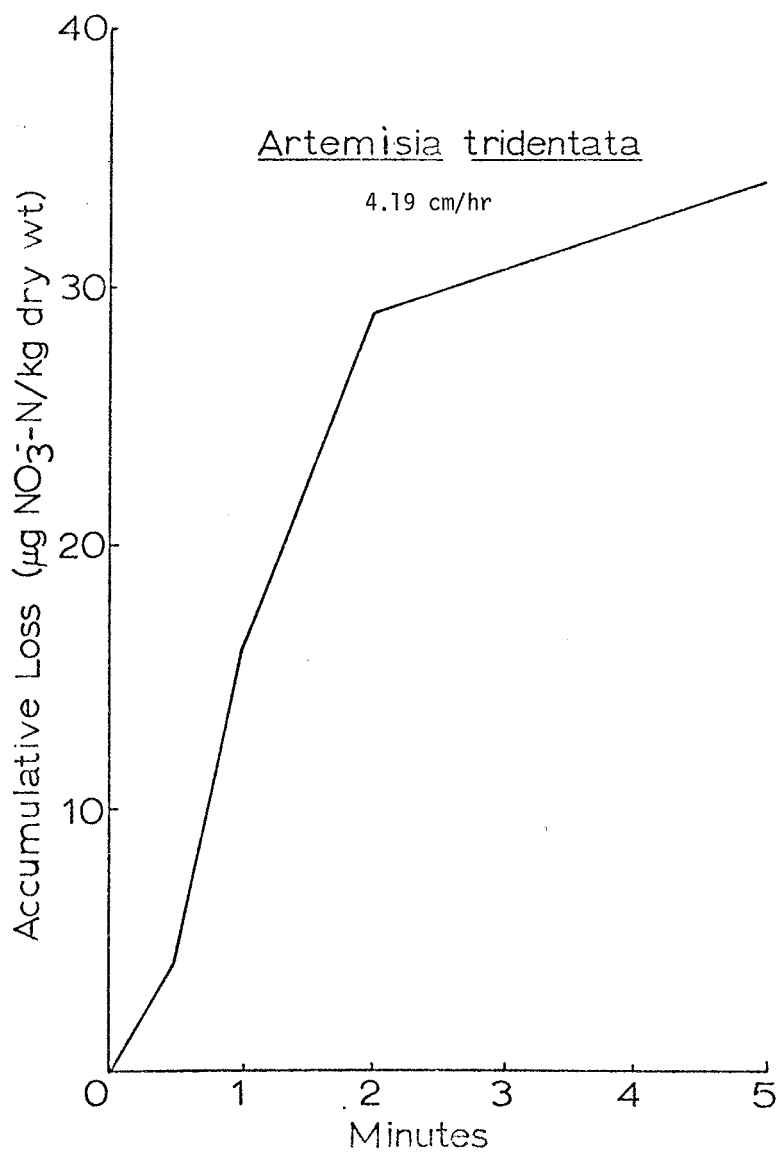


Figure 11 Accumulative loss of $\text{NO}_3\text{-N}$ from foliage of *Artemisia tridentata* from simulated rainfall of 4.19 cm/hr, August 23, 1972. Mean of 5 replications. (DSCODE A3USQ21)

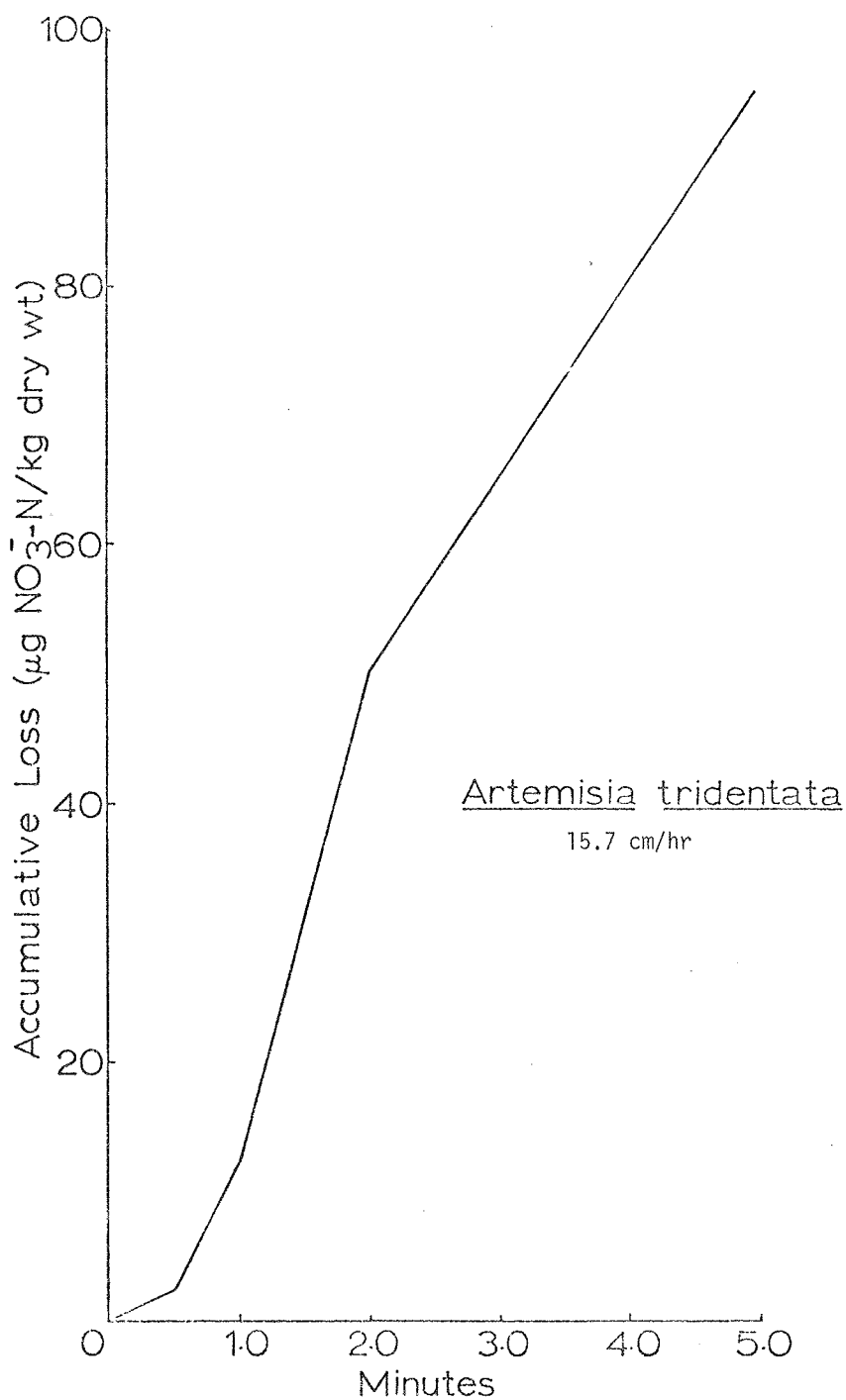


Figure 12. Accumulative loss of $\text{NO}_3\text{-N}$ from foliage of *Artemisia tridentata* from simulated rainfall of 15.7 cm/hr, August 23, 1972. Mean of 5 replications. (DSCODE A3USQ21)

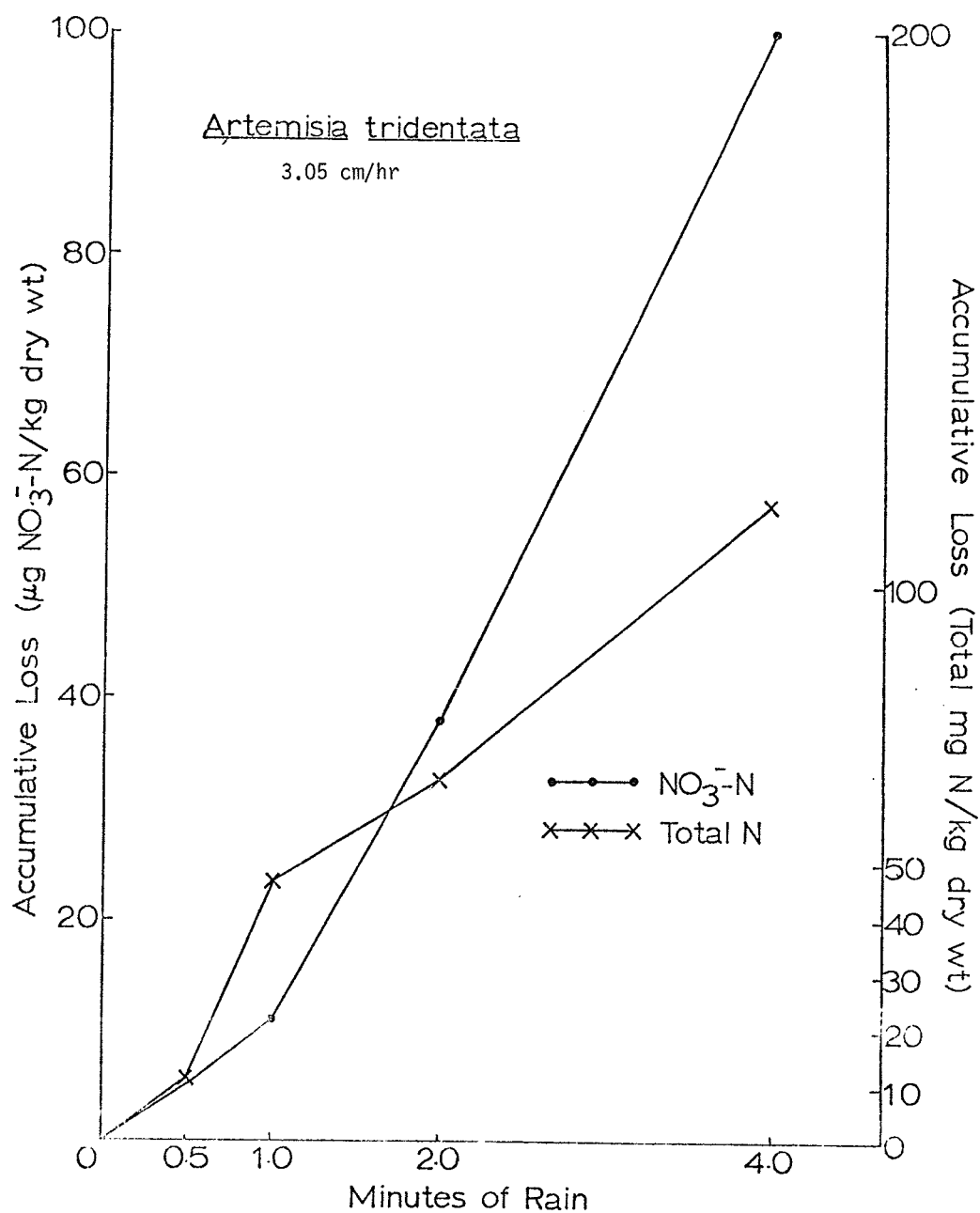


Figure 13. Accumulative loss of $\text{NO}_3\text{-N}$ and total N from foliage of *Artemisia tridentata* from simulated rainfall of 3.05 cm/hr, October 25, 1972. Mean of 10 replications. (DSCODE A3USQ21)

Table 8. Moisture and plant cover influence on denitrification from the sagebrush site #5 in Curlew Valley

Location	Moisture	Time in Days					
		1	4	8	1	4	8
		mg NO_3^- -N			% of applied		
Between canopies	5%	1.93	1.99	2.04	96.5	99.5	102.0
Between canopies	15%	2.00	2.16	2.48	100	108	124
Between canopies 1	30%	1.96	1.98	2.27	98	99	113.5
Between canopies 2	30%	1.98	1.96	2.03	99	98	101.5
	average	1.97	1.97	2.15	98.5	98.5	107.5
Under canopy 1	30%	2.23	2.66	2.73	111.5	133	136.5
Under canopy 2	30%	2.29	2.42	3.45	114.5	121	172.5
	average	2.26	2.54	3.09	113	127	154.5

Table 9. Curlew Valley ammonium-N, values expressed as $\mu\text{g NH}_4^+$ -N/g soil (DSCODE A3USQ01)

Site	Depth (cm)	May 11*	June 14*	August 24*
5	0 - 3	4.1	6.8	3.1
5	5 - 20	0.0	0.0	0.0
5	40 - 50	4.3	1.0	0.0
5	70 - 80	3.4	2.6	0.0
6	0 - 3	6.8	5.5	1.2
6	5 - 20	2.4	0.0	0.0
6	40 - 50	2.7	1.9	0.0
6	70 - 80	3.8	3.8	0.0
7	0 - 3	3.1	2.9	2.6
7	5 - 20	0.0	2.7	2.6
7	40 - 50	3.4	1.9	0.7
7	70 - 80	1.7	0.9	2.6

* Kjeldahl method

2.3.4.1.-30

Table 9. (continued)

Site	Depth (cm)	September 15**	October 14**	November 14**
5	0 - 3	0.6	3.9	6.8
5	0 - 3 (under canopy)	-	1.7	-
5	5 - 20	0.2	2.0	10.3
5	5 - 20 (under canopy)	-	1.1	-
5	40 - 50	0.1	1.5	6.3
5	40 - 50 (under canopy)	-	1.1	-
5	70 - 80	0.0	0.9	9.1
5	70 - 80 (under canopy)	-	0.9	-
6	0 - 3	0.1	1.0	5.5
6	5 - 20	0.1	0.7	4.6
6	40 - 50	0.0	0.7	4.3
6	70 - 80	0.0	0.7	5.1
7	0 - 3	0.0	0.7	3.4
7	5 - 20	0.0	0.5	3.4
7	40 - 50	0.0	0.5	3.3
7	70 - 80	0.0	0.5	3.4

** Ammonia electrode method

Table 10. Nitrite (expressed as $\mu\text{g NO}_2^- \text{-N/g soil}$), Curlew Valley soils, DSCODE A3USQ01

Site	Depth (cm)	September 15	October 14	November 14
5	0 - 3	0.3	0.0	0.1
5	0 - 3 (under canopy)	-	0.0	-
5	5 - 20	0.1	0.0	0.1
5	5 - 20 (under canopy)	-	0.0	-
5	40 - 50	0.2	0.0	0.1
5	40 - 50 (under canopy)	-	0.1	-
5	70 - 80	0.2	0.2	0.1
5	70 - 80 (under canopy)	-	0.1	-
6	0 - 3	0.2	0.0	0.3
6	5 - 20	0.2	0.0	0.0
6	40 - 50	0.0	0.4	0.2
6	70 - 80	0.2	0.1	0.1
7	0 - 3	0.2	0.0	0.0
7	5 - 20	0.2	0.0	0.0
7	40 - 50	0.5	0.0	0.2
7	70 - 80	0.1	0.2	0.0

Nitrogen fixation (DSCODE A3USQ04)

Results on nitrogen fixation as determined by the acetylene reduction method by soil crusts are shown in Tables 11 to 13. Potentiation of N-fixation by the addition of glucose (i.e., heterotrophic fixation) is shown in Tables 14 and 15, the influence of moisture content in Tables 16 and 17; fixation as a function of temperature is found in Figure 14; and the canopy effect is shown in Tables 18 and 19.

Table 11. Nitrogen fixation by acetylene reduction: Curlew Valley August 24, 1972 incubated at 22 C in the light and moistened with water, except where noted (DSCODE A3USQ04)

Sample	C ₂ H ₄ peak (mm)	Time elapsed (hrs.)	Nanomoles C ₂ H ₄ /hr.
5-crust	4.0	22.05	.0155
6-crust	20.0	22.4	.1445
7-crust	0.0	23.2	0.0
6-crust (not moistened)	0.0	21.2	0.0
6-crust (dark incubation)	3.5	21.9	.0132
6:0-3 cm depth	0.0	21.4	0.0
6:5-20 cm depth	0.0	21.6	0.0

Table 12. Nitrogen fixation: Curlew Valley soils, Sept. 15, moistened with water and incubated at 30 C (DSCODE A3USQ04)

Sample	Conditions	Activity: nanomoles C ₂ H ₄ /g soil/24 hrs.*
5-crust	Light	23.4
6-crust	Light	5.0
7-crust	Light	173.0
<i>Artemisia</i> (branches and leaves)	Light	0.0015
<i>Eurotia</i> (branches and leaves)	Light	0.0015
<i>Atriplex</i> (branches and leaves)	Light	0.0027
<i>Artemisia</i> (roots)	Dark	0.0
Lichen (found on dead sagebrush)	Light	less than 0.001

* means of triplicate assays

2.3.4.1.-32

Table 13. Nitrogen fixation -- light/dark fixation: NH_4^+ inhibition; Site 7 crust, Oct. 15, incubated at 22 C for 24 hr, moistened with water or NH_4^+ solution, light = 100 foot-candles (DSCODE A3USQ04)

Conditions	C_2H_4 peak (mm)	Mean C_2H_4 peak	Nanomoles C_2H_4 24 hours	kg N fixed/hectare/hr
Light	517			
"	307	341	154.5	.0045
"	227			
"	312			
Dark	40			
"	63	45	9.3	.000273
"	61			
"	16			
Light + 50 μg NH_4^+ -N/g soil	186			
	223	184	-	-
	124			
	172			
Light + 100 μg NH_4^+ -N	269			
	111	184	-	-
	125			
g soil	321			
% dark N-fixation = 13 light N-fixation				
% Inhibition:				
50 μg NH_4^+ -N/g soil = 48				
100 μg NH_4^+ -N/g soil = 46				

Table 14. Glucose potentiation of nitrogen fixation: Site #6 soils, Aug. 24, incubated in light (except where noted), and moistened with 5 drops of distilled water or 5 drops of a 2% glucose solution, 24 hr (DSCODE A3USQ04)

Sample	Conditions	Activity: nanomoles C_2H_4 /g soil/hr
Crust	Light	.0237
Crust	Light/glucose	.183
Crust	Dark	.0076
Crust	Dark/glucose	.210
0-3 cm depth	Dark	.000
0-3 cm depth	Dark/glucose	.000
5-20 cm	Dark	.000
5-20 cm	Dark/glucose	.000

Table 15. Glucose potentiation of nitrogen fixation: Curlew Valley, Sept. 15, moistened with water or 2% glucose solution, and incubated at 30 C (DSCODE A3USQ04)

Sample	Conditions	Activity: nanomoles C ₂ H ₄ /g soil*		
		24 hours	48 hours	70 hours
5-crust	Light	9.9	65.0	
6-crust	Light	0.11	0.22	
7-crust	Light	2.1	1.7	
5-crust	Light/glucose	7.4	235.0	
6-crust	Light/glucose	0.46	10.0	
7-crust	Light/glucose	170.0	710.0	
5: 0-3 cm	Dark/glucose	0.0	17.5	
6: 0-3 cm	Dark/glucose	0.0	10.5	
7: 0-3 cm	Dark/glucose	6.3	290.0	
5: 5-20 cm	Dark/glucose	0.0	5.9	32.0
6: 5-20 cm	Dark/glucose	0.0	0.15	3.3
7: 5-20 cm	Dark/glucose	0.0	0.45	2.0

* means of duplicate assays

Table 16. Nitrogen fixation: water potential and moisture influence; 0-3 cm cores collected Nov. 26, site #5 (sagebrush) between canopies, moistened and incubated for 10 hr at 22 C in light (DSCODE A3USQ04)

No.	% Moisture	Activity: C ₂ H ₄ peak ht. (nm)
1	--	11
2	20	9
3	20	2
4	--	156
5	20	3
6	23	930
7	--	86
8	20	15
9	35	60
10	--	34
11	34	1376
12	36	270

Treatment: 1- 3 air dried 10 hours
 4- 6 none
 7- 9 0.4 ml distilled water added
 10-12 0.8 ml distilled water added

2.3.4.1.-34

Table 17. Water potential: between and under plant canopy, Aug. 15 (DSCODE A3USQ04)

Site	Bar Pressure
5-between canopies	-12
5-under canopy	-11
6-between canopies	-13
6-under canopy	-10
7-between canopies	-11
7-under canopy	-10

Table 18. Nitrogen fixation: canopy effect; crusts collected Oct. 15, moistened and incubated in light (100 ft.-c.) at 22 C for 24 hr (DSCODE A3USQ04)

Sample	Peak ht. (mm)	Mean peak	Nanomoles C ₂ H ₄ /24 hrs.	g N fixed hectare/hr.
5-between canopies	233 152 146	177	63.0	1.86
5-under canopy	1 6 65	24	3.84	0.114
6-between canopies	10 16 3	10	1.155	0.033
6-under canopy	14 0 0	5	0.435	0.0126
6-between canopies outside rabbit fence	16 17 19	17	2.085	0.060
7-between canopies	153 157 216	175	61.5	1.80
7-under canopy	14 73 50	46	9.54	0.279
7-between canopies outside rabbit fence	355 241 228	275	114.6	3.36

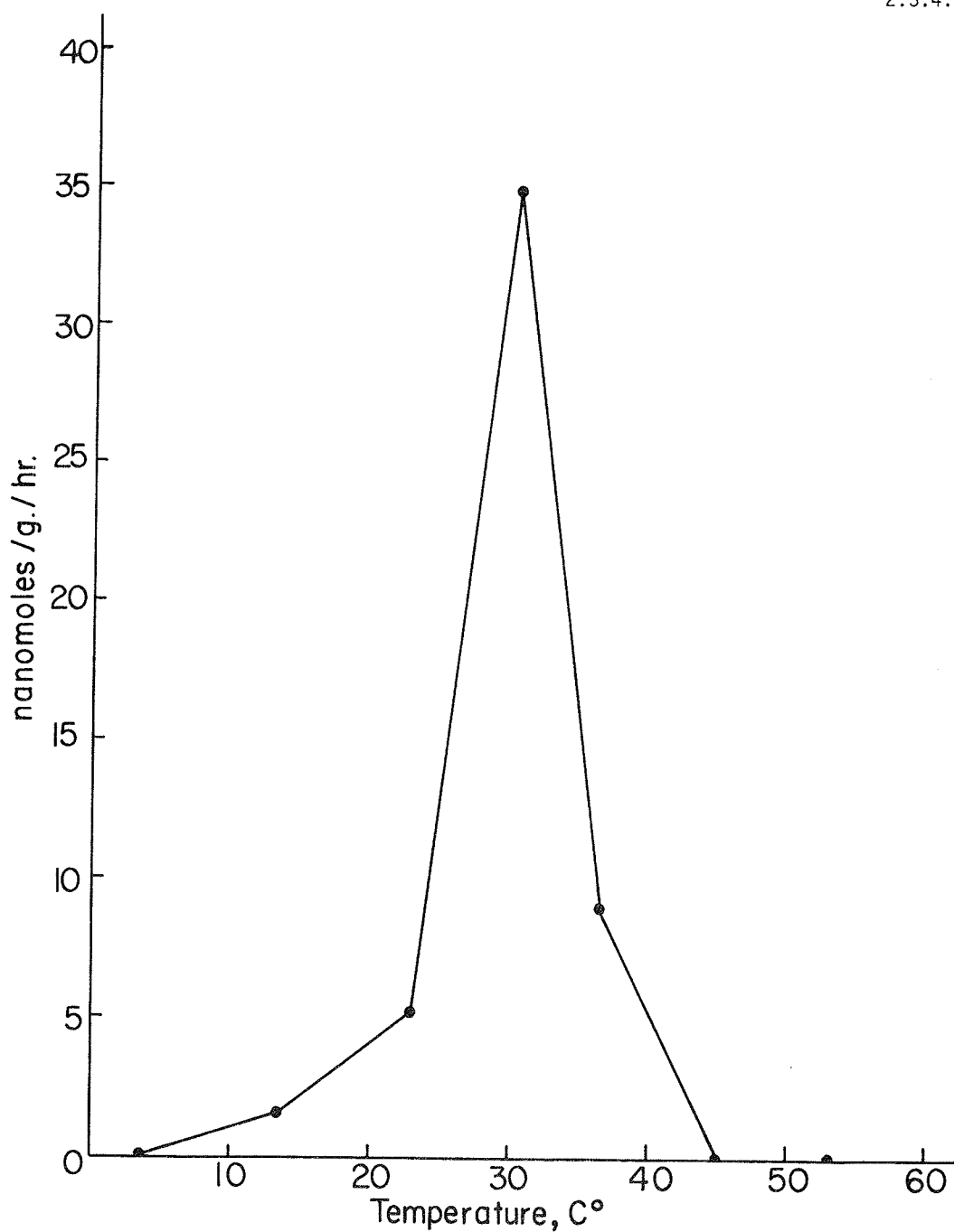


Figure 14. Site 7 crust; collected 9-15-72; C₂H₄ reduction as a function of temperature, incubated in the dark and moistened with 2% glucose solution (DSCODE A3USQ04)

2.3.4.1.-36

Table 19. Nitrogen fixation: canopy effect; 0-3 cm soil cores collected Nov. 26, moistened and incubated in light (100 ft.-c.) at 22 C for 12 hr (DSCODE A3USQ04)

Sample	Peak ht. (mm)	Mean peak ht.	Nanomoles C H 12 hrs	Grams N fixed Hectare/hr
5-between canopies	33.5 1376.0 270.0	560	612.0	36.0
5-under canopy	1.5 1.0 6.0 19.0	7	1.392	0.0816
5-between canopies outside grazing fence (no rabbit fence)	352.0 752.0 9.0 31.0	286	243.0	14.28
6-between canopies	23.0 3.0 7.0 31.0	16	4.44	0.264
6-under canopy	1.5 1.0 2.0 1.0	1.4	0.150	0.0084
6-between canopies outside rabbit fence	22.0 2.0 9.0 24.0	14	3.66	0.216
7-between canopies	14.0 308.0 112.0 508.0	236	186.0	10.92
7-under canopy	0.0 115.0 1.0 5.0	30	10.5	0.612
7-between canopies outside rabbit fence	250.0 45.0 73.0 54.5	108	63.0	3.72

Nitrification potential (DSCODE A3USQ05)

Nitrification potential was measured *in vitro* by the perfusion method as a function of seasons (Table 20). Nitrification rate was highest in the 0-3 cm surface layer and was dependent on the site of sampling.

Table 20. Nitrification potential: samples collected on 1 April 1972 (DSCODE A3USQ05)

Incubation Days	Depth cm	NO ₃ ⁻ -N µg/g soil		
		Site 5	6	7
2	0-3	2	0	0
4		3.7	1	0
6		5	3.7	2
8		4.5	2	1
10		7.0	3.7	2
12		9.3	4.5	3.7
15		12.5	5.7	4.5
2	5-20	0	0	0
4		1	0	1.5
6		0	1	2
8		1.5	2	0
10		2	2.5	3.7
12		3	3	4.5
15		3	4.5	5.7
2	40-50	1	0	0
4		0	1	0
6		0	0	1
8		1	1.5	0
10		0	2	1
12		1	1.5	2.0
15		2	3	2.5
2	70-80	0	1	0
4		1	0	1
6		1.5	0	1
8		2	1.5	0
10		1	0	0
12		2	1.5	0
15		0	2	1.0

Initial NO₃⁻-N = 0

Initial NH₄⁺-N = 2333 µg/g soil

Ammonification potential

Results of ammonification (i.e., degradation of organic matter with subsequent release of ammonia) potential at various water potentials of Curlew Valley soils are shown in Table 21 and Figures 15 to 20 (DSCODE A3USQ03).

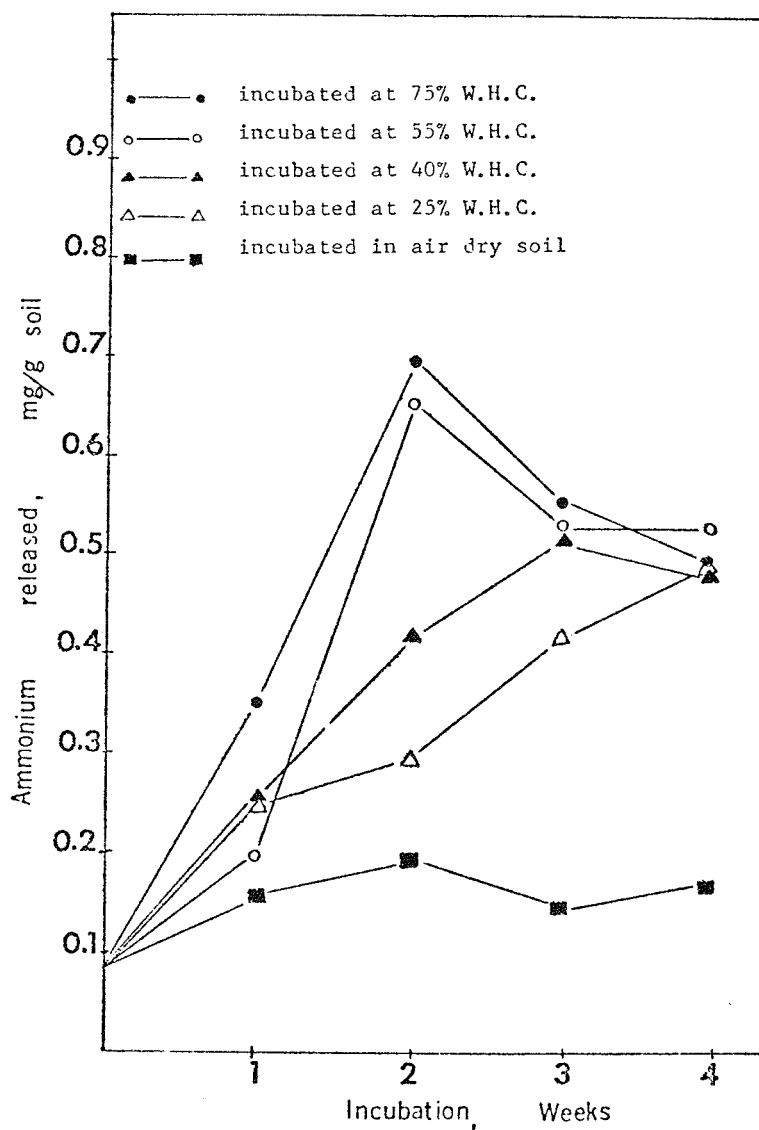


Figure 15. The effect of moisture on the production of ammonium-N during incubation of 0-3 cm shadscale site soil amended with casein. DSCODE A3USQ03

Table 21. Ammonification potential at various moisture contents (DSCODE A3USQ03)

Sampling Site	Incubated Soil	Ammonification in air dry soil					NH ₄ ⁺ -N trapped in tubes, µg	Org-N at the end of experiment mg/g soil	% org-N mineralized
		Initial org-N mg/g soil	1 NH ₄ ⁺ -N	2 released, mg/g soil	3 released, mg/g soil	4 released, mg/g soil			
0 - 3 cm shadscale	control	1.116	0.056	0.084	0.14	0.084	0	0.945	15.4
	soil + casein (0.8 mgN/g soil)	1.916	0.154	0.196	0.14	0.168	2	1.302	32.1
5 - 20 cm shadscale	soil + litter (0.86 mgN/g soil)	1.976	0.098	0.154	0.14	0.168	0	1.8	9.0
	control	0.83	0.042	0.070	0.070	0.056	0	0.434	47.7
5 - 20 cm cultivated soil	soil + casein	1.63	0.126	0.14	0.112	0.154	1	1.386	15.0
	soil + litter	1.69	0.112	0.14	0.168	0.14	0	1.50	11.2
5 - 20 cm cultivated soil	control	1.632	0.112	0.14	0.14	0.126	0	1.064	34.8
	soil + casein	2.432	0.168	0.238	0.196	0.224	2	1.806	25.75
	soil + litter	2.49	0.196	0.238	0.224	0.196	0	2.5	17.7
Ammonification Potential at 25% Water Holding Capacity (W.H.C)									
0 - 3 cm shadscale	control	1.116	0.084	0.084	0.112	0.084	2	0.838	24.9
	soil + casein	1.916	0.244	0.294	0.42	0.488	29	0.84	56.2
5 - 20 cm shadscale	soil + litter	1.976	0.154	0.14	0.14	0.168	2	1.6	19.0
	control	0.830	0.042	0.042	0.084	0.056	2	0.747	10.0
5 - 20 cm cultivated soil	soil + casein	1.63	0.182	0.28	0.448	0.532	22	1.0	38.0
	soil + litter	1.69	0.098	0.112	0.126	0.147	3.5	1.5	11.25
5 - 20 cm cultivated soil	control	1.632	0.112	0.112	0.14	0.112	3.4	0.77	52.8
	soil + casein	2.432	0.42	0.504	0.588	0.602	25	1.57	35.5
	soil + litter	2.49	0.168	0.224	0.28	0.224	3.5	2.17	12.86

Table 21. continued

Sampling Site	Incubated Soil	Initial org-N mg/g soil	Ammonification Potential at 40% W.H.C.				NH ₄ ⁺ -N Trapped in tubes, µg	Org-N at the end of experiment mg/g soil	% org-N mineralized
			Incubation, Weeks						
			1 NH ₄ ⁺ -N released, mg/g soil	2	3	4			
0 - 3 cm shadscale	control	1.116	0.56	0.042	0.084	0.112	4	0.735	34.1
	soil + casein	1.916	0.252	0.42	0.518	0.49	45	0.63	67.1
	soil + litter	1.976	0.14	0.168	0.196	0.196	2	1.414	28.45
5 - 20 cm shadscale	control	0.8	0.042	0.028	0.042	0.042	2	0.7	15.67
	soil + casein	1.63	0.252	0.392	0.532	0.56	25	1.05	35.6
	soil + litter	1.69	0.084	0.126	0.126	0.112	2	1.428	15.5
5 - 20 cm cultivated soil	control	1.632	0.112	0.14	0.14	0.126	1.5	1.4	14.2
	soil + casein	2.432	0.308	0.42	0.588	0.616	48	1.064	56.25
	soil + litter	2.49	0.168	0.168	0.196	0.182	3	2.1	15.7
Ammonification Potential at 55% W.H.C.									
0 - 3 cm shadscale	control	1.116	0.056	0.126	0.112	0.084	3	0.54	51.6
	soil + casein	1.916	0.196	9.658	0.532	0.532	28	0.84	56.2
	soil + litter	1.976	0.14	0.308	0.182	0.252	2	1.54	22.1
5 - 20 cm shadscale	control	0.83	0.028	0.056	0.056	0.028	2	0.63	24.1
	soil + casein	1.63	0.196	0.546	0.504	0.49	20	0.98	39.5
	soil + litter	1.69	0.112	0.238	0.196	0.294	2	1.36	19.5
5 - 20 cm cultivated soil	control	1.632	0.084	0.126	0.126	0.084	4	0.342	79
	soil + casein	2.432	0.364	0.714	0.91	0.65	24	0.63	74.1
	soil + litter	2.49	0.14	0.308	0.28	0.336	1.2	1.9	23.7

Table 21. continued

Ammonification Potential at 75% W.H.C.									
Sampling Site	Incubated Soil	Initial org-N mg/g soil	1 NH_4^+ -N	2 released, mg/g soil	3	4	NH_4^+ -N trapped in tubes, μg	Org-N at the end of experiment mg/g soil	% org-N mineralized
0 - 3 cm shadscale	control	1.116	0.07	0.084	0.084	0.098	5	0.21	81.2
	soil + casein	1.916	0.35	0.70	0.578	0.504	28	0.525	72.6
	soil + litter	1.976	0.168	0.325	0.21	0.21	10	1.5	24.1
5 - 20 cm shadscale	control	0.83	0.042	0.07	0.07	0.56	3	0.455	45.2
	soil + casein	1.63	0.266	0.6	0.448	0.476	14	0.961	41.0
	soil + litter	1.69	0.14	0.392	0.224	0.182	2	1.35	20.0
5 - 20 cm cultivated soil	control	1.632	0.112	0.154	0.112	0.112	2.5	0.19	88.25
	soil + casein	2.432	0.364	0.8	1.025	0.712	21	0.435	82.0
	soil + litter	2.49	0.252	0.28	0.224	0.266	7	1.95	21.3

Initial NH_4^+ -N, 0 - 3 cm shadscale soil = 0.084 mg/g soil
 5 - 20 cm shadscale soil = 0.054 mg/g soil
 5 - 20 cm cultivated soil = 0.140 mg/g soil

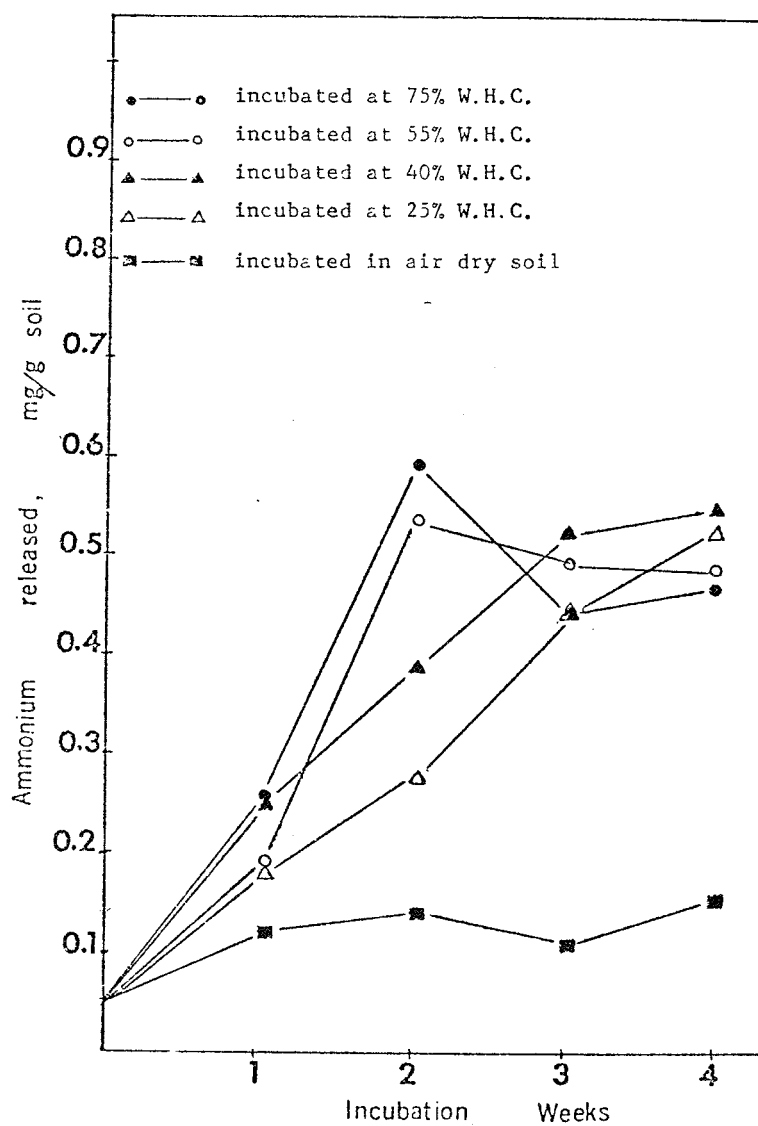


Figure 16. The effect of moisture on the production of ammonium-N during incubation of 5 - 20 cm shadscale site soil amended with casein (DSCODE A3USQ03)

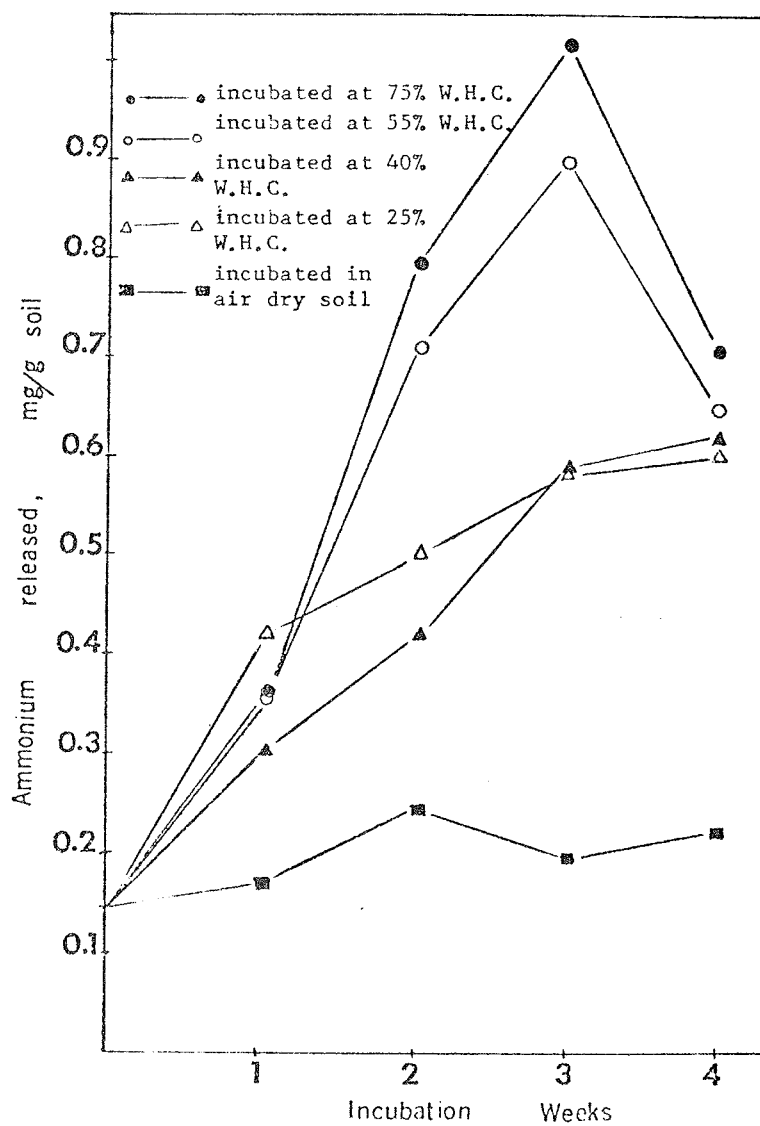


Figure 17. The effect of moisture on the production of ammonium-N during incubation of 0 - 20 cm cultivated (garden) soil amended with casein (DSCODE A3USQ03)

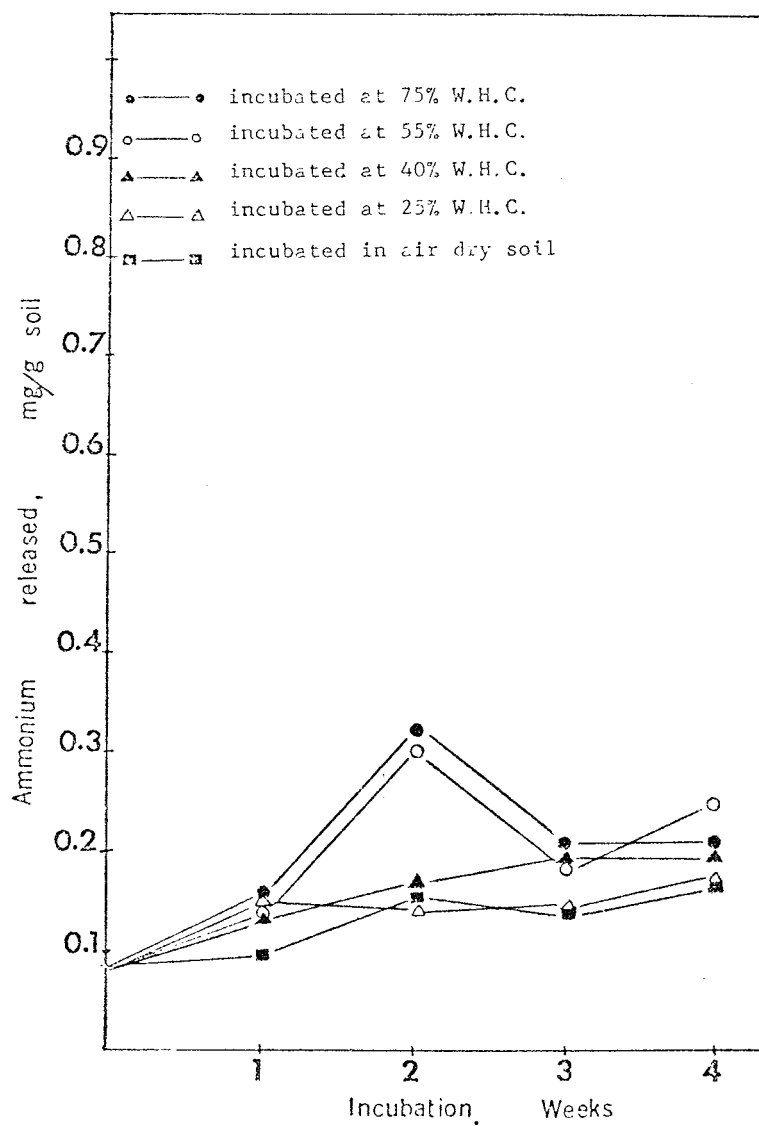


Figure 18. The effect of moisture on the production of ammonium-N during incubation of 0-3 cm shadscale site soil amended with litter (DSOCDE A3USQ03)

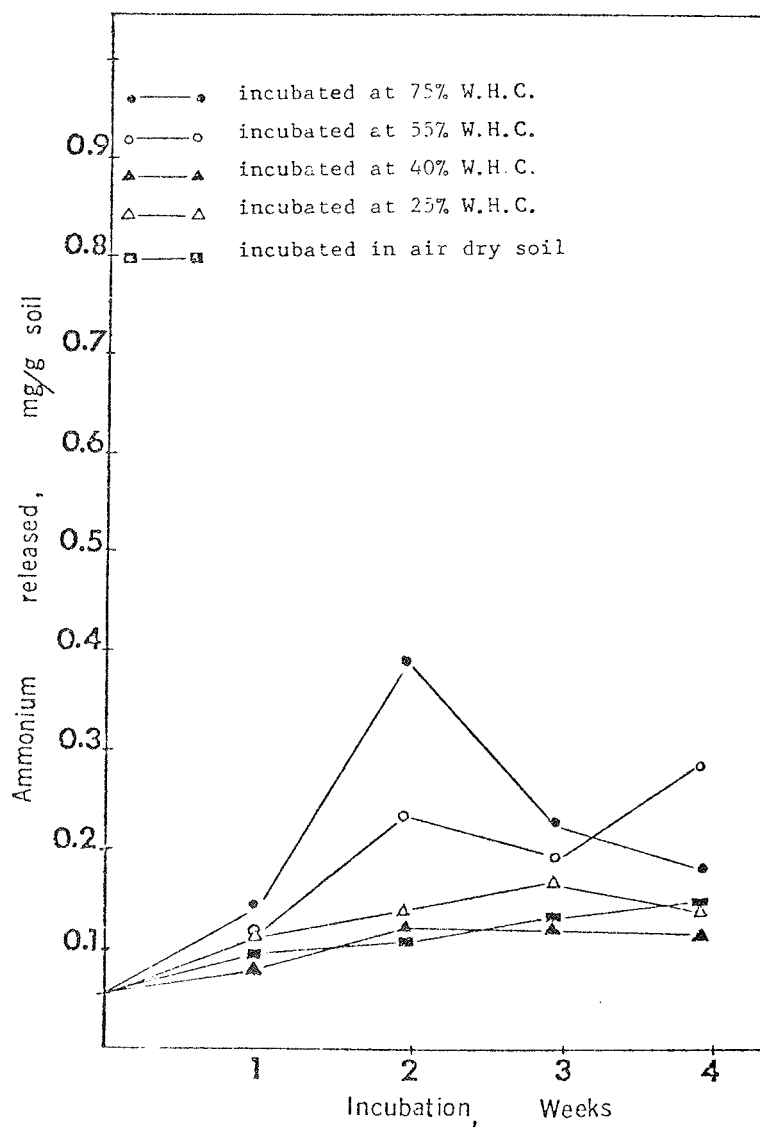


Figure 19. The effect of moisture on the production of ammonium-N during incubation of 5-20 cm shadscale site soil amended with litter (DSCODE A3USQ03)

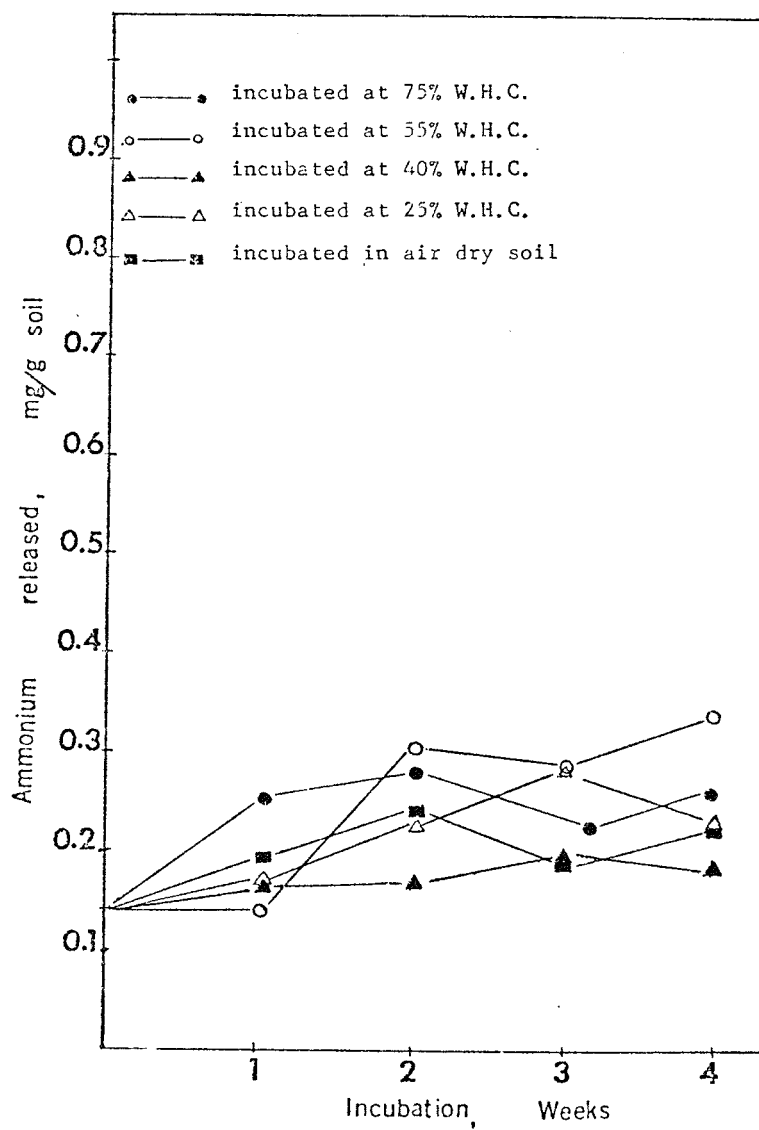


Figure 20. The effect of moisture on the production of ammonium-N during incubation of 0-20 cm cultivated (garden) soil amended with litter (DSCODE A3USQ03)

DISCUSSION

Data indicate that summer precipitation yields about 0.2 ppm of Total N, 0.5 ppm of $\text{NO}_3\text{-N}$ and 0.12 ppm of $\text{NH}_3\text{-N}$. Fall rains yielded about 17.7 ppm of Total N, 15.8 ppm of $\text{NO}_3\text{-N}$, and 0 ppm of $\text{NH}_3\text{-N}$. The nitrogen associated with dust accounted for a very high fraction of the total input. Extrapolating from this sketchy data to average annual rainfall, we could expect a flux of about 2 g/m^2 of nitrogen input via wet precipitation. Whether or not we have a net gain of dust on the desert land surfaces themselves is questionable. The net input due to dust is probably related to vegetal cover. In any event, precipitation seems to be contributing almost as much N to the system as the nitrogen-fixing microbes and cryptogams. Another year's data with a fuller record should further define this input and allow us to relate Curlew Valley with the longer runs of data available in the literature (Gosz, 1969).

The leaching experiments do not fully reflect the natural phenomena for several reasons. First, the lowest storm intensity possible with the artificial rainmaker is much higher than the gentlest storm likely to produce stem flow, or leaf drip. Furthermore, the cutting of the shrubs causes problems of shaking leaves from the shrub, killing of the plant and the consequent alteration of turgor and absorption. Most of the nitrogen detected by this technique is probably coming from the dust and debris washed from the plant. Although fluxes are minor, better definition is required to provide numbers for the model. Plants are presently growing in the greenhouse in preparation for experiments on live plants following techniques recently developed by Clements, Jones and Hopper (1972).

A significant amount of NH_3 appears to be volatilized from soils. The graph (Figure 4) is based on non-isotopic N data and needs to be validated by the ^{15}N analysis that is currently in progress. These ^{15}N data will also indicate if any "priming effect" is evident from the added $(\text{NH}_4)_2\text{SO}_4$.

Soil analysis will also give an indication of the amount of NH_4^+ immobilized during this period and also the amount nitrified. The quantity of ^{15}N remaining in the NH_4^+ will complete the picture.

If, indeed, after replication, the results are essentially the same as Figure 4, the effect of the plant canopy shows some startling variations. The winterfat and sagebrush canopy reduces the amount of NH_3 lost by volatilization whereas the shadscale canopy increases the loss. An explanation for this fact is not now evident and further investigation is necessary.

2.3.4.1.-48

Table 8 shows the results of KNO_3 -addition to the sagebrush site soils in Curlew Valley. This denitrification experiment was disrupted by incubator failure and therefore the temperature was not constant during the sampling period.

However, the "priming effect" of KNO_3 can be seen. More N was released from the organic matter from under the canopy than from the samples between the canopies. This may be expected since a higher organic matter content is present under the canopy than in the interspaces between the plants. Isotope-ratio analysis would confirm this conclusion.

Moisture influence on the "priming effect" is interesting. At low moisture little, if any, release of N from organic N is evident. At high moisture content the N release is significant but not as large as the release at intermediate moisture.

No influence of moisture on denitrification can be seen without the aid of ^{15}N data. There is some suggestion of a differential in activity with respect to temperature, moisture and pH with the nitrifying bacteria; particularly that *Nitrobacter* is less active than *Nitrosomonas* at high pH (Barkworth and Bateson, 1965). This might result in an accumulation of nitrite.

The soil samples examined thus far exhibit no striking nitrite concentrations. All values are much less than $1 \mu\text{g NO}_2^- \text{-N/g of soil}$.

Dark or endogenous N-fixation is on the order of 10-13% of light fixation, and there is not significant fixation beneath the surface due to a limitation in carbohydrate supply.

Glucose can potentiate N-fixation on the surface and in the soil depths. However, there is an increasing lag in this potentiation as the soil depth increases. Thus, there is a heterotrophic N-fixing potential in the Curlew Valley soils that is perhaps not realized since it is dependent upon a readily available supply of carbohydrate to provide the energy and structural components (carbon skeleton) to the system.

The values for dark N-fixation agree with Hardy et al. (1968) who found that soybean roots had 15% of their light activity after 64 hr of darkness.

Negligible N-fixation was found when the leaves and branches of the three site plants were examined; i.e., no phyllosphere N-fixing organisms were present.

Although there has been a report of symbiotic nitrogen fixation with *Artemisia ludoviciana* (Farnsworth and Clawson, 1972) and *A. tridentata* (Wallace and Romney, 1972) roots collected in the spring, no activity was found with our *Artemisia tridentata* roots, although this could have been due to the time of sampling (fall).

The temperature optimum for this N-fixing system appears to be about 30 C.

There are reports of ammonium ion inhibition of N-fixation (Spiff and Odu, 1971), and our data (in Table 13) suggest a 50% inhibition of N-fixation at 50 and 100 $\mu\text{g NH}_4^+\text{-N/g}$ of soil. These values and the concentration effect require further verification since it is somewhat of an anomaly that both concentrations of ammonium ion have such similar inhibition values. The ammonium values for the Curlew soils, however, (see $\text{NH}_4^+\text{-N}$ Tables) do not appear to even approach the above values for ammonium ion.

The data in Table 16 indicate that N-fixation is significantly reduced at 20% moisture from 34 to 36% moisture.

Tables 18 and 19 demonstrate a large increase in N-fixation on all sites from October to November (the period of the onset of this fall's rainy period). Tables 16 and 17 show the increase in water potential from October to November.

The N-fixation data indicate that there is a small order of difference between the sagebrush and shadscale sites with respect to N-fixation, but that the winterfat site (with the exception of the August assays) is of a large order of magnitude reduced (50 to 100 times lower).

One of the most dramatic effects observed (see Tables 18 and 19) is the reduction in N-fixation under all plant canopies. It is unlikely that ammonium ion inhibition is responsible since the levels of NH_4^+ are not very high. Equally unlikely is a light reduction due to shading, since it is not very great either. The reduction in N-fixation under the canopy is either due to a specific inhibitor or due to osmotic effects perhaps coupled with specific ion effects. Xerophytes are notorious for their ability to concentrate salts. However, the water potential data of Table 11 indicate that if anything there is slightly more water available under the plant canopy. Electrical conductivity studies may elucidate an osmotic effect, if it is present.

While most of the assays were performed under a 100 ft.-c. of light, Wolk and Wohciuch (1971), using *Anabaena cylindrica*, found that there was an approximate two-fold increase in N-fixation when the light was increased from 100 to 5000 ft.-c. Thus the values reported for N-fixation in the light may require a consideration of light, but this awaits further studies.

2.3.4.1.-50

Within a site the assays are quite variable, particularly with the soil cores. This, in large part, is due to the irregular growth of the algal mat on the soil surface.

The values for November are much higher than October values due in part, as discussed previously, to the increase in soil moisture. However, the November samples were soil cores with intact surface crusts which would optimize the surface area available in the assay of crust N-fixation (in comparison with some loss of surface crust area with the serum bottle assays).

MacGregor and Johnson (1971) report a value of 3-4 g of nitrogen fixed/ha/hr following a rainfall, with algal crusts from the Sonoran Desert. At 22 C and approximately 100 ft.-c. of light, the following N-fixation values are representative for the Curlew Valley sites (November samples; expressed as g of nitrogen fixed per ha per hr):

sagebrush site	36.0 g N/ha/hr
winterfat site	0.264 g N/ha/hr
shadscale site	10.9 g N/ha/hr

The above values would be somewhat higher if light and temperature considerations were optimized.

A more reliable estimate requires further validation and quantification of the N-fixation parameters by using ^{15}N methods.

As shown in Table 21, the ammonification rate was greatly influenced by moisture content, when soils were amended with casein (Figures 15, 16 and 17). The ammonification of plant materials was influenced less by changes in moisture content (Figures 18, 19 and 20). It was also observed that the amount of ammonium released was higher in cultivated garden soils collected from the shadscale site. Shadscale site soil samples (0-3 cm) were more efficient in ammonification than 5-20 cm shadscale soil samples. In cultivated soils the ammonium release leveled off after two weeks when soils were amended with casein.

Gaseous ammonia from casein-amended soil was greatly influenced by moisture content. Release of gaseous ammonia was highest at 40% water-holding capacity (W.H.C.) and decreased with further increasing or decreasing moisture content. Soils amended with litter did not show any considerable amount of gaseous ammonia release (Table 21).

Rate of organic nitrogen mineralization increased as the moisture content of soils was increased from air dry to 75% W.H.C. Recovery of Total N was much less from casein-amended soils than from litter-amended soils.

Sindhu and Cornfield (1967) and Johnson and Guenzi (1963) showed that an increase in the osmotic tension reduces the nitrate accumulation. For the soils used in our experiments, soluble salt content increased with the depth of profile. It was observed that the surface layer (0-3 cm) samples had a higher nitrification rate than samples from other profiles. In addition to salt content, inadequate aeration may be one of the reasons for suppression of nitrification rate in deeper profiles. Biological activity (nitrification and ammonification) was higher in the top 3 cm layer than in the rest of the profile.

Lees and Quastel (1946) concluded that the rate of nitrification of a given quantity of ammonification sulphate is a fraction of the degree to which the ammonium ions are held in base exchange sites. In the presently described experiments about 3-35% ammonium was fixed by perfused soils. These soils had a high exchangeable Na^+ and K^+ content, which could be replaced by ammonium ions. In the first five hr 30% of the total ammonium was fixed by soils and after that the decrease in ammonium was comparatively slow and linear.

Lees and Quastel (1946) studied the nitrification of a previously air-dried soil by perfusion technique and observed that the nitrification process may be of a long duration. After a lag period, a logarithmic growth phase takes place. At some point, a condition is reached where the soil becomes saturated with nitrifying bacteria and the rate becomes constant. In most of the soils used in the perfusion experiment, the nitrate accumulation passed through a lag period of about 8-10 days, followed by the logarithmic phase.

The overall balance sheet for added ammonium-N may be obtained by adding volatilized ammonia, ammonium fixed by clay particles and the detected nitrate and nitrite.

It was observed that 0-3 cm profile samples had more NH_4^+ -N than samples from 5-20, 40-50, 70-80, and 110-130 cm in the profile. The ammonium-N estimated was the total NH_4^+ -N which is available to plants and microorganisms and includes the clay-fixed NH_4^+ -N.

Air drying and subsequent re-wetting is known to produce a temporary stimulating effect on the decomposition of the organic matter. The stimulating effect is greatest when drying and re-wetting is repeated. Birch and Friend (1961) showed that after 204 cycles, 46.4% nitrogen was mineralized. Ammonification rate was increased as the moisture content was increased from 25 to 75% W.H.C. in casein-amended soils. Little decomposition took place when soil was amended with litter.

2.3.4.1.-52

Ekpete and Cornfield (1966) showed that with increasing moisture, up to 50% W.H.C., mineral-N was almost entirely nitrate and that with further increase in moisture to waterlogging, nitrate decreased and ammonium accumulated. In our experiments, there was no nitrite and nitrate detected due to addition of 2-chloro-6 (trichloromethyl) pyridine, which inhibits oxidation of NH_4^+ to NO_2^- .

Peaks of ammonium production from some casein-amended soils were evident during the third week, and those for litter-amended soils were evident during the second week of the incubation period. After the maximum accumulation of NH_4^+ the microbial population increased and a subsequent decline in NH_4^+ accumulation resulted, which may be due to increased nutrient demands by the microflora. It was suggested by Float (1970) that the decline is due to the excess of immobilization over gross mineralization of nitrogen.

The results obtained for the mineralization of nitrogen from casein and plant materials show that when the upper 3 cm of shadscale and cultivated soils were amended with casein, recovery of Total N was much less than from soils amended with litter. Such discrepancy was not observed when the 5-20 cm depths of shadscale site soils samples were amended with casein or litter.

It was shown by Jewitt (1942) that gaseous ammonia was lost in considerable quantities when NH_4^+ -containing fertilizers were applied to certain alkaline soils. The results obtained show that a release of ammonia (gaseous) was optimal at 40% W.H.C., and at the moisture level above that volatilization decreased. In a dry soil, evolution of ammonia was the least. The volatilization of ammonia was detected in casein-amended soil whereas in litter-amended soils there was no volatilized ammonia detected

EXPECTATIONS

Having worked out procedural and equipment problems, we now propose to collect a full year's data on each process.

Nitrogen content of as many storms as possible will be separately analyzed throughout the year. Leaching will be done with live plants and more uniform water application under controlled conditions. This will allow throughfall, stem flow, leaf drip, and absorption components to be separated without dust and debris contamination. We can then relate back to field conditions on a dry weight basis. A field study on live plants will be designed to check out the correspondence of the greenhouse work. Comparisons will give insight into the degree that dust plays in the N input. Detection

of total gaseous loss of NH_3 will be attempted under field conditions at some time during the growing season. This work will be correlated with use of ^{15}N in small chambers without temperature and humidity control. By next year, a much more complete assessment of the importance of these processes in the nitrogen cycle will be available.

Most of the equipment, supply and procedure problems for ^{15}N work have been solved by now and ^{15}N methods will be used next year to examine and verify the nitrogen flux and pool data obtained so far with chemical and biological methods. This will include N-fixation, N-release from litter, ammonification, nitrification, denitrification, and ammonia volatilization. It is expected that the presently reported data will be essentially verified. Any deviation would be most interesting in the elucidation of the nitrogen cycling in desert soils.

ACKNOWLEDGEMENTS

Next to the Project Leaders, the following personnel participated in the investigations described above: Dr. P. Eberhardt; Miss H. Patel, M.A.; Mr. R. Rychert, M.A.; Miss S. Cotter, B.A.; Mr. L. B. Camp, M.S.

We also wish to acknowledge the assistance of Mr. Randy Shinn, Mr. Jeff Knudsen, and Mr. Steve Hibbler in collecting precipitation samples following storms at Snowville. We appreciate the use of the Utah State Department of Highways shed at Snowville for our leaching experiments.

A series of soil analyses were performed by the Soils Laboratory, Agricultural Experimental Station, USU, and interpreted by Dr. A. Southard.

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PART II

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A B S T R A C T

This report describes the results of the biological and biochemical tests on soils of sites 5, 6 and 7, Curlew Valley. The parameters measured were: microbial numbers, dehydrogenase activity, proteolytic activity, carbon dioxide release, pH, and the content of nitrate, total nitrogen and organic carbon.

The results show that, similar to other desert soils, the biological activities are concentrated in the top cm; the activities decrease drastically with depth. Activities were higher in the rainy periods and were also higher in the soils under the sagebrush canopy.

Considerable metabolism and decomposition takes place in soils with water tensions lower than -15 bars.

The C/N ratios were low, indicating that all of the available organic carbon has been used to immobilize nitrogen, and further immobilization of additional nitrogen (by N-fixation) would be limited.

INTRODUCTION

Our 1972 IBP Desert Biome process studies have been directed towards nitrogen cycling and associated activities in arid area soils. Results are from Curlew Valley sites numbered 5, 6 and 7, established in January of 1972. Site #5 is a sagebrush (*Artemesia tridentata*) dominated area; site #6 is winterfat (*Eurotia lanata*) dominated; and site #7 is dominated by shadscale (*Atriplex confertifolia*).

Part I of this report describes the process studies on nitrogen cycling. In this second part we have described our results on general biological activities of these soils as they pertain to nitrogen transformation and decomposition.

MATERIALS AND METHODS

This report describes results obtained at a South Curlew Valley site, west of the Wildcat mountains, located in T13N-R29E, Sec. 14 and 15. The soils and sampling sites are described in Part I of this report.

Determination of microbial numbers

One g of each sample was placed in a 250 ml screw-cap Erlenmeyer flask containing 99 ml sterile distilled water to give a 1:100 dilution. After vigorous shaking, further dilutions of 10^{-3} , 10^{-4} , 10^{-5} and/or 10^{-6} as desired, were made in screw-cap tubes containing 9 ml of sterile distilled water. Five plates were made for each dilution. Plates with 10^{-2} , 10^{-3} and 10^{-4} dilutions were poured with Martin's Medium for the enumeration of fungi. Plates with 10^{-4} , 10^{-5} and/or 10^{-6} dilutions were poured with Soil Extract Agar for the enumeration of bacteria and streptomycetes.

After thorough mixing, the agar was allowed to harden, and the plates were incubated at 22 C. The plates were stacked and inverted during incubation time.

The fungal plates were counted after 5 days; the bacterial colonies on the soil extract agar plates were counted after 5 days and the streptomycetes after 8 days.

For microaerophilic plate counts soil dilutions of 10^{-3} and 10^{-4} were plated with Brewer's Anaerobic Agar (Difco). The solidified plates were placed right side up in large desiccator jars. The desiccators contained a small amount of 0.5M sulfuric acid in a water reservoir below, to obtain a less-than-saturated water vapor atmosphere. The lid was placed on the jars with a sealant and the jars evacuated. Nitrogen was then allowed to fill the jar from a nitrogen tank. This process was repeated three times. After 14 days the plates were removed and counted.

All microbial counts are reported on an oven-dry soil weight basis.

Preparation of Soil Extract Agar (based on Fred and Waksman, 1928):

Agar	15.0 g
K ₂ HPO ₄	0.5 g
Soil extract	100 ml
Tap water	800 ml
Glucose	1.0 g in 100 ml water

Soil extract was prepared by autoclaving 1000 g garden soil with 1000 ml tap water for 30 min; about 10 g CaCO₃ was added, stirred, and the mixture was filtered on a Buchner funnel with double Whatman #5 filter paper or other retentive filter paper. The filtrate may have to be refiltered to obtain a clear solution. The filtrate was sterilized in 100 ml quantities and stored in refrigerator.

The medium was heated until agar dissolved, cooled enough to adjust pH to 6.8 - 7.2, and sterilized at 15 psi, 121 C, for 15 min. Glucose was sterilized separately in 100 ml tap water, and added to medium after sterilization.

Preparation of Martin's Medium for fungi (Allen, 1957):

Glucose	10.0 g in 100 ml water
Peptone	5.0 g
KH ₂ PO ₄	1.0 g
Mg SO ₄	0.5 g
Rose Bengal	0.033 g
Agar	20.0 g
Streptomycin solution	1.0 ml
Distilled water	to 1000 ml total volume

Glucose is dissolved in 100 ml distilled water and sterilized separately, then added to the medium after both are sterilized. The medium was heated to dissolve agar and then sterilized for 15 min. at 15 psi. The pH is adjusted to between 6.8 and 7.2 before sterilization.

Streptomycin is weighed out under aseptic conditions; 4 g dissolved in 100 ml of sterile distilled water and then poured into a 0.20 μ Millipore filter,

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filtered and poured into a presterilized 250 ml screw-cap Erlenmyer flask. This is stored in a refrigerator and 0.01 ml added to each plate for each 10 ml of agar before pouring plates (careful not to mix in with the 1 ml of soil samples); it may be added to this cooled sterile medium immediately before using. Stable for 6-10 weeks.

Soil respiration

The technique used follows the method of Elkan and Moore (1962). Ten g of soil sample were placed in a 125 ml screw-cap Erlenmyer flask with a center well. Enough distilled water was added to bring the soil to approximately 30% moisture by weight. Then 1 ml of 0.04N $\text{Ba}(\text{OH})_2$ solution was placed in the center well. A blank contained no soil but 2 ml of distilled water.

The flasks were capped tightly and incubated at 30 C while being rocked fast -- enough to agitate the $\text{Ba}(\text{OH})_2$ solution to facilitate CO_2 absorption by the $\text{Ba}(\text{OH})_2$. Time of incubation was 90 minutes, after which all the caps were loosened to stop the reaction.

Titration was carried out with 0.02N HCl until a clear solution resulted. One ml of the freshly made unreacted $\text{Ba}(\text{OH})_2$ solution was also titrated to obtain the original N of the solution used. The 0.02N HCl was prepared fresh each day.

Before each incubation run, the negative water potential of each soil sample was measured. The water potentials were again measured at the end of the incubation time for each soil. The average -bar reading between the beginning and ending reading is the approximate negative bar pressure of the sample during the reaction time.

Determination of phosphatase activity

The method described is adapted from Ramírez-Martínez and McLaren (1966). 1.5 g of a soil sample was placed in each of 3 screw-cap test tubes. To each tube was added 2 ml of Modified Universal Buffer (MUB), pH 7.0. The tubes were numbered and the following reagents were added to a total of 8 ml:

- Tube #1 - 2 ml 0.005M Na- β -naphthyl phosphate
1 ml toluene
3 ml distilled water
- Tube #2 - 2 ml 0.005M Na- β -naphthyl phosphate
4 ml distilled water
- Tube #3 - 1 ml toluene
5 ml distilled water

The tubes were capped (Parafilm and filter paper disks inserted in each cap to insure tight seal) and placed on a rotating wheel (approx. 4 rpm) for 16 hr in a 30 C water bath. After incubation 2 ml of 0.5M NaOH were added to each tube to bring the pH above 11 and to stop the reaction. After shaking, the suspensions were centrifuged at 15,000 rpm for 15 min. Then the supernatants were drawn off with capillary pipettes into photometer tubes, and assayed for the presence of β -naphthol by Aminco-Bowman spectrophotofluorometer (courtesy of Dr. Sharma, Dept. of Veterinary Sciences, USU).

A standard β -naphthol solution of 5×10^{-4} M (0.0072 g/100 ml), pH > 11, was used as a standard to adjust the instrument each day to 76% transmission according to the standard curve.

Modified Universal Buffer (Skujins et al., 1962):

A. Stock Solution Reagents:

Tris (hydroxymethyl) aminomethane	3.025 g
Maleic Acid	2.90 g
Citric Acid	3.50 g
Boric Acid	1.57 g
1N NaOH	122 ml
Distilled water	+0 250 ml

B. Working Solution:

To 20 ml of stock solution add 10 ml of 0.1N HCl, titrate to desired pH (7.0), and make up to volume to 100 ml with distilled water.

Proteolytic activity

Proteolysis was studied with the method of Hoffmann and Teicher (1957). For the assay 10 g of soil sample were placed in each of two 100 ml screw-cap volumetric flasks. 500 mg of calcium carbonate was added to each flask and mixed in; 1.5 ml of toluene was then carefully added drop by drop so that most of the soil was dampened. After standing for 15 minutes, 20 ml of a freshly made 2% gelatin solution was added to one flask, and 20 ml of distilled water to the other flask. After thorough mixing, the flasks were placed on a rotating apparatus in a 37 C incubator.

After 20 hr incubation the flasks were removed from the incubator and filled to the mark with 37 C distilled water. The toluene must be above the mark. After shaking, the contents of each flask were gravity filtered through a double filter paper consisting of Whatman #5 on the outside and a fast filtering crepe type on the inside.

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To assay for the amount of hydrolyzed gelatin, 5 ml of each filtrate was placed in a centrifuge tube. To each was added 5 ml of a cupric phosphate suspension. The mixture of filtrate and cupric phosphate suspension was allowed to stand for 5 minutes with occasional shaking, then centrifuged at 7000 rpm for 5 minutes and the supernatant decanted into photometer tubes. The absorbance at 660 m μ was read on a B & L Spectronic 20.

The standard solution for this assay was a 2% solution containing the appropriate amino acids by weight that make up gelatin. Since the 2% gelatin used in the assay is diluted 1:5 before the absorbance is read, portions of the above solution were also diluted 1:5. This dilution was then considered to represent 100% hydrolysis of gelatin.

Cupric Phosphate Suspension:

Cupric chloride	28 g/l
Sodium phosphate	68.5 g/l
Sodium borate	10.1 g/l, pH adjusted to 9.1 to 9.2
Sodium chloride	6 g/100 ml

To 40 ml of sodium phosphate solution add 20 ml of cupric chloride solution with stirring. Centrifuge the mixture at 7000 rpm for 5 minutes. Discard the supernatant and wash the precipitate twice by resuspending in 60 ml of sodium borate buffer and centrifuging after each washing. Resuspend washed precipitate in 100 ml of borate buffer and add the 6 g of NaCl. Stir until dissolved and store in glass-stoppered bottle. Unstable after 10 days.

Dehydrogenase activity

The method follows that of Casida et al. (1964). Each soil sample was weighed into three sterile screw-cap tubes, 6 g per tube. To two of the tubes were added 2.5 ml sterile distilled water and 1.0 ml 3% aqueous solution of triphenyltetrazolium chloride. To the third tube (control) 3.5 ml sterile distilled water was added. The tubes were mixed thoroughly with a Vortex mixer and then incubated in a 30 C incubator for 24 hr.

Extraction of the triphenyltetrazolium formazan produced was carried out with methanol. The samples were removed from the tubes by shaking with methanol onto a 125 ml Buchner funnel fitted with Whatman #5 filter paper. The soil was washed with methanol until no more color could be extracted. During this procedure it was necessary to keep the sample wet at all times until extraction was complete to avoid air being drawn through the soil.

The filtrate was then poured into a 100 ml vol. flask and made up to volume with methanol. After mixing, approximately 20 ml was poured into tubes for the determination of absorbance. The absorbance was read on a B and L Spectronic 20 at 485 m μ . In some cases, due to suspended soil particles which were not removed by filtration, it was necessary to centrifuge the filtrate at 14,000 rpm for 10 minutes before reading the absorbance.

The readings were compared to a standard formazan curve in order to determine the amount of formazan in the diluted filtrate. The results are reported as mg of formazan in 100 ml of filtrate.

2,3,5-Triphenyltetrazolium chloride (TTC), 3% aqueous solution:
Dissolve 3 g of reagent in 100 ml of distilled water. Triphenyltetrazolium formazan, for a standard formazan curve: 1.5 mg of Triphenyltetrazolium formazan dissolved in 50 ml methanol, for a concentration of 0.03 mg/ml formazan. Serial 1:2 dilutions of this solution were made to develop a standard formazan curve.

Determination of total nitrogen

Total nitrogen was determined by microKjeldahl digestion of soil samples with selenium catalysts and a subsequent microKjeldahl distillation as detailed by Bremner (1965).

Determination of nitrate - nitrogen

The method is reported in a USU Soil Laboratory Manual (undated). Soil samples (50 g) were extracted with 250 ml of 2N KCl as follows: 50 ml of 2N KCl solution was added to a flask containing 50 g of soil, placed on a shaker for 30 minutes and extracted with the remaining 200 ml on Whatman #42 filter paper.

Upon extraction of soil samples the procedure is as follows:

1. Pipette 5 ml of the filtered 2N KCl extract into 100 ml tall beakers and 5 ml of the 2N KCl extracting solution into an extra beaker.
2. Add 5 drops of 4.3N acetic acid; swirl to mix, then add 0.5 ml of 0.5% ammonium sulfamate solution; swirl to mix and place on a hot plate.
3. When warmed to 60 or 80 C, add five drops of 10% NaOH solution; swirl to mix and let contents evaporate to dryness.
4. After removing beakers from hot plate add 2 ml of phenoldisulfonic acid to the beakers in such a way that the residue is moistened quickly and thoroughly. Rub sides of beakers with a stirring rod to bring the

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phenoldisulfonic acid in contact with any of the nitrates that may have spattered onto the wall on drying and let stand at least 20 minutes until the residue is dissolved.

5. Add 34 ml of distilled water and 7 N NH_4OH to beaker until a permanent yellow color remains (14 ml). Let cool. Make further dilution if color is too intense and read absorbance at 420 m μ .

Phenoldisulfonic acid, $\text{C}_6\text{H}_3\text{OH}(\text{HSO}_3)_2$: Dissolve 200 g pure white phenol in 1200 ml concentrated H_2SO_4 . Add 600 ml fuming sulfuric acid (15% free SO_3); stir well; heat for two hours on hot water bath.

Standard KNO_3 solution (stock). Dissolve 0.722 g anhydrous KNO_3 and dilute to 1 liter with distilled water. Contains 0.1 mg N/ml.

Determination of organic carbon

The procedure described below is based on the Walkely-Black (Allison, 1965) and modified Schollenberger (Jackson, 1958) methods.

Subsample the collected soil sample, taking a total of about 15 g from different portions of the soil. Grind this subsample as fine as possible (about 6 mesh fineness) until thoroughly mixed. Remove sticks, straw and other material which is not an integral part of the soil. Use porcelain mortar and pestle, and brass or stainless steel sieve. Avoid iron utensils.

Weigh out duplicate 1 g portions of soil and transfer to 400 ml beakers. If organic matter exceeds about 3.5% or organic carbon about 2.0% weigh a 0.5 g portion of soil. Three blanks should be run in the series to obtain a correction factor.

To each beaker add 10 ml 5% potassium dichromate solution. Use fresh solution daily. Rotate each beaker to insure complete wetting of the sample. Add 20 ml concentrated H_2SO_4 containing 2.5% Ag_2SO_4 , swirl, and place on hot plate immediately. Heat to 150 C; remove from heat, swirl, and place on asbestos pad. Cool to room temperature then dilute to 200-250 ml -- the samples may be left at this point for several hours. Add 25 ml of ferrous solution to each beaker using a pipette. Be sure to drain the syphon and pipette and fill with fresh solution from the bottle at the start of each day's analysis.

The titration may now be begun with the permanganate solution. The end point of the blank is about the same as the permanganate standardization. Titrate until the color changes from the green to a purple-red and persists. In order to detect the end

point a strong light under the sample and vigorous stirring of the sample is necessary. Note: after adding the ferrous solution and before titration the sides of the beaker should be washed down with water.

Dilute both blank and sample to same volume. If this is not done, other solutions besides the permanganate must be standardized.

Overheating the sample causes decomposition of the dichromate. If the sample is overheated, it should be rerun.

As the Curlew Valley samples contain appreciable quantities of salt ($EC_e < 3.0$), H_2SO_4 containing 25.0 g Ag_2SO_4 per liter of acid was used instead of just H_2SO_4 . This is to precipitate the chloride which interferes with the reaction.

Ferrous ammonium sulfate solution: Dissolve 195 g $FeSO_4 (NH_4)_2SO_4 \cdot 6H_2O$ and 30 ml H_2SO_4 (conc.) in distilled water and dilute to one liter.

Potassium permanganate solution: Dissolve 12.5 g of $KMnO_4$ in one liter of water, boil for 10-15 minutes, cool and filter through a washed asbestos pad. An alternate method is to let the solution stand for three or four days at room temperature and filter as above. Standing at room temperature over the prolonged period allows the MnO_2 to form as does the boiling. The MnO_2 is removed by filtering.

The potassium permanganate solution is standardized in the following way. Dry sodium oxalate at 105 C for several hours. Weigh accurately about 1 g samples of $Na_2C_2O_4$, dissolve in 200-250 ml of water, add 10 ml H_2SO_4 (conc.), heat to 85 C and titrate immediately with the permanganate solution. When the end point is being approached add the permanganate dropwise until a faint pink color remains for about one minute. If the same volume (200-250 ml) of solution is used in the organic matter titrations, no blank correction is necessary.

$$\text{Normality } KMnO_4 = \frac{\text{Wt. of sodium oxalate}}{0.067 \times \text{Vol. } KMnO_4 \text{ used}}$$

$$\text{Milliequivalent weight sodium oxalate} = 0.067$$

Calculations:

In the blank titration there are two oxidizers ($KMnO_4$ and $K_2Cr_2O_7$) and one reducer, ferrous ammonium sulfate. In the titration of a soil sample the same quantity of ferrous and the dichromate solutions is used as in the blank, but since a second reducer (organic matter) is present more of the permanganate is required. The extra permanganate solution is a measure of the organic matter which has been oxidized.

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If a blank is run for each set of samples, using the same volumes of dichromate and ferrous solutions as are used for the soil sample, the percent organic carbon is the product of the extra permanganate solution used and factor determined as follows:

$$\text{Milliequivalent wt. carbon} = 0.003$$

$$\% \text{ organic carbon in organic matter} = 58$$

$$\% \text{ organic carbon recovered} = 89$$

$$\frac{\text{meq. wt. carbon} \times \text{normality KMnO}_4}{(.89) (\text{wt. soil sample})} \times 100 = \text{Factor}$$

$$(\text{Factor}) \times (\text{Vol. of extra KMnO}_4) = \% \text{ Organic Carbon}$$

If it is desired to express the results as organic matter, then $\% \text{ organic carbon} \times 1.724 = \text{organic matter } \%$.

The result obtained is usually on an air-dry basis. To convert to oven-dry basis multiply the percent organic carbon on an air dry basis by the moisture factor, which is 1.00 plus percent moisture on dry weight basis expressed as a decimal fraction.

Soil moisture content

One g of each soil sample was placed into weighing bottles. With lids ajar the bottles were placed in a drying oven at 110 C. After two days the samples were removed, allowed to cool, and reweighed. The amount of weight loss was calculated as the number of g of water per 100 g of soil:

$$\frac{(\text{Moist Weight} - \text{Dry Weight})}{\text{Dry Weight}} \times 100 = \% \text{ Moisture}$$

Soil pH determination

The pH values of soil samples were determined by weighing 5 g of a soil sample into a 15 ml beaker, adding 5 ml of distilled water, and stirring the contents. After standing approximately ten minutes, the contents were swirled, and the pH was read with a Beckman pH meter using small electrodes.

Water potential measurements

The MJ55 Model Psychrometric Microvoltmeter was used with a sample chamber psychrometer.

Before measuring the water potential of a soil sample, the temperature was measured. This is done by connecting the copper constantan thermocouple wires of the chamber to the red and blue binding posts of the microvoltmeter. The

"reference junction" switch must be in the "up" position and the range switch on the one millivolt full scale; the meter will read the voltage corresponding to the chamber temperature where the sample is held. The voltage reading can be converted to C by using Table 1.

Table 1. Copper constantan conversion chart

Temp. C	0	1	2	3	4	5	6	7	8	9	10	Temp. C
Millivolts												
(+)0	0.000	0.038	0.077	0.116	0.154	0.193	0.232	0.271	0.311	0.350	0.389	(+)0
10	0.389	0.429	0.468	0.508	0.547	0.587	0.627	0.667	0.707	0.747	0.787	10
20	0.787	0.808	0.827	0.908	0.949	0.990	1.030	1.071	1.112	1.153	1.194	20
30	1.194	1.235	1.277	1.318	1.360	1.401	1.443	1.485	1.526	1.568	1.610	30
40	1.610	1.652	1.694	1.737	1.779	1.821	1.864	1.907	1.949	1.992	2.035	40

Temperatures in C, based on the International Temperature Scale of 1948. Reference junctions at 0 C.

To read the voltage corresponding to water potential of the soil, the "reference junction" toggle must be in the off (down) position. Disconnect the copper thermocouple and constantan wires. Next, connect the copper wire of the psychrometer to the red input terminal and the silver wire of the psychrometer to the black input terminal of the meter. Turn power switch "on" and set the meter to proper scale, usually 10 μ volts.

The meter should be zeroed with the zero control knob and, with the power switch back to the "on" position, the temperature and vapor pressure within the sample chamber is allowed to come to equilibrium -- the needle should come back to zero position.

After allowing for equilibration the "cool" switch is held down for 15 sec. When the "cool" switch is released a reading from the proper scale is taken. This μ volt reading is converted to -bars by referring to standard calibration curves corresponding to the temperature (Figure 1).

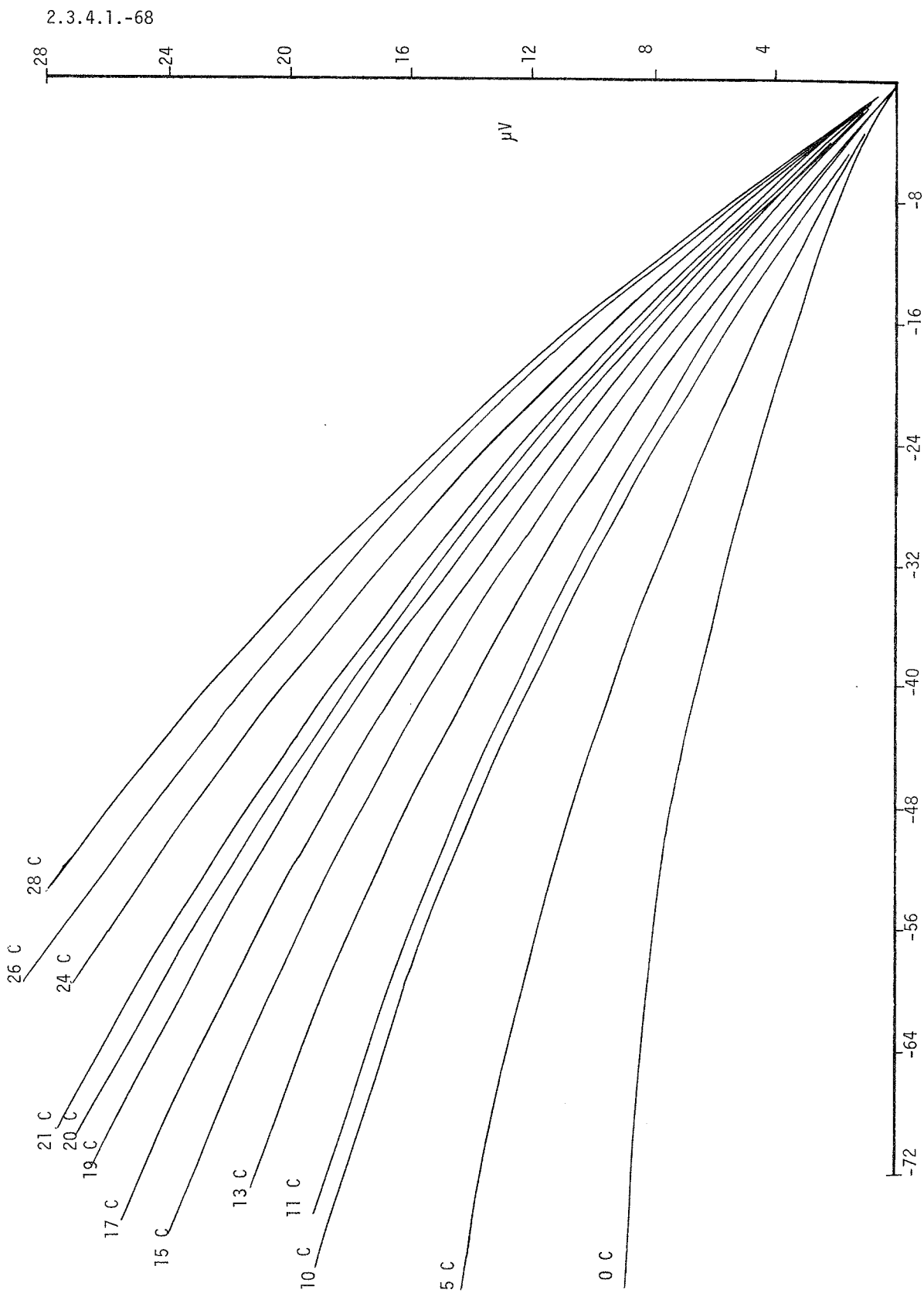


Figure 1. Standard calibration curves for determination of water potential.

Calibration curve for psychrometer

The curve was developed from methods of Wiebe et al. (1971). A 2 molal stock solution was prepared by dissolving 116.90 g of NaCl (reagent grade) in 1000 g of distilled water. This gives a 9.5543 g solution per g NaCl. The mass of NaCl required for any solution is the molality multiplied by the molecular weight. Multiplying the molality times the molecular weight times the mass of stock solution per unit mass of NaCl gives the mass of solution required. The mass of NaCl plus 1000 g gives the total mass of the solution, so the amount of water required to add was obtained by subtraction of the stock solution mass from the total mass. Table 1A shows the stock solution mass, mass of water required, and total mass for NaCl solution. For our measurements, standard solutions were made up at temperatures from 0 to 34 C. The temperature of the chamber was first read, and then of the solutions. Equilibration time between chamber and solution was 15 sec. For water potentials between 0 and -40 bars, the output was essentially linear (Figure 1 and Table 2).

Table 1A. Development of standard solutions for calibration curve for psychrometer

Molality of NaCl	Mass of 2-molal stock solution (g)	Mass of water (g)	Total mass (g)
0.1	55.84	950.00	1005.84
0.2	111.69	900.00	1011.69
0.3	167.53	850.00	1017.53
0.4	223.38	800.00	1023.38
0.5	279.32	750.00	1029.22
0.6	335.07	700.00	1035.07
0.7	390.91	650.00	1040.91
0.8	446.76	600.00	1046.76
0.9	502.60	550.00	1052.60
1.0	558.45	500.00	1058.45
1.5	837.67	250.00	1087.67
2.0	1116.90	0.00	1116.90

2.3.4.1.-70

Table 2. Water potentials of NaCl solutions (Lang, 1967) at temperatures between 0-40 C

Molality	Water Potential (J/kg)*								
	Temperature (C)								
	0	5	10	15	20	25	30	35	40
0.05	- 214	- 218	- 222	- 226	- 230	- 234	- 238	- 242	- 245
0.1	- 423	- 431	- 439	- 447	- 454	- 462	- 470	- 477	- 485
0.2	- 836	- 852	- 868	- 884	- 900	- 915	- 930	- 946	- 961
0.3	-1247	-1272	-1297	-1321	-1344	-1368	-1391	- 1415	- 1437
0.4	-1658	-1693	-1727	-1759	-1791	-1823	-1855	- 1886	- 1917
0.5	-2070	-2115	-2158	-2200	-2241	-2281	-2322	- 2362	- 2402
0.6	-2484	-2539	-2593	-2644	-2694	-2744	-2794	- 2843	- 2891
0.7	-2901	-2967	-3030	-3091	-3151	-3210	-3270	- 3328	- 3385
0.8	-3320	-3398	-3472	-3543	-3612	-3682	-3751	- 3818	- 3885
0.9	-3743	-3832	-3917	-3998	-4079	-4158	-4327	- 4314	- 4390
1.0	-4169	-4270	-4366	-4459	-4550	-4640	-4729	- 4815	- 4001
1.1	-4599	-4713	-4820	-4924	-5026	-5127	-5226	- 5322	- 5418
1.2	-5032	-5160	-5278	-5394	-5507	-5620	-5730	- 5835	- 5941
1.3	-5470	-5611	-5742	-5869	-5994	-6110	-6239	- 6354	- 6471
1.4	-5912	-6068	-6210	-6350	-6487	-6623	-6754	- 6880	- 7006
1.5	-6359	-6529	-6684	-6837	-6986	-7134	-7276	- 7411	- 7548
1.6	-6811	-6996	-7163	-7330	-7491	-7652	-7805	- 7950	- 8007
1.7	-7260	-7460	-7640	-7820	-8000	-8170	-8330	- 8490	- 8650
1.8	-7730	-7940	-8130	-8330	-8520	-8700	-8880	- 9040	- 9210
1.9	-8190	-8430	-8630	-8840	-9040	-9240	-9430	- 9600	- 9780
2.0	-8670	-8920	-9130	-9360	-9570	-9780	-9980	-10160	-10350

* 1 bar = 100 J/kg

RESULTS

Numbers of microorganisms

The numbers of microorganisms in soils are shown in Table 3 (aerobic bacteria), Table 4 (streptomycetes), Table 5 (microaerophilic bacteria), and Table 6 (fungi).

Results of the dates studied showed that numbers of aerobic bacteria were generally two to four times greater than were numbers of streptomycetes. Site #6 (winterfat) had the greatest numbers of bacteria of the three study sites, with most found in the 0-3 cm layer. Site #5 (sagebrush) had only slightly greater numbers of bacteria and streptomycetes than the soils from site #7 (shadscale). The highest numbers of organisms for the sagebrush soils were at the 40-50 cm depth in June, but at the 0-3 and 5-20 cm depths in August. Site #7 (shadscale) showed the greatest numbers in the 5-20 cm depth, dropping sharply at the next lower depths for June. The 40-50 cm depth had high

numbers of bacteria but not streptomycetes for August samples. Most of the streptomycetes for both June and August were found in the 5-20 cm layer with two- to ten-fold lower numbers in the other layers of the soil profile.

Table 3. Number of aerobic bacteria per g of soil (DSCODE A3UBJJ5)

Sample	<u>#/g dry soil</u>			
	1 April 1972	11 May 1972	14 June 1972	25 August 1972
Site #5-1 (surface)	7,060,000	9,290,000	570,000	2,200,000
2 (5-20 cm)	5,910,000	3,280,000	460,000	2,700,000
3 (40-50 cm)	1,180,000	4,310,000	4,100,000	1,200,000
4 (70-80 cm)	1,070,000	2,640,000	980,000	3,300,000
5 (100-120 cm)	47,800			
Site #6-1 (surface)	15,300,000	3,230,000	5,300,000	4,900,000
2 (5-20 cm)	31,000,000	5,810,000	1,900,000	2,600,000
3 (40-50 cm)	14,900,000	3,120,000	1,700,000	2,700,000
4 (70-80 cm)	5,520,000	1,380,000	280,000	210,000
5 (100-120 cm)	2,230,000			
Site #7-1 (surface)	6,730,000	4,850,000	960,000	2,500,000
2 (5-20 cm)	5,840,000	3,200,000	2,200,000	2,900,000
3 (40-50 cm)	3,490,000	1,390,000	410,000	2,900,000
4 (70-80 cm)	253,000	1,650,000	120,000	700,000
5 (100-120 cm)	159,000			

2.3.4.1.-72

Table 4. Number of streptomycetes per g of soil (DSCODE A3UBJJ5)

Sample	<u>#/g dry soil</u>			
	1 April 1972	11 May 1972	14 June 1972	25 August 1972
Site #5-1 (surface)	1,330,000	1,620,000	390,000	1,100,000
2 (5-20 cm)	1,780,000	4,530,000	580,000	1,700,000
3 (40-50 cm)	70,600	1,800,000	4,300,000	960,000
4 (70-80 cm)	455,000	1,700,000	320,000	230,000
5 (100-120 cm)	<100			
Site #6-1 (surface)	4,970,000	1,010,000	1,600,000	1,100,000
2 (5-20 cm)	7,470,000	645,000	2,000,000	910,000
3 (40-50 cm)	14,700,000	2,020,000	1,500,000	2,200,000
4 (70-80 cm)	4,990,000	237,000	110,000	110,000
5 (100-120 cm)	1,940,000			
Site #7-1 (surface)	5,310,000	4,040,000	760,000	440,000
2 (5-20 cm)	674,000	3,620,000	1,700,000	1,600,000
3 (40-50 cm)	930,000	776,000	410,000	580,000
4 (70-80 cm)	25,300	3,060,000	46,000	270,000
5 (100-120 cm)	68,200			

Table 5. Numbers of microaerophilic bacteria for Curlew Valley soils, expressed as counts per g of dry soil (DSCODE A3UBJJ5)

Sample	#/g dry soil		
	1 April 1972	11 May 1972	14 June 1972
Site #5-1	102,000	1,900,000	530,000
2	22,000	1,700,000	350,000
3	706,000	230,000	370,000
4	1,000,000	170,000	2,700,000
5	143,000	no data	no data
Site #6-1	619,000	3,100,000	220,000
2	286,000	900,000	1,100,000
3	754,000	300,000	no data
4	308,000	190,000	
5	316,000	no data	
Site #7-1	327,000	770,000	
2	265,000	1,000,000	
3	488,000	260,000	
4	597,000	94,000	

Table 6. Number of fungi per g of soil (DSCODE A3UBJJ5)

Sample	#/g dry soil			
	1 April 1972	11 May 1972	14 June 1972	25 August 1972
Site #5-1	122,000	6,900	6,100	17,000
2	94,500	37,000	5,800	79,000
3	7,100	500	110,000	86,000
4	1,400	2,100	6,800	1,400
5	90			
Site #6-1	5,000	2,700	4,700	10,700
2	17,800	30,000	13,000	28,000
3	47,600	29,000	24,000	33,000
4	5,100	8,600	900	632
5	1,200			
Site #7-1	3,500	3,400	5,500	8,100
2	27,000	240,000	42,000	23,000
3	700	2,300	1,600	1,700
4	250	<100	0	1,700
5	40			

Aerobic bacteria for April, 1972, were generally two to four times greater than numbers of streptomycetes. The highest numbers for bacteria were in the 0-3 and 5-20 cm depths. For streptomycetes the highest numbers were mostly in the 0-3 cm and 40-50 cm depths. Most bacteria were found in the shadscale soil rather than in either winterfat or sagebrush, both of which had about the same numbers. Most of the streptomycetes were in the shadscale and winterfat soils.

In May more bacteria and streptomycetes were found in sagebrush soil, with highest numbers in the 0-3 cm layer for bacteria and the 5-20 cm layer for streptomycetes. The shadscale site and winterfat site had about equal numbers of bacteria with most being found in the 0-5 cm and 5-20 cm layers. Streptomycetes at these two sites were lower than bacteria at the shadscale site, but about the same or somewhat higher numbers than bacteria at the winterfat site.

Numbers of anaerobic bacteria varied from site to site and throughout the soil profile. Their numbers in May and June ranged from 3.1×10^6 down and to 9.4×10^4 . There was generally a decrease from May to June counts, but numbers were still slightly higher for June than April counts.

Similarly, numbers of fungi varied from site to site, and throughout the season and profile. Significantly, fungal numbers were not concentrated in the surface layer (except for the April sampling, sagebrush station).

Dehydrogenase activity

It is evident that most of the activity is located in the top 0-3 cm layer, with generally negligible rates below.

The activity was higher for sagebrush than shadscale soils for January, 1972, samples (not shown in the Table). Samples from sites 5, 6 and 7 had 10-fold higher activity in the surface 3 cm layer than the rest of the profile (Table 7), as has been found in previous studies.

In sampling for October an extra group was taken at the sagebrush site (#5). Samples were taken from directly under the canopy of the plants to determine if an increase in activity would be found. The first two depths (5-10 and 5-20 cm) from under the canopy, as compared with the same depths not under the canopy, had an increase of only one-third with no difference at lower depths.

Proteolytic activity

The proteolysis procedure is based on the rate of gelatin hydrolysis and reported as percent hydrolysis after 20 hr incubation. The values are shown in Table 8.

Table 7. Dehydrogenase activity, as measured by mg of formazan produced from reduction of triphenyltetrazolium (DSCODE A3UBJJ4)

Sample No.	1 April	11 May	14 June
	mg formazan	mg formazan	mg formazan
Site #5-1 (surface)	.74	.62	.88
2 (5-20 cm)	.05	.05	.17
3 (40-50cm)	.036	.03	.08
4 (70-80cm)	.02	.02	trace
5 (100-120cm)	.026		
Site #6-1	.92	1.33	1.08
2	.02	.12	.13
3	.04	.08	.11
4	.01	.02	.02
5	.04		
Site #7-1	.91	2.5	1.64
2	.11	.03	.42
3	.04	.02	.01
4	.02	.00	trace
5	.01		

Sample No.	24 August	15 Sept.	14 Oct.	14 Nov.
	mg formazan	mg formazan	mg formazan	mg formazan
Site #5-1 (surface)	1.54	1.29	1.08	0.7
2 (5-20 cm)	.11	.06	.05	.05
3 (40-50cm)	.06	.04	.02	.03
4 (70-80cm)	trace	.035	.01	.02
Site #6-1	1.25	1.52	1.15	1.21
2	.10	.12	.03	.12
3	.08	.03	.04	.06
4	.06	.036	.02	.03
Site #7-1	2.16	1.94	2.0	2.50
2	.12	.12	.15	.14
3	.06	0.18	.05	.08
4	.00	.00	.01	.01

Site #5-1C (under canopy)		1.5	
2C		.07	
3C	not sampled	.02	
4C		.02	not sampled

Table 8. Proteolytic activity (DSCODE A3USQ02)

Sample	1 April 1972	11 May 1972
	% Hydrolysis	
Site #5-1 (surface)	25	24
2 (5-20 cm)	5	10
3 (40-50 cm)	14	12
4 (70-80 cm)	4	3
5 (100-120 cm)	9	
Site #6-1	36	35
2	16	13
3	23	13
4	8	5
5	9	
Site #7-1	17	38
2	11	15
3	14	12
4	7	8
5	3	

Sample No.	24 August 1972	15 Sept. 1972	14 Oct. 1972	14 Nov. 1972
	% Hydrolysis			
Site #5-1	29	35.5	31.5	31.5
2	9	9.8	12.5	4.4
3	0	12.0	7.0	7.5
4	0	9.8	4.0	2.0
Site #6-1	23	27	25	41
2	7	5	7	9.8
3	9	7.4	4.2	10.5
4	7	2	2	9.0
Site #7-1	23	35	36	47
2	9	7	7.2	12
3	10	4.4	12.4	8
4	5	4.0	4.2	3
Site #5-1C (under canopy)			47	
2C			9	
3C	not sampled		7	not sampled
4C			3	

As in dehydrogenase, the activity was higher in the top 0-3 cm layer by a third to a sixth than in the 5-20 cm layer. There is generally a decrease with each deeper layer.

Phosphatase activity

Phosphatase activity in April and May, 1972, in sites 5, 6 and 7 was highest in the surface layer, dropping by about half in the 5-20 cm depth and being nearly as high again in 40-50 cm depth as in the surface 3 cm. The lower two depths had decreasing activity (Table 9).

Table 9. Phosphatase activity (DSCODE A3UBJJ2, BJJ3)

Sample	1 April 1972		$\mu\text{moles/g } \beta\text{-naphthol}$ 11 May 1972	
	w/Toluene	w/o Toluene	w/Toluene	w/o Toluene
Site #5-1 (surface)	.64	1.36	.93	1.16
2 (5-20 cm)	.56	.50	.50	.34
3 (40-50 cm)	.70	.76	.64	.50
4 (70-80 cm)	.20	.16	.30	.16
5 (110-120cm)	.11	.10		
Site #6-1	.80	1.06	.70	.90
2	.60	.52	.47	.46
3	.80	.80	.50	.44
4	.40	.40	.16	.14
5	.20	.20		
Site #7-1	.60	1.16	.70	1.32
2	.40	.40	.20	.26
3	.70	.60	.60	.56
4	.20	.16	.20	.18
5	.10	.10		

Soil respiration

The amounts of CO_2 evolved from the soils studied are found in Table 10. Results were obtained under optimum temperature and moisture conditions in the soils. For Curlew Valley soils at all three sites it was found that maximum CO_2 evolution occurred with the soils at approximately 30% moisture.

In the top 3 cm layer the values are two to four times higher, depending upon the site.

Table 10. CO₂ evolution from Curlew Valley soils (DSCODE A3UBJJ1)

Sample No.	24 August 1972		15 Sept. 1972	
	Water Potential Bars	CO ₂ Evolved μmoles/g/min	Water Potential Bars	CO ₂ Evolved μmoles/g/min
Site #5-1 (surface)	- 5.0	45.2	- 3.4	52.9
2 (5-20 cm)	- 5.6	12.0	- 3.0	15.6
3 (40-50 cm)	-10.0	17.6	- 8.8	17.3
4 (70-80 cm)	-26	8.0	-15.7	18.2
Site #6-1	- 5.2	48.4	- 4.9	59.1
2	- 5.0	8.9	- 8.8	21.8
3	- 4.6	10.2	- 5.7	15.1
4	- 6.0	5.8	- 4.5	19.1
Site #7-1	- 7.5	11.6	- 5.2	19.6
2	-14.5	5.8	- 9.2	18.7
3	-34	14.7	-28.9	14.6
4	-37.6	9.8	-26.6	14.2

Sample No.	14 Oct. 72		14 Nov. 72	
	Water Potential Bars	CO ₂ Evolved μmoles/g/min	Water Potential Bars	CO ₂ Evolved μmoles/g/min
Site #5-1	- 5.3	56.0	-12.1	22.2
2	- 4.8	21.2	- 6.1	8.0
3	-22.8	27.4	-18.2	27.0
4	-17.3	15.0	-26.6	19.4
Site #6-1	- 7.9	20.8	- 8.5	29.6
2	- 6.7	17.2	-10.0	15.4
3	- 6.0	14.6	-11.3	40.4
4	- 8.0	12.0	-13.4	15.0
Site #7-1	-10.2	19.0	- 8.0	36.0
2	-12.7	8.8	-10.4	10.2
3	-14.6	15.0	-23.0	16.4
4	-20.7	10.2	-24.0	6.6
Site #5-1C (under canopy)	- 7.9	60.4	not sampled	
2C	-10.3	20.8		
3C	-16.4	27.4		
4C	-20.4	19.4		

Respiration of soil with added glucose or glycine was studied (Figure 2). Soils showed an increase in CO₂ evolved with up to 6 or 8% concentration of amendment, but activity dropped sharply when higher percentages of glucose or glycine were added (Figure 2). The results are shown in Tables 11 and 12. Soil samples to which no amendments were added, at 45% soil moisture, showed highest amount of CO₂ evolved

after 2 hr, dropping down after 2.5, 3.0 and 4.0 hr. Surface 3 cm layer samples showed highest total CO_2 evolved after 110-130 min. Soils from deeper layers (40-50 cm) in the profile gave highest evolution after 140 min incubation. The optimal time for these soils to evolve maximum amount of CO_2 was 90-130 min. (Figure 3).

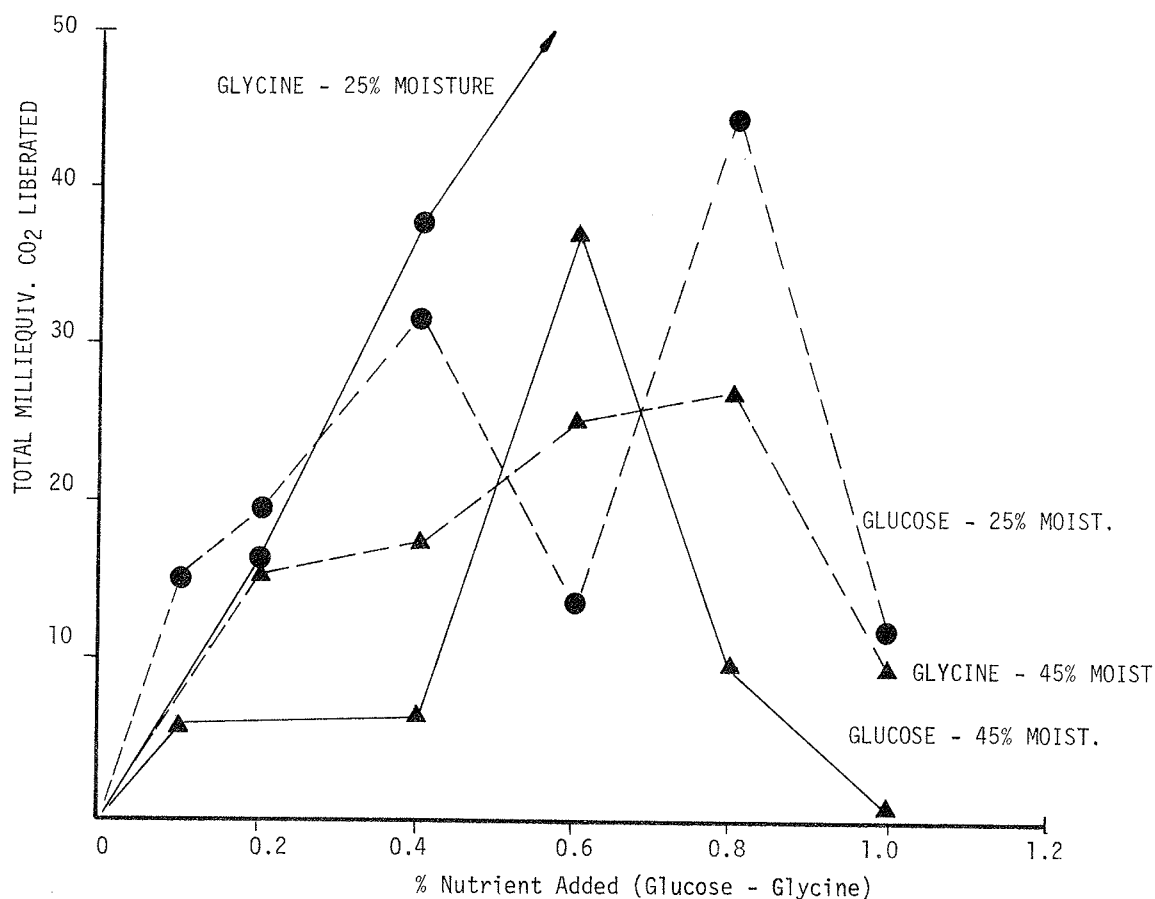


Figure 2. Respiration of amended soils.

Table 11. CO₂ evolution from unamended soils (DSCODE A3UBJJ1)

Sample*	Bar Pressure	CO ₂ evolved μ moles/g/min
1N-shadscale type 0-2 cm	- 6	59
2N-shadscale type 3-15 cm	-11	68
3N-sagebrush type 0-2 cm	- 6	63
4N-garden soil 0-15 cm	- 2.8	82

*Samples collected on January 20, 1972 from nonspecified stations at the site.

Table 12. CO₂ evolution in soils amended with 6% glucose (DSCODE A3UBJJ1)

Sample*	Soil Water Content (%)	Bar Pressure	CO ₂ evolved μ moles/g/min
1N	25	-15	81.8
1N	45	- 6	121.4
2N	25	-20	59.2
2N	45	-11	71.2

*Samples as in Table 11.

Respiration in a shadscale soil was studied with respect to moisture content as expressed in negative water tension (Figure 4).

Generally, the shadscale soil (SS) retained its respiratory activity at considerably higher levels as compared with a garden soil (GS) at the same negative water tension values.

In measuring the amount of CO₂ respired from soils amended with *Eurotia lanata* roots and shoots, it was found that soils with shoots gave higher amounts of CO₂ than those with roots (Table 13).

Soil pH

Table 14 gives the pH values for the soil samples collected. These values are determined in a 1:1 water suspension and ranged from pH 8.11 to 9.65. The pH increased in alkalinity from August to November in most of the samples. The surface layer generally had a lower pH than the deeper layers.

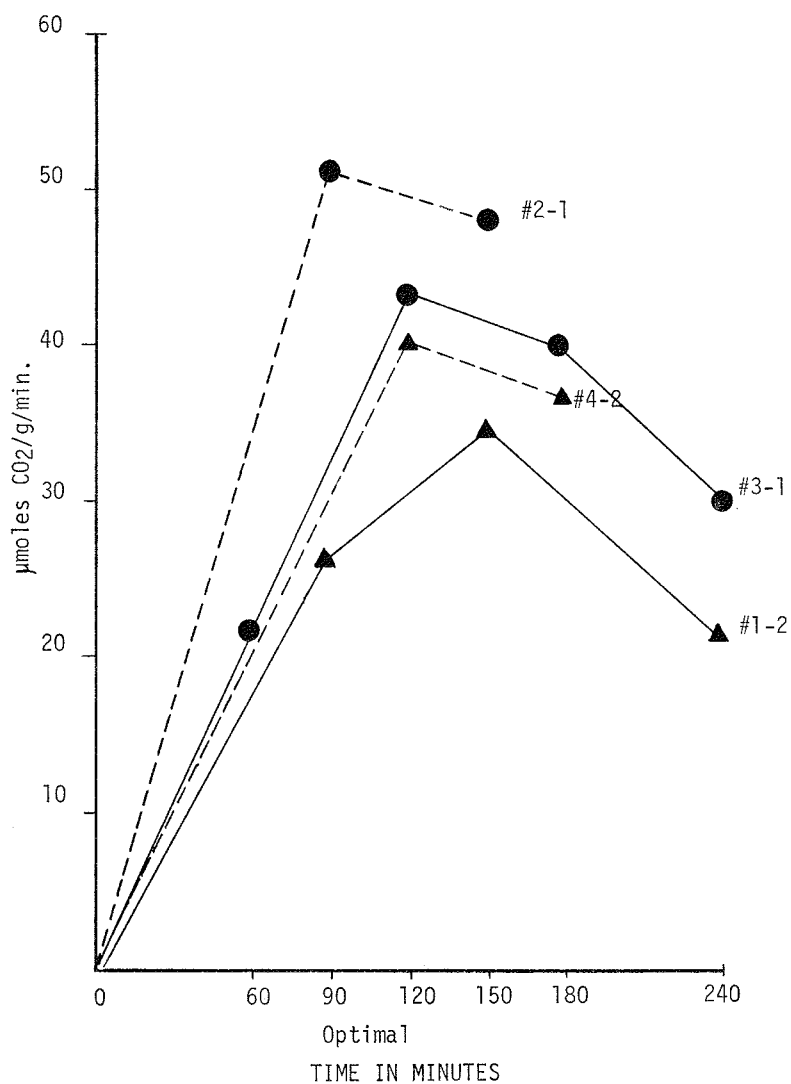


Figure 3. CO₂ evolution vs time.

Table 13. CO₂ evolution from soils amended with *Eurotia* roots and shoots (DSCODE A3UBJJ1)

Sample*	Bar Pressure	CO ₂ evolved μ moles/g/min
1N ₁ + 5% roots	-1.0	61.4
1N ₁ + 5% shoots	-1.0	104.0
1N ₁ + 2% roots	-0.8	41.8
1N ₁ + 2% shoots	-0.8	57.8
2N ₁ + 5% roots	-0.6	91.4
2N ₁ + 5% shoots	-0.6	114.6

* As in Table 11.

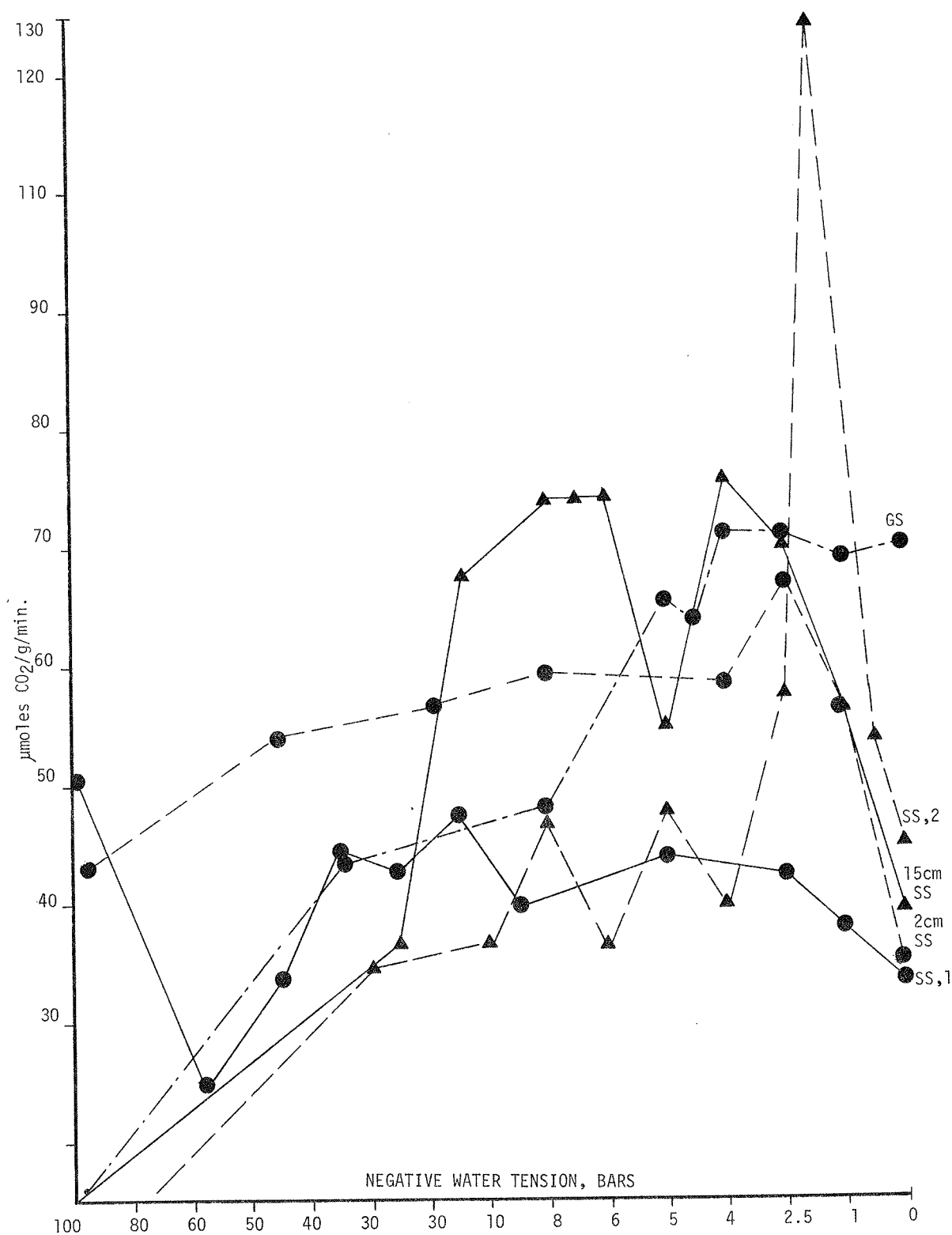
Figure 4. CO₂ evolution vs. soil moisture in bars.

Table 14. pH in Curlew Valley soils (DSCODE A3UBJJ6)

Sample No.	pH			
	24 August 1972	15 Sept. 1972	14 Oct. 1972	14 Nov. 1972
Site #5-1	8.52	8.38	8.72	8.83
2	8.68	8.88	9.09	9.48
3	8.85	9.08	9.62	9.45
4	9.21	9.09	9.69	9.29
Site #6-1	8.60	8.11	9.00	8.82
2	8.95	8.49	9.15	8.70
3	9.12	8.52	9.22	9.15
4	9.50	8.62	9.82	8.82
Site #7-1	9.29	8.88	9.12	8.85
2	8.56	8.49	--	9.21
3	8.75	8.54	9.15	8.99
4	8.68	8.61	9.11	9.01
Site #5-1C (under 2C canopy) not sampled			8.78	
3C			9.02	
4C			9.10	
			9.12	not sampled

Percent water

The water content in samples taken on the dates indicated are shown in Table 15. The values increase at all three sites in the surface layer from a low of 1.4% at site #7 in June, to a high of 19.7% for the same site in November.

Table 15. Water content in Curlew Valley soils

Sample No.	% Water				
	14 June 1972	24 August 1972	15 Sept. 1972	14 Oct. 1972	14 Nov. 1972
Site #5-1	1.6	2.77	2.14	4.00	16.5
2	4.7	8.45	6.60	6.40	13.5
3	7.9	8.34	11.48	41.8	12.9
4	22	16.68	13.63	14.2	20.8
Site #6-1	1.8	1.42	1.83	3.20	16.4
2	4.1	3.62	4.49	4.40	14.1
3	6.3	4.93	4.60	4.90	18.8
4	8.0	4.93	5.48	6.80	8.6
Site #7-1	1.7	1.44	2.04	2.90	19.7
2	4.5	7.52	8.22	3.14	15.7
3	15	18.27	16.95	12.7	15.7
4	15	17.25	15.07	16.1	14.2
Site #5-1C (under 2C canopy) not sampled				4.49	
3C				7.23	
4C				13.80	
				20.30	

2.3.4.1.-84

The highest percent water at all sites for all depths was found in the 40-50 cm depth at site #5 in the month of October. Most of the water was held in the lower depths at all the sites.

Chemical analysis

The amounts of nitrate, total nitrogen and total organic carbon in site #5, #6 and #7 soils during the season are shown in Table 16. [The amount of ammonium in the same soils is shown in Table 9, and that of nitrite in Table 10, this report, Part 1.]

The C/N ratios are included in Table 16.

Table 16. Chemical analysis of Curlew Valley soils (DSCODE A3USQ01)

11 May 1972	NO ₃ -N (PPM)	Total % N	% Organic Carbon	C/N Ratio
Site #5-1	1.3	.12	1.07	8.9
2	.2	.06	.54	9.0
3	.1	.06	.54	9.0
4	.2	.03	.29	9.7
Site #6-1	1.2	.13	1.58	12.1
2	.4	.06	.65	10.8
3	<.1	.05	.49	9.8
4	1.7	.02	.23	11.5
Site #7-1	5.0	.13	1.46	11.2
2	<.1	.07	.67	9.6
3	.3	.06	.57	9.5
4	.2	.04	.40	10.0
<u>14 June 1972</u>				
Site #5-1	3.1	.17	1.66	9.8
2	1.3	.09	.82	9.1
3	.4	.06	.61	10.2
4	.6	.05	.43	8.6
Site #6-1	1.8	.12	1.13	9.4
2	1.6	.06	.65	10.8
3	1.1	.07	.74	10.5
4	.9	.03	.27	9.0
Site #7-1	3.0	.10	.91	9.1
2	6.0	.09	.89	9.9
3	.4	.06	.62	10.3
4	.4	.04	.46	11.5

Table 16. (cont).

24 August 1972	NO ₃ -N (ppm)	Total % N	% Organic Carbon	C/N Ratio
Site #5-1	4.5	.14	1.79	12.8
2	2.6	.07	.74	10.4
3	.2	.06	.73	12.2
4	2.0	.03	.28	9.3
Site #6-1	.7	.12	1.27	10.6
2	1.3	.06	.62	10.3
3	.5	.06	.54	9.0
4	.4	.02	.25	12.5
Site #7-1	2.4	.12	1.27	10.6
2	.1	.07	.63	9.0
3	<.1	.07	.75	10.7
4	7.9	.04	.39	9.8
<hr/> 15 Oct. 1972 <hr/>				
Site #5-1	1.3	.15	1.9	12.6
2	.88	.08	.8	10.0
3	.38	.06	.7	11.7
4	1.8	.04	.4	10.0
Site #6-1	.25	.14	1.6	11.4
2	3.0	.07	.7	10.0
3	<.1	.06	.5	8.3
4	<.1	.05	.5	10.0
Site #7-1	1.0	.13	1.4	10.8
2	1.8	.08	.6	7.5
3	.5	.08	.7	8.8
4	.5	.06	.5	8.3
<hr/> 14 Nov. 1972 <hr/>				
Site #5-1	.25	.15	1.8	12.0
2	.88	.07	.5	7.2
3	.38	.06	.5	8.3
4	1.6	.03	.3	10.0
Site #5-1C (under canopy)	5.0	.21	2.8	13.3
2C	1.5	.08	.8	10.0
3C	1.3	.09	.9	10.0
4C	5.1	.04	.4	10.0
Site #6-1	<.1	.11	1.0	9.1
2	1.0	.06	.5	8.3
3	<.1	.06	.4	6.7
4	.13	.04	.3	7.5
Site #7-1	.5	.16	1.6	10.0
2	1.0	.07	.7	10.0
3	.88	.08	.7	8.8
4	.5	.05	.4	8.0

Microbial numbers

The plate counts for 1972 show that there were about two-to four-fold more bacteria than streptomycetes in these soils.

Bacteria decreased with increasing depth in the profile but the highest number was often in the 5-20 cm depth rather than the surface 0-3 cm, where most of the algal and lichen activities are located. The numbers reached $<5 \times 10^6/\text{g}$ and decreased to $1.2 \times 10^4/\text{g}$ at the 70-80 cm depths.

Station #5 (sagebrush) had the highest bacteria and streptomycetes counts at the 40-50 cm depth in June, but in August the highest numbers were at the 0-3 cm and 5-20 cm depths.

The shadscale samples (station #7) of August had a nearly three-fold increase in numbers in the 0-3 cm layer over the June counts. The 5-20 cm depth had the greatest number of bacteria in June and was slightly higher in August.

Streptomycetes generally followed the same patterns of distribution with depths and from station to station as bacteria. The highest numbers were from $2 \times 10^6/\text{g}$ in the 5-20 cm layers with two- to ten-fold decrease in the other layers of the soil profile. The only exception was at station #5 in June where streptomycetes showed a high count of $4 \times 10^6/\text{g}$ with 40-50 cm depth.

The June and August distribution of fungal numbers remained the same between the three soil types studied. The surface 0-3 cm layer in August showed an increase of over two-fold from the numbers found for June. However, the highest numbers were still found in the 40-50 cm layers for sagebrush and winterfat soils, and in the 5-20 cm layer for the shadscale soils, but with no increase over the June numbers.

This increase of numbers in the surface two depths from June to August reflects the increasing moisture as the dry summer period comes into the slightly wetter month of August and on into the wet fall months. The numbers in the 40-50 cm layer from June to August remained the same, probably because any moisture received during August never penetrated to the deeper layers.

Generally, the microbial numbers are somewhat lower in these soils than in cultivated soils; it has not been possible to correlate the microbial numbers with any of the other measured biological parameters.

Dehydrogenase activity

Determination of dehydrogenase activity is based on the ability of soil to reduce triphenyltetrazolium chloride to the respective formazan. The amount of formazan produced is directly related to the dehydrogenase activity. It represents the "total biological activity".

At all three stations the surface 0-3 cm layer had from 10- to 20-fold higher activity over the rest of the profile. There was a steady, nearly linear decrease from August through November samples from station #5. Station #6 had the highest activity occurring in the September samples. Station #7 had higher activity for all four months than did soils from stations #5 and #6. Here the activity decreased from August to September but showed an increase in October through November samples.

It is felt that the most substantial index of the biological activity of soil is its enzymatic activity, and that the study of the latter rather than numbers of microorganisms can give an indication about the processes occurring in the soil. Our results show that the one enzymatic measurement which best characterizes the total biological status and activity is dehydrogenase. Our correlation indices of dehydrogenase with several other soil activities were between 0.84 and 0.99. (See J. Skujins, in Balph, 1972).

Proteolytic activity

This parameter is an index of the rate of hydrolysis of proteinaceous compounds, an important process in the nitrogen cycle of soils.

The results for August through November showed higher activity in November, except for station #5 soils which had higher activity in September.

Station #7, shadscale soil, had slightly higher activity than both winterfat and sagebrush soils for these four months. The lowest activity was found in winterfat soil throughout, except where the activity increased sharply in November. This was also the pattern shown for dehydrogenase activity over the same period.

For station #5 sampled under the canopy, only the surface 0-3 cm layer showed any increase of activity over the same soil not under the canopy.

Phosphatase activity

Measurements were made for some spring samples for reference values only. It has been shown by our previous studies on desert biome soils that phosphatase values may not be correlated with any other parameters measured presently.

Respiration values

CO₂ evolution in these soils followed the same pattern as the other biological activities in being highest in the surface 0-3 cm layer.

There was an increase in soil respiration from August to October for station #5 samples; October samples for stations #5 and #6 showed a decrease.

After the initial decrease in activity from the 0-3 cm layer to the next 5-20 cm layer there was no further decrease with succeeding depths. Instead, there was a small increase at the 40-50 cm depth and it generally decreased again at the 70-80 cm depth.

The canopy 0-3 cm layer showed only a slight increase over the same layer not under the canopy. No increase in canopy samples was found in lower depths over the non-canopy samples.

Other results indicate that a considerable respiratory activity (i.e., decomposition of organic matter) in desert soils takes place below the agriculturally accepted water content, below the negative water tension of 15 bars. These results indicate that significant biological activities take place in the so-called air-dry soils in the desert.

The preliminary data show also that the shoots are decomposed faster than the roots. This phenomenon was brought out also by experiments with ¹⁴C-labelled *Eurotia* plants (not reported herein).

Soil moisture

The amount of moisture held in the soil varied from station to station. This is mostly due to differences in textural characteristics of soils which vary on all three stations. Within each station, the greatest variability in soil moisture, throughout the year, occurred at the 30-40 cm depth and was minimal at the 70-80 cm depth and deeper, indicating that 30 to 40 cm was the average maximum penetration depth of surface precipitation.

Water potential measurements

It is now well accepted that, in relating soil moisture to activities occurring within the soils, the total water potential is a better measure than the beforehand commonly used moisture percent by weight.

In a water potential study in our area, Juan Casto asked the question: What is the actual permanent wilting percentage and the available moisture in the Curlew Valley soils from the areas of the different plant communities? He concluded that the wilting point is not -1500 Joules (-15 bars) per kg as it is generally accepted for most mesophyte species; for example, winterfat and shadscale grew well during most of the growing season with moisture below -1500 Joules per kg.

pH

The pH values of these soils are high and have a definite influence on biological activities and chemical properties of these soils; for example, on the volatilization of ammonia (see Part I, this report).

Averages of several activities are shown in Table 17.

Table 17. Some biological activities in Curlew Valley soils (1972 averages)

Sampling Site & Depth	Respiration ($\mu\text{m CO}_2/\text{g}/\text{min}$)	Proteolysis (% Hydrolysis)	Dehydrogenase (gm Formazan)
5-1 (0-3cm)	47	30	.98
5-2 (5-20cm)	14	9	.08
5-3 (40-50cm)	21	9	.04
5-4 (70-80cm)	19	6	.02
6-1 (0-3cm)	40	30	1.21
6-2 (5-20cm)	18	10	.10
6-3 (40-50cm)	19	11	.08
6-4 (70-80cm)	11	8	.03
7-1 (0-3cm)	24	32	1.95
7-2 (5-20cm)	15	10	.16
7-3 (40-50cm)	20	10	.06
7-4 (70-80cm)	9	5	trace
Canopy effect*			
5-1C (0-3 cm)	60	47	1.50
5-2C (5-20 cm)	21	9	.07
5-3C (40-50 cm)	27	7	.02
5-4C (70-80 cm)	19	3	.02

*These values are from October samples only.

CONCLUSIONS

It is apparent from our examination of the biological activities in several desert soils that the biological activities are concentrated in the top cm layer of these soils. It is in this layer that most of the organic matter turnover has been demonstrated to take place. The activities decrease drastically with depth. (Skujins, 1972).

It was shown by comparing soils sampled directly under the canopy of plants with samples taken from between the plants that the activity was higher in soils under the canopy (Table 17). It should be noted, however, that the nitrogen fixation under the canopy was negligible compared with that in the bare areas (Part I, this report).

Significant, although preliminary, results show that considerable metabolism and decomposition take place in "air-dry" soils with water tension below -15 bars.

Data compiled from the comparative studies between the Biome soils showed great variability in the biological activity between sampling dates, sites and plants species studied. The main factors which influence differences or similarities of biological activities in soils do not seem to be due to specific sampling dates, sites, or species as such; it seems more likely due to changing temperatures and moisture levels of the soils, and to other chemical, physical, and/or environmental factors.

The conclusions reported herein are based on empirical evaluations of observed data. Proper evaluation of the data requires rigorous statistical treatment and regression analysis (computerized). Also, at least one full year biological cycle is necessary for such an evaluation.

ACKNOWLEDGEMENTS

Most of the analyses reported herein were performed by Sally Cotter, Martha Clark and Hasu Patel.

Chemical analyses on nitrate, nitrogen and carbon were done by the USU Soils Laboratory.

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1972 PROGRESS REPORT

NITROGEN AND CARBON FLUX IN A SOIL-VEGETATION COMPLEX
IN THE DESERT BIOME

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Research Memorandum, RM 73-36

MAY 1973

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Report Volume 3

Page 2.3.4.2.

A B S T R A C T

The pathway of nitrogen and carbon compounds in ecosystems is important to understanding biological control mechanisms and interactions. As a first approximation of their role in the desert biome the areal nitrogen and carbon concentration, fixation, and loss are being analyzed with respect to precipitation and runoff at different sites in Curlew Valley, Utah. These data will be used to assess the nitrogen and carbon flux in cold desert shrub-dominated communities. The initial phases of the study were devoted to development of methods for measuring nitrogen and carbon fixation.

The first results indicated that relatively uniform nitrogen and carbon distribution occurs throughout Curlew Valley but it changes seasonally with temperature, light and moisture levels. Potential nitrogen fixation is on the order of ten times the actual fixation. Considerable variation in rainfall exists at the different sites.

INTRODUCTION

The work described in this report represents the first year of research on attempting to define the relationships between biological fixation of nitrogen and carbon and the loss of that nitrogen and carbon.

The mechanisms of loss would include excretion, volatilization, decomposition, and removal, via runoff waters, of dead and alive particulate materials and of soluble compounds.

Owing to methods development and equipment delivery delays affecting site setup, sampling did not commence until July 15, 1972, and the sites were not completely fixed until September 8, 1972, when sampling of all sites began. Development of methods for field measurement of potential nitrogen and carbon analyses is continuing. Cutoff time for samples for this project was arbitrarily defined for convenience as the end of October, 1972. All results described in this report except that for runoff and potential fixation are currently in the data bank.

OBJECTIVES

The study proposed to determine nitrogen and carbon fixation rates of a soil-vegetation complex in the desert biome and their disposition by:

1. Determining the field production rates of nitrogen and carbon by microflora.
2. Determining the potential nitrogen and carbon fixation under aerobic conditions for the same sites.
3. Determining the amounts of nitrogen and carbon removed by the runoff water.

These objectives were to be accomplished at seven specific sites within Curlew Valley by the following:

1. Weekly measurement of nitrogen and carbon on an area basis.
2. Biweekly measurement of acetylene reduction (N_2 fixation) and CO_2 fixation ($^{14}CO_2$ uptake) *in situ* on an area basis.
3. Weekly measurement of rainfall, runoff and nutrient concentration in the runoff from plots located in the selected sites.

METHODS

Site design selection

Seven specific sites were selected for study and were set up as shown in Figure 1. The sites were selected to represent different shrub-dominated areas (Tidestrom, 1925) and to be relatively close geographically (Figure 2). Generally sites were selected which had only slight slope and were representative of the total area. Studies conducted on Sites 1, 3 and 5 were coordinated with that of Lynn (1973).

Site 1 was set up on May 25, 1972, and is called the Locomotive Springs site. It is located approximately 35 m north and 35 m west of the intersection of the old Central Pacific Railroad bed and the Snowville-Loomotive Springs Road, and oriented in a north-south direction. The dominant shrub is greasewood (*Sarcobatus vermiculatus* Hook). Soil-crust appears to be generally free of lichenous growth. It was relatively easy to dig to a depth of 75-90 cm so soil depth was good. The slope at the site was very slight; the runoff collection vessels (polyethylene tanks and glass collection jars) were placed at the down-slope end of the plots.

Site 2 (Wildcat Hills site) was set up on May 25, 1972, approximately 2.7 km up the dirt road following the base of the Wildcat Hills north and west of the bench mark (XX89-1934, in Section 8, T-12N-R-10W of Kelton Park Quadrangle, USCS map). The site was approximately 35 m north (uphill) of the dirt road and oriented in a north-south direction. Layout was essentially identical to site 1 but the dominant shrub was shadscale (*Atriplex confertifolia* Torr. and Frem.). The soil-crust was heavily covered with lichens. A layer of hard soil and shale prevented digging below 45 cm.

Site 3 is called the sagebrush site and was set up on May 31, 1972, approximately 9.4 km north of the intersection of the Central Pacific Railroad bed and the Locomotive Springs Road. The specific location was about 90 m west of the Locomotive Springs Road and about 60 m south of the powerlines running east-west. The area is dominated by big sagebrush (*Artemisia tridentata* Nutt.) and the soil crust was heavily lichenous. Hard soil was encountered at 45-60 cm depths. Layout otherwise similar to Site 2.

Site 4 was the grassland site established on August 11, 1972, north of Snowville, Utah and located on the northern edge near the midpoint within the "Sharptailed Grouse Experimental Enclosure" in Southfield 13 of the USDA National Grasslands. No fence enclosure was needed but the site was otherwise similar to Site 1. Grasses (crested wheat and canadian wild rye) were dominant and no lichens were noted on the soil-crust. Shrubs were sparse but more varied than the previous three sites.

2.3.4.2.-4

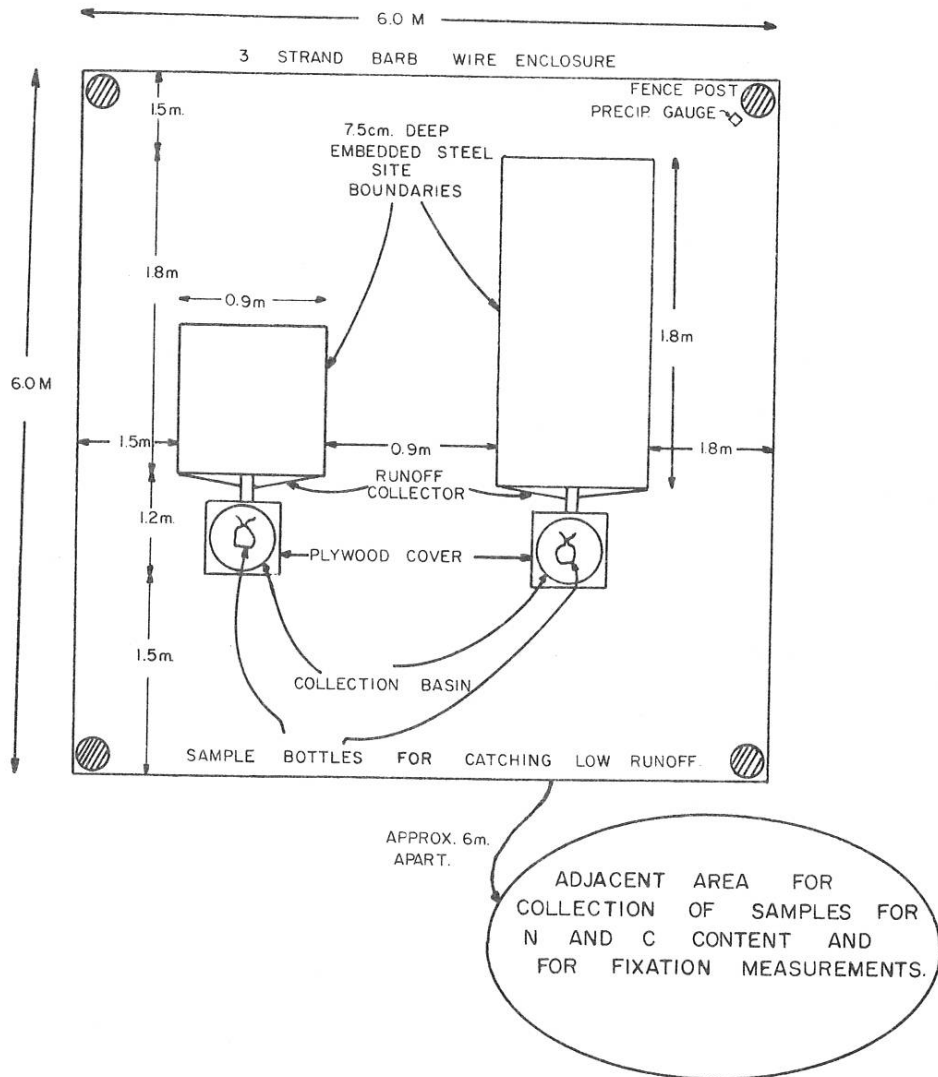


Figure 1. Overhead view of site layout for runoff collection and measurement of nitrogen and carbon flux (not to scale).

2.3.4.2.-6

Established on September 15, 1972, Site 5 was located about 6 m east of the Lynn (1972) killed site. This area is about 30 m north and east of the parking area north of the validation site. The shrub community is a mixture dominated by shade scale and sagebrush.

Site 6 was established on September 15, 1972, and was located just east of the center road and south of the validation site amid crested wheat grass.

Established on September 15, 1972, Site 7 was located just west of the center road and south of the validation site in the sagebrush (*Artemisia tridentata* Nutt.) dominated community.

Sampling

Soil samples methods for weekly measurement of nitrogen and carbon: A marked plot was set off about 6 m from the runoff plots and encompassing a similar soil-vegetation complex to those of the runoff plots. From these plots, five weekly samples were taken randomly with a 1.5 cm diameter (i.d.) cork borer to a depth of 1 cm. Care was taken to prevent resampling the same hole. These five samples were placed in sterile plastic bags (Whirlpaks) and later analyzed in the laboratory for total organic carbon (TOC) and total nitrogen (TN).

Fixation sampling points: Fixation measurements using reaction vessels designed for field operations were made in the same plot as that from which the soil samples were collected, from undisturbed surfaces by the cork bore sampling.

Runoff: When runoff occurred it was collected in glass bottles placed within a 30 gallon polyethylene lidded tank. When runoff overflowed the glass bottle, it was caught in the polyethylene tank where it could be collected. All material, including water, sediment and debris in the tank, bottle, and collection basin, was collected to determine the effects of microflora on components of runoff, rainfall and sheet erosion and sediment on uncultivated lands.

Routine field and chemical measurements (See Data Sets A3UFA01 and A3UFA02)

Measurements taken at the sites: The following list of parameters were measured at each site:

	Weekly
A3UFA01	Time of sampling
	Precipitation
	Soil-crust temperature (≤ 1 cm depth)

Soil-crust moisture (≤ 1 cm depth)
 Total nitrogen of soil-crust (≤ 1 cm depth)
 Total organic carbon of soil-crust (≤ 1 cm depth)

Runoff volume

Runoff characteristics

Suspended material

Total C

Total N

Total P

Total particulate N

A3UFA02 Soluble $\text{NO}_3\text{-N}$, $\text{NH}_3\text{-N}$

Soluble $\text{PO}_4\text{-P}$

Soluble Inorganic C

Total Soluble C

K^+

Na^+

Biweekly

Carbon fixation

A3UFA01 Nitrogen fixation

Quarterly

Diurnal carbon and nitrogen fixation

Analytical methods: A schematic flow chart of the analytical measurements is shown in Figure 3. Measurements taken in the field included precipitation measured with a Truchek fence post gauge overlaid with olive oil at ambient temperature above 5 C. For less than 5 C a known amount of polyethylene glycol (Prestone antifreeze) was added and overlaid with Rinder oil. Soil-crust temperature was measured using a standard thermometer (-20 to 120 C) with the bulb inserted to a depth of 1 cm. Soil-crust moisture was measured using the carbide-acetylene method (Parks Speedy Moisture apparatus). The total volume of runoff was collected and taken to the laboratory for measurement of volume. The suspended solids were removed by filtering through a series of graded filters culminating in a Millipore filter (HA, 0.45 μ). After drying the solid material at 103 C it was weighed to determine the suspended solids.

Laboratory analyses of NO_3^- , NH_3 , PO_3^{3-} , Na^+ , and K^+ in water were adapted from methods listed in the literature (Golterman, 1969; Strickland and Parsons, 1968; APHA, 1971) and specifically detailed in an unpublished report (Cowan and Porcella, 1972). For the soil crust samples and unfiltered runoff samples total organic carbon (TOC) was measured using the dichromate technique of Walkely and Black (1934). This

2.3.4.2.-8

method as used by the Soils Lab at USU normally underestimates the total value by about 10%. Because reproducible results were obtained without heating, this step was eliminated. This caused a further 10% underestimate of total organic carbon. Thus the results reported herein are an underestimate of the "true" total organic carbon content of soils and represent only about 80% of that total. In later reports this underestimate will be corrected using an actually measured factor.

Measurements of total nitrogen (TN) were made on samples from the surface cm of the soil crust and on raw surface runoff waters. Runoff samples were analyzed using the direct pipeting method. A Coleman Model 29 nitrogen analyzer was used for these measurements. The instrument employs an automation of the micro-Dumas nitrogen analysis. It essentially converts all nitrogen forms to nitrogen gas by a series of catalyzed oxidations and reductions. Materials and methods for the operation of this instrument are best described in the operation manual available from Coleman Instruments Company.

The TOC and TN measure non-living as well as living material and thus do not reflect biomass entirely. These data will be correlated where possible with estimates of chlorophyll made by Lynn (1973) for the same sites in order to obtain a better understanding of what TOC and TN actually measure.

Measurements of soluble total and inorganic carbon in the runoff water were accomplished using a Beckman Model 915 Total Organic Carbon Analyzer.

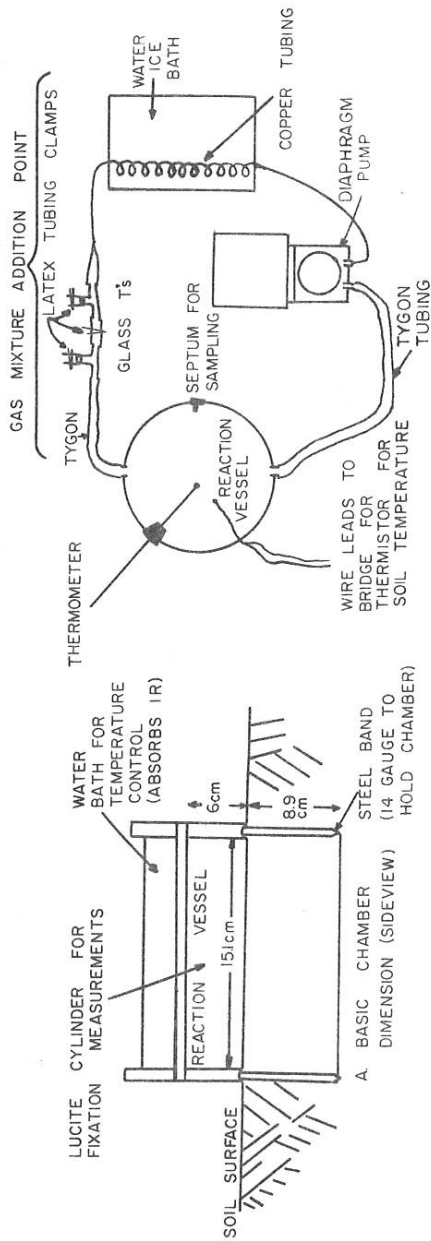
Apparatus for fixation measurements: The basic apparatus used in both carbon and nitrogen fixation experiments is shown in Figure 4. A 14 gauge steel circular band 15.3 cm in diameter and 8.9 cm high was placed in the soil to a depth of approximately 8 cm. Over the area of soil-crust circumscribed by this metal boundary was placed a 6.3 mm walled Lucite cylinder closed at one end. The cylinder was grooved at the end placed next to the soil so as to receive the wall of the steel boundary described above. This groove was filled with modeling clay which, when the cylinder was pressed onto the metal band, made a gas-tight seal between the Lucite cylinder and steel boundary. Clamps made of small latex tubing were used to maintain pressure at the joint to insure a good seal. The resultant chamber was about 7 cm high with a gas volume of approximately 1250 cc. This system allowed the measurement of activity of the crust without removing it from its natural placement and results could be easily related to the surface area exposed.

During the development of the apparatus and technique, extreme buildup in temperature was observed inside the above-described vessel when exposed to direct sunlight. This was even more apparent when ambient temperatures were high. An ice or water bath above the vessel in combination with circulating the chamber atmosphere through a heat sink,

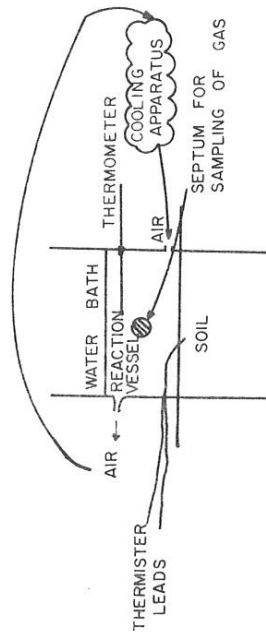
provided the best results in controlling inside air and soil temperatures to maintain approximate ambient conditions. A diaphragm-activated electric pump (Dyapump) capable of circulating approximately 9 liters of gas per minute, was employed to propel the atmosphere through the vessel and then through 658 cm of coiled 3.2 mm i.d. copper refrigeration tubing immersed in water or ice water. This system allowed the inside atmosphere temperature to be maintained within ± 3 C ambient temperatures for a period of time in excess of 2 hr for ambient temperatures up to 45 C. The shadowing of the soil caused by the bath above the chamber was not believed to be of great significance to the reactions since the blue-green algae, the organisms thought to be principally involved, are typically light saturated at intensities far below that of full sunlight (e.g., Brown and Richardson, 1968). Atmospheric temperature was monitored with a thermometer through the wall of the vessel. Soil temperature was monitored by a small thermistor placed against the soil. A septum in the side of the vessel was used for withdrawing samples. This septum is of the type used with Virtis lyophilizing equipment and can be withdrawn part way to allow for the passage of gases around the septum. The Lucite was checked spectrophotometrically (Beckman DB-GT) to determine the light transmissibility. Light transmission was between 85 and 91% T between wavelengths of 360 and 800 n.m.

Operation of fixation apparatus: During experimental operation, the natural atmosphere was replaced with an artificial argon-based atmosphere (Matheson Co.) composed of 22.103% O₂, 0.042% CO₂, and the balance being argon. This replacement was carried out by flushing the system for not less than one and one-half minutes with the argon atmosphere. This was done by attaching a tube from the gas bottle to one of the glass "T"'s shown in Figure 4 and pulling out the septum part way. The gas was then turned on at a rate easily detectable by placing the fingers in the area of the septum. This was continued with the pump running for 1 min. After 1 min the gas was shut off with a pinch clamp and the septum replaced tightly. The pump was allowed to continue circulation for 30 sec. After this, the flushing was continued for another 30 sec. In order to prevent short-circuiting of the gasses through the vessel, the inlet and vent of the system were placed at the bottom and top respectively on opposite sides of the vessel.

As a control for CO₂ fixation, a black vessel was constructed as described in Figure 4 but was spray-painted black, wrapped with black plastic tape and then sprayed with aluminum paint to retard heat adsorption. Thermistors were used to check both soil and atmospheric temperatures in this vessel in order to lessen the chances for light leaks.



B. LUCITE CYLINDER FOR THE FIXATION CHAMBER SHOWING METHOD FOR COOLING AIR, ADDING GAS AND SAMPLING.



C. SCHEMATIC OF CHAMBER DESIGN (SIDE VIEW)

Figure 4. Design of *in situ* Lucite fixation chambers.

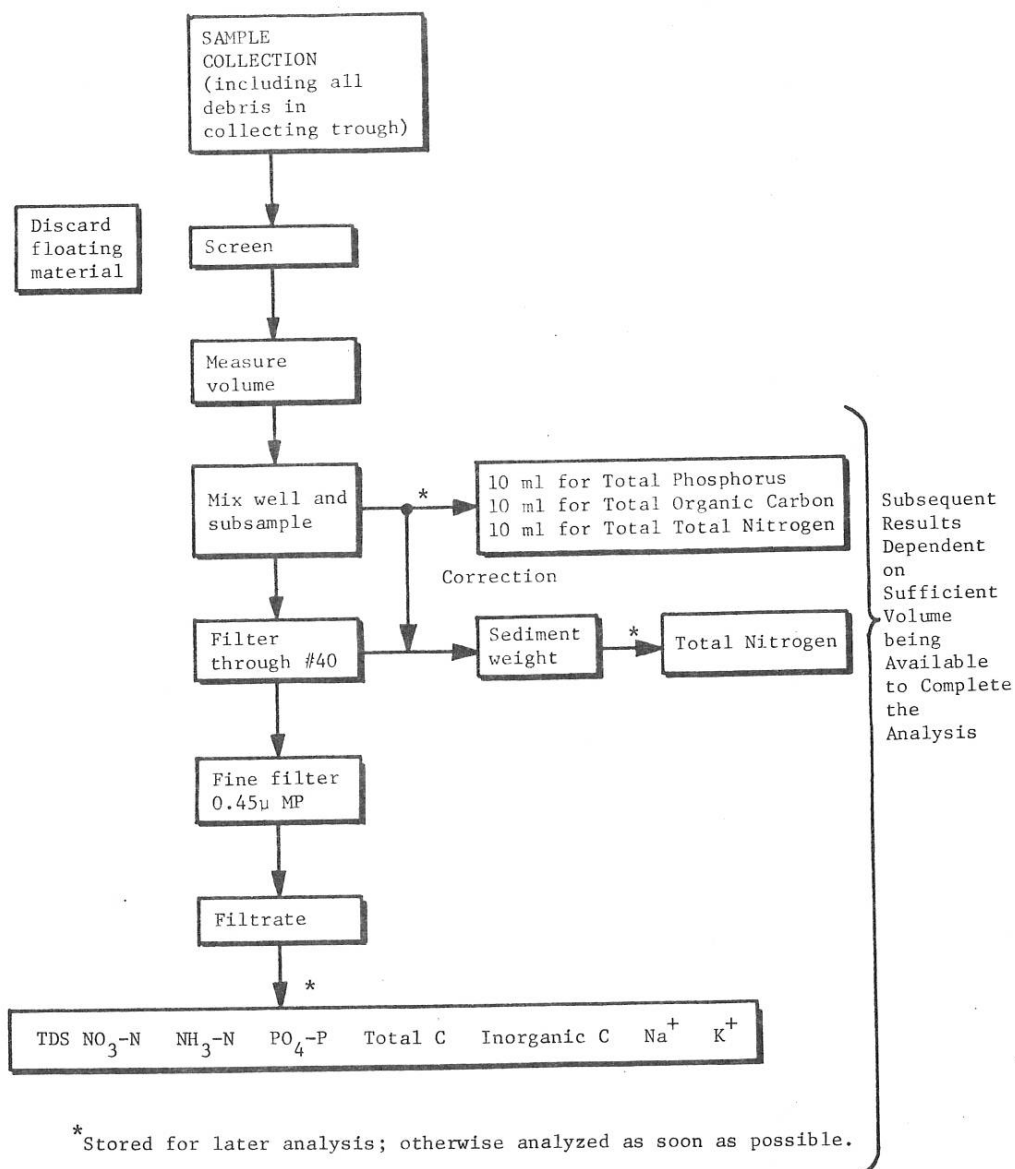


Figure 3. Schematic showing runoff analytical scheme.

2.3.4.2.-12

Because ambient temperatures in the field are cool and solar intensity is low during much of the year, vessels are being used in which the atmospheres are not circulated or cooled in any way except by exchange through the Lucite wall. This allows more freedom as to the number of vessels which can be built and conveniently operated, therefore increasing the amount of data collected. Also, it is not necessary to have a portable 115 volt power supply for running the pumps. Comparison with ambient soil and air temperatures indicates satisfactory operation of these closed chambers. In these systems the argon atmosphere is added first and then the acetylene or $^{14}\text{CO}_2$ added, using a large volume syringe.

Estimation of nitrogen fixation

Acetylene reduction has become a well accepted and widely used tool for the estimation of nitrogenase activity in almost all known nitrogen-fixing environments including soil crusts (Stewart et al., 1967). The relative simplicity of the acetylene reduction test for nitrogen fixation made it the chosen method for our study.

The π bonding systems and size of the dinitrogen ($\text{N} = \text{N}$) and the acetylene ($\text{HC} = \text{CH}$) molecules make acetylene a good competitor for the enzyme sites of the nitrogenase system. The nitrogen is removed from a test system and acetylene introduced to a partial pressure of approximately 0.2 atm. The nitrogenase system accepts the acetylene and reduces it to ethylene. The ethylene is left free in the system and its rate of appearance can be monitored using a gas chromatograph. It is thought by some investigators that approximately 3 moles of ethylene ($\text{H}_2\text{C} = \text{CH}_2$) are produced for each mole of N_2 that would be reduced to ammonia in the same amount of time. The reduction of N_2 to 2NH_3 requires the transfer of six electrons where the reduction of one acetylene to one ethylene requires the transfer of two electrons, hence the theory that there should exist a three to one ratio in the reduction of the two species C_2H_2 and N_2 respectively. The correlation between actual nitrogen fixation and acetylene reduction is not as firmly established as it ought to be and it likely may change with species and the system. However, for purposes of gross estimation, the factor of three will be utilized in these studies with the reservation that the relation may be changed.

After the reaction vessels (Lucite chambers shown in Figure 4) were flushed with the argon atmosphere described above, the system was connected to a flask containing approximately 270 cc of purified acetylene (Matheson Co.) at atmospheric pressure. This was flushed into the system by routing the circulating atmosphere through the "T"'s shown in Figure 4 and through tubing into and out of the flask for 30 sec. After this, the circulation of the atmosphere was returned to the closed system by closing the clamps. This procedure brought the partial pressure of acetylene in the system to approximately

0.15 atm. The time when the acetylene began flushing into the system was assigned time zero and gas samples were taken periodically up until 30 min had elapsed. Three samples were usually taken during this interval. For example, samples would be taken at 4, 15 and 31 min.

The samples were taken using 5 cc vacutainers for extracting gas samples from the reaction vessel and transporting the sample to the laboratory for gas chromatography. Three samples of this volume (5 cc) could be taken without lowering the pressure inside the vessel more than 0.2%. Also, enough sample was present in the vacutainer to supply a 0.5 cc sample for injection in the gas chromatograph without lowering the pressure inside the tube more than 10%. However, it was discovered that the 5 cc vacutainers were not highly evacuated as they come from the manufacturer, and will draw only about 5 cc into a total volume of about 6.2 cc. This represented a considerable dilution, and the inconsistency of the draw made the dilution unpredictable. It was found that if the vacutainers were highly evacuated (to less than 0.1 mm Hg) and then the stopper and end of the tube sealed by dipping it into melted beeswax, a much more efficient draw could be made more consistently. By processing 10 tubes as described above, storing them overnight (as was done with actual experiments), and then measuring the draw with boiled water, a dilution factor of 1.06 ($S_x = 0.03$) was arrived at from an average of the draws. This factor is used to multiply the amount of ethylene detected in the gas sample to more exactly determine the rate of acetylene reduction.

Flame-ionization gas chromatography for the detection of ethylene was carried out using a 3.2 mm o.d. 2.4 m Porapak R column in a Hewlett-Packard Model 1550 gas chromatograph having a dual column (A and B) mode. The B column was packed as identically as possible to A and was used for reference only. Helium carrier gas flow was set at about 30 cc per min; the column oven was run isothermally at 50 C; the detector temperature was 115 C; the injector temperature was 90 C. The electrometer range was 1 with the mode dual.

A standard curve for ethylene detection was prepared using chemically pure ethylene (Matheson Co.). By using bottles of approximately 145 cc volume fitted with serum bottle stoppers, serial dilutions of ethylene gas were made. The dilutions were prepared in triplicate, and duplicate injections were made from each dilution in order to obtain some estimate of variability in the technique. Injections of 1 cc and 0.1 cc of gas were made to the column to achieve the desired amount of ethylene in the column. Amounts of ethylene injected to the column were 1.6×10^{-6} moles, 1.6×10^{-7} moles, 1.1×10^{-8} moles, and 1.1×10^{-9} moles. The lowest level gave a peak height of 2-2.5 mm. Baseline instability at attenuations needed for this sensitivity often makes a peak of this height unreliable. Because of this a lower level of reliable detection on this instrument

2.3.4.2.-14

would be five times this amount or 6×10^{-9} moles of ethylene. Peak height was taken directly as a measure of the amount of ethylene in the injection because the peak obtained was symmetrical and good reproducibility has been obtained using peak height measurements. For peak heights greater than 40 mm, the coefficients of variation ($CV = (S_x/\bar{X}) 100$) were <2%. The CV increases <12% as peak height decreases <10 mm. Typically the peak heights measured on field samples were usually greater than 50 mm.

The samples collected in the vacutainers in the field were returned to the laboratory where a 0.5 cc aliquot of the gas was withdrawn and injected to the gas chromatograph column with a gas-tight syringe. The resultant ethylene peak allowed the calculation of the concentration of ethylene in the reaction vessel and cooling system. The volume of the reaction system was known and thus the rate of ethylene production was related to the surface area of soil-crust exposed. The rate of ethylene production was then related to nitrogen fixing potential *in situ*.

Estimation of CO_2 fixation

Fixation of CO_2 was estimated by measuring the rate of $^{14}CO_2$ disappearance from the fixation chamber with time. This tracer technique is based on photosynthetic reactions as well as on non-photosynthetic uptake (reviewed in Stanier et al., 1970). The argon atmosphere was utilized so that the initial stable CO_2 would be known (0.042% CO_2). The CO_2 was added by the same techniques described for nitrogen fixation measurements. A dark reaction vessel (see Figure 4 and Discussion) was utilized to measure non-photosynthetic uptake of $^{14}CO_2$.

Preparation of $^{14}CO_2$: The $NaH^{14}CO_3$ was obtained from Amersham-Searle, diluted with an equimolar solution of $NaHCO_3$, and placed in individual ampoules. Each ampoule contained 1 ml of 0.003M $NaHCO_3$ having an activity of $2 \mu C$ $^{14}CO_2$ removal.

One opened ampoule was placed in an upright position and 1 ml of concentrated H_2SO_4 was added to a 50 ml erlenmeyer flask. The flask was then sealed with a two-hole stopper having intake and outflow tubes with either septums or clamped surgical latex tubing. The intake tube extends to the bottom of the flask and the outflow tube to just below the stopper base to insure good $^{14}CO_2$ removal.

Injection of $^{14}CO_2$ was accomplished using the flow system described above or by placing a 60 ml syringe into the outflow septum of the flask and a needle into the intake septum. Then 60 ml of gas was withdrawn from the flask (the syringe needle was inserted all the way into the reaction vessel septum) and a needle placed in the same septum just penetrating the septum. The contents of the syringe were then injected into the reaction vessel. The needle was removed immediately; then the syringe.

Sampling and counting of $^{14}\text{CO}_2$: The first sample was taken one minute after injection of $^{14}\text{CO}_2$ into the reaction vessel. Additional samples were taken at six min, 11 min, 16 min, and 31 min after injection of $^{14}\text{CO}_2$. For sampling, 1.5 ml of ethanolamine plus 2-methoxyethanol (1:2 v/v) solution was drawn into a 10 ml syringe, the syringe inserted into the reaction vessel, and 2 ml of gas was withdrawn. After removal of the syringe from the reaction vessel, the syringe was shaken to trap all CO_2 and the solution placed in a scintillation vial containing 15 ml scintillation medium. The vial was returned and counted on a liquid scintillation counter.

Liquid scintillation counting of the trapped $^{14}\text{CO}_2$ was based on techniques described by Jeffay and Alvarez (1961). A solution of ethanolamine in 2-methoxyethanol (1:2 v/v) was used to trap the carbon dioxide. The scintillation medium used was a toluene, 2-methoxyethanol solution 2:1 v/v containing 5.5 g/l of 2,5-diphenyloxazole (DPO). Counting was done at the Bacteriology Department with a Nuclear-Chicago Isocap 300 liquid scintillation spectrometer operated at room temperature. An external standard was used to correct for temperature effects on efficiency.

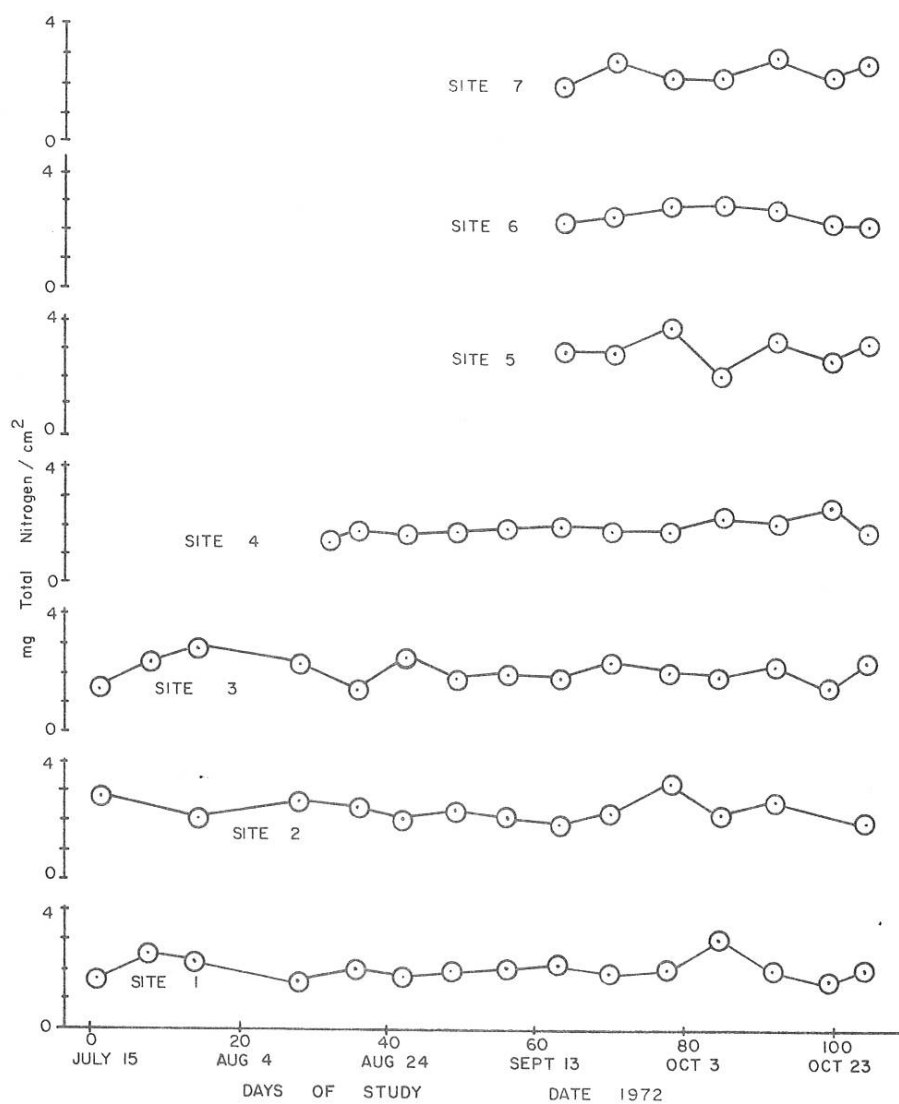


Figure 5. Changes in total nitrogen at different sites in Curlew Valley, Utah (DSCODE A3UFA01).

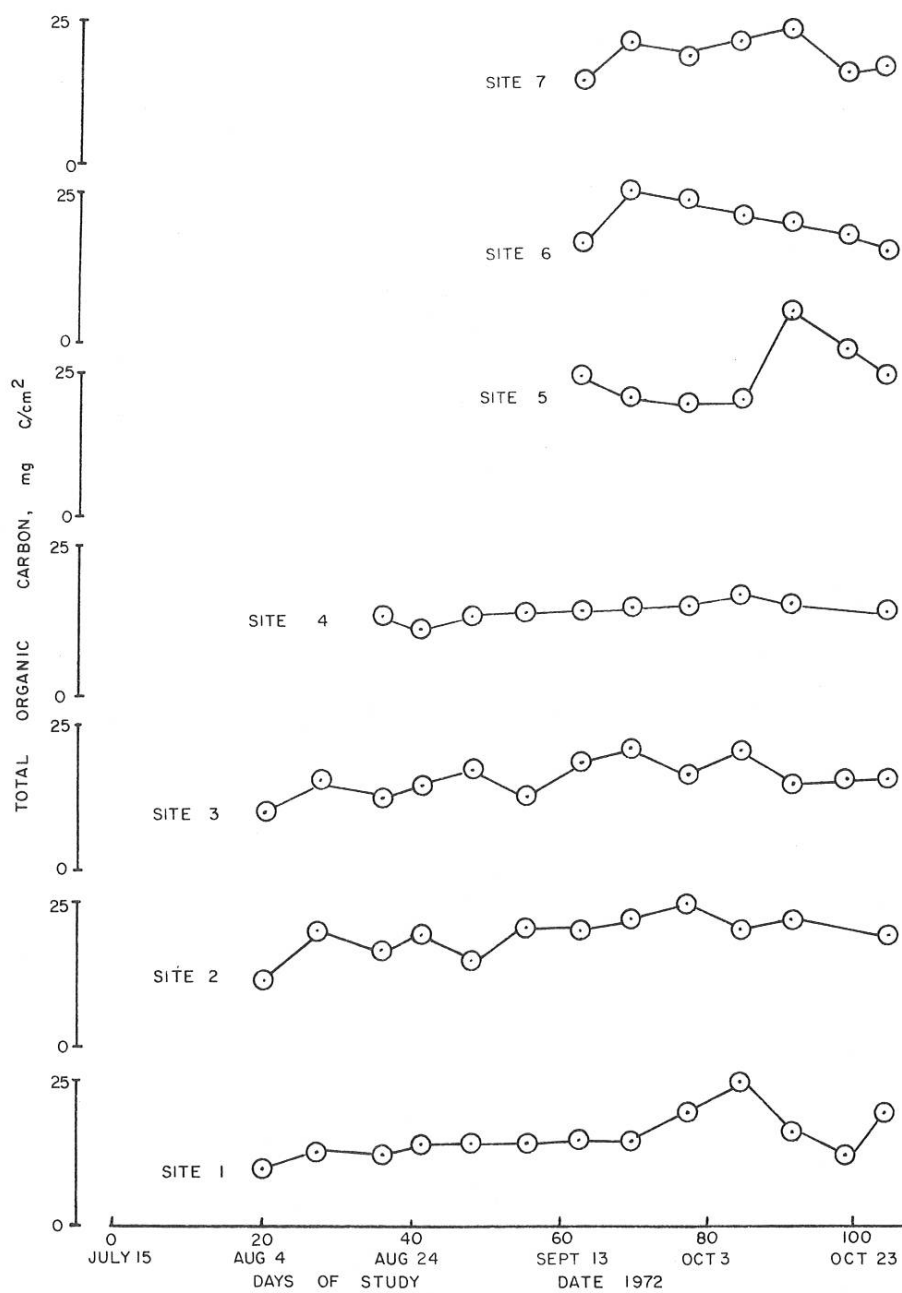


Figure 6. Change in total organic carbon at different sites in Curlew Valley, Utah (DSCODE A3UFA01).

RESULTS

Nitrogen and carbon standing crop

In Curlew Valley both nitrogen and carbon fixation in the algal-soil crust are affected considerably by at least the following major variables: light, crust moisture, and temperature (Lynn, 1973; Skujins, 1972). This is reflected in the patterns of increase in total nitrogen (TN) and total organic carbon (TOC) areal concentrations shown in Figures 5 and 6. For all sites there is a steady but gradual rise in TN and TOC with time until soil temperatures dropped consistently below 2 C between the October 14 and 21, 1972, sampling dates. The gradual increase was probably due to the higher soil moisture, resulting from the autumnal rainfall. Shortening of day length may have resulted in sufficient light decrease to prevent larger increases in the TN and TOC standing crop. Larger increases are expected during the spring when light, temperature and moisture all are increasing. When the data are more complete, they will be analyzed further with respect to nitrogen and carbon flux.

Site variation

Although the results are not yet confirmed, it is likely that significant differences will be shown to exist for the interspace algal-soil crust TN and TOC (Table 1). A portion of these differences will be found to be due to dominant shrub and soil differences; e.g., the northerlymost area (site 4) is atypical (the most highly vegetated site) compared to the rest of the sites and has the lowest TN and TOC.

The typical, highly-variable rainfall (Table 1) and consequently runoff will also have considerable influence, not only on the rates of fixation but upon the rate at which the products of that fixation are removed in the runoff.

The highest standing crops of TN and TOC were found at Site 5 near the validation site. Otherwise Site 5 was not remarkable in terms of rainfall.

Ratios of mean TOC/TN for the same time interval were relatively constant, varying from 7.1 to 8.8 (mean 7.9). Because of the TOC under-estimate (see Methods section) this ratio is actually lower than typical. The TOC will be corrected in later reports upon calculation of the appropriate factor. An autumnal mean TN and TOC study crop can be estimated for Curlew Valley by averaging the mean values from each site in Table 1 for the time period September 15 to the end of October, 1972: $TN = 2.38 \text{ mg/N/cm}^2$ and $TOC = 19.0 \text{ mg/C/cm}^2$. Using these estimates would give a coefficient of variation of less than 90%.

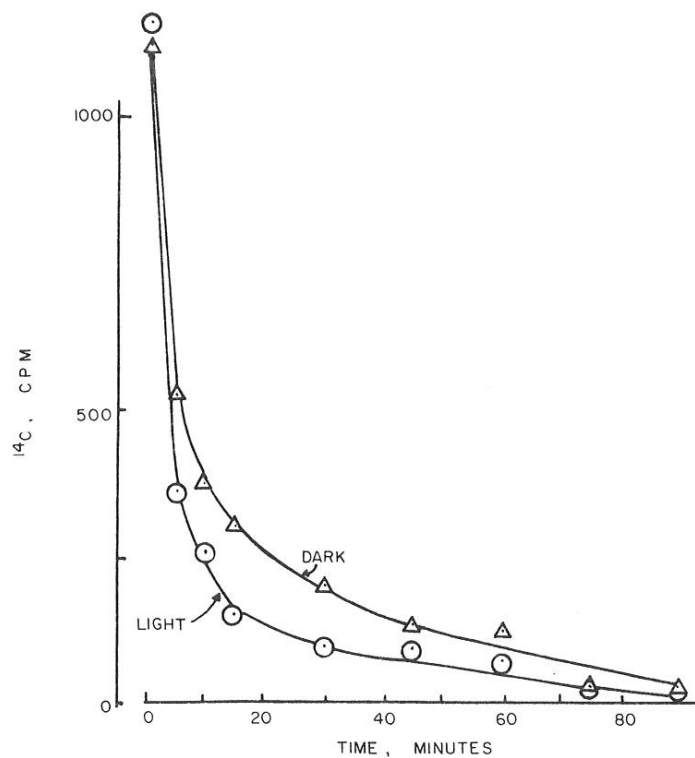


Figure 7. Light/dark effects on uptake of $^{14}\text{CO}_2$ by *in situ* algae-soil crust (Site 5, October 27, 1972).

Table 1. Variation of total nitrogen, total organic carbon, and rainfall for different sites in Curlew Valley, Utah DSCODE—A3UFA01

Site** Number	Dominant Shrub-Type	$\bar{X} \pm 1 Sx^*$		Total Rainfall [†] cm
		Total N ₂ mg N/cm ²	Total Organic C mg C/cm ²	
1 A	Greasewood	2.06 ± 0.37 (15)	14.9 ± 3.9 (13)	9.23 (13)
B		2.17 ± 0.43 (7)	16.9 ± 4.2 (7)	5.68 (7)
2 A	Shadscale	2.38 ± 0.38 (13)	19.2 ± 3.4 (12)	13.01 (13)
B		2.41 ± 0.50 (6)	21.1 ± 2.0 (6)	6.94 (7)
3 A	Sagebrush	2.07 ± 0.38 (15)	15.9 ± 3.1 (13)	8.15 (13)
B		2.08 ± 0.28 (7)	17.6 ± 2.6 (7)	6.32 (7)
4 A	Grasses Shadscale- Sagebrush	1.91 ± 0.33 (12)	12.3 ± 4.5 (10)	10.42 (11)
B		2.07 ± 0.32 (7)	14.7 ± 1.4 (6)	8.92 (7)
5 B		2.96 ± 0.53 (7)	24.2 ± 5.7 (7)	8.30 (7)
6 B	Crested Wheat	2.58 ± 0.31 (7)	19.8 ± 3.7 (7)	8.21 (7)
7 B	Sagebrush	2.42 ± 0.39 (7)	18.5 ± 3.2 (7)	7.82 (7)

*Number in parentheses represents number of samples averaged.

**The B values all represent means and totals beginning on the September 15, 1972 sampling date. A values represent means and totals beginning on the starting date for that site.

†Number in parentheses represents the number of weeks over which rainfall was summed.

Runoff volume and sediment also varies considerably with site location (Table 2). However, the data are too sparse at present to warrant further examination. Because of freezing conditions during the winter months, these studies will provide very little data until spring. At that time intensity recorders will be operational for rainfall and runoff.

Estimates of potential nitrogen and carbon fixation

Results of these measurements are very preliminary because considerable laboratory work is needed to explain the field results. A crude estimate of gross potential nitrogen fixation based on *in situ* autumnal acetylene reduction measurements indicated an annual potential fixation of about 10000 kg/ha/yr. This compares with estimates of actual net fixation of 820 kg/ha/yr (Fletcher, 1972). This would indicate that only about 10% of the gross nitrogen fixation remains as net.

Table 2. Runoff volumes and suspended solids weights for different sites in Curlew Valley, Utah* DSCODE—A3UFA02

Site No.	Weeks Observed	Total Runoff** Volume, ml		Suspended Solids Carried in Runoff, g	
		Large Plot	Small Plot	Large Plot	Small Plot
1	16	2260 (5)	1235 (3)	43.8	21.0
2	16	5859 (4)	2203 (3)	65.6	4.1
3	16	936 (7)	1005 (5)	0.6	0.6
4	12	1492 (3)	1004 (3)	4.8	7.4
5	7	1124 (1)	1084 (1)	2.0	1.9
6	7	7101 (3)	5369 (3)	---†	89.4
7	7	2217 (2)	1415 (2)	3.7	----†

*The area of the large plot is 1.67m^2 and the small plot is 0.836m^2 .

**Runoff occurrences observed are noted by the number in parentheses.

†Data not available at this time.

The gross potential carbon fixation has not been estimated because of difficulties in interpretation of results (see Figure 7). The light-dark relationships indicate rapid removal of CO_2 and it is not clear whether the rate of uptake becomes limited by available CO_2 . The rapid uptake is probably caused by equilibration of the $^{14}\text{CO}_2$ with the alkaline soils of Curlew Valley; this and other possible effects on carbon fixation will be determined in the laboratory.

DISCUSSION

The results presented herein are still too incomplete to satisfy the objectives; however, they indicate several areas of laboratory research which are required to make adequate interpretations of the results, particularly for the fixation measurements. At this point, the results seem to provide reasonable estimates of nitrogen and carbon areal concentration changes and of their rates of fixation. Removal rates in runoff will be used to estimate loss rates except for those materials which are volatilized. These latter losses will be estimated by difference.

EXPECTATIONS

Briefly, the analysis of samples for nitrogen and carbon will continue concomitantly with estimations of potential fixation rates of nitrogen and carbon for the seven sites in Curlew Valley, Utah. Laboratory studies (Lynn, 1973; Skujins, 1973) will be used to determine the appropriate estimation of the fixation rates. These results will then be utilized to estimate the nitrogen and carbon flux as affected by fixation and runoff. Then actual areal concentrations of nitrogen and carbon flux will be compared to estimates derived from fixation and runoff.

ACKNOWLEDGEMENTS

We are thankful for Prof. Ray Lynn's (USU) help in developing biomass measurement techniques and in site selection and to Prof. John Skujins (USU) for his time in helping us to set up the acetylene reduction measurement. We have been able to coordinate our studies with Ray Lynn, and Prof. Eugene Staffeldt's encouragement in having process meetings to eliminate duplication and to coordinate studies has helped us significantly.

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1972 PROGRESS REPORT

GASEOUS LOSSES OF NITROGEN FROM THE SOIL OF SEMI-ARID REGIONS

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and

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University of Arizona

Research Memorandum, RM 73-37

MAY 1973

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Report Volume 3

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A B S T R A C T

Soil profile samples were selected for laboratory studies of gaseous nitrogen (N) losses from two soil types at each Sonoran Desert Validation Site near Tucson. Oxygen consumption, gaseous evolution during anerobic incubation employing $^{15}\text{NO}_3$, changes in the N fractions, and most probable number (MPN) of denitrifying organisms were examined to determine N loss potential. The potential for gaseous loss of N was observed in all soils at all depths and resulted in $^{15}\text{N}_2$ and $^{15}\text{N}_2\text{O}$ evolution. The calculated loss in 18 days of added $^{15}\text{NO}_3$ ranged from approximately one-tenth to more than two-thirds of the total amendment. An organic carbon energy source was included in portions of these studies. Glucose additions increased N in the gaseous phase and increased the calculated loss based on ^{15}N remaining in the soil after incubation. Oxygen consumption increased, indicating biological and/or chemical activity, when the soils were moistened. Although oxygen was consumed in soils from all profile depths within 24 hr, the rate of consumption was higher in the surface soils of all profiles except the one having the buried A horizon. The number of denitrifying organisms under saturated moisture increased with soil depth, incubation time, and additions of $\text{NO}_3\text{-N}$ and organic carbon.

INTRODUCTION

This study was conducted to determine the potential for gaseous losses of nitrogen (N) from native desert soils and to quantify these losses in relation to the various parameters of the system. The previous work was concerned with the potential for gaseous loss and the identity of the gaseous products evolved, as well as techniques for the study. Some of this work was continued during 1972. The biological and non-biological contributions to gaseous N losses were studied and satisfactory techniques have been developed to differentiate between these two processes. Initial studies on rates of gaseous N loss as a function of temperature, moisture, nitrate concentrations, and organic carbon have been initiated and will be continued.

OBJECTIVES

The objectives for 1972 were:

1. To complete the study of denitrification potential on soil samples from various profile depths of two soils from each Sonoran Validation Site -- Santa Rita and Silverbell.
2. To determine the relative contributions of non-biological and biological gaseous losses.
3. To initiate rate studies of the gaseous loss process in relation to moisture, temperature, nitrate concentration and organic carbon source. This phase of the study will be continued and completed in 1973.

METHODS

Soil profile samples (DSCODE A3UTH-) were taken from two locations on the Santa Rita site (Sonoita sandy loam - SR-1, Anthony sandy loam - SR-2), and two from the Silverbell site (Rillito loam - SB-1, Rillito loam, eroded - SB-2). Sampling depths were 0-5, 15-20, 30-35, 60-65, and 90-95 cm, with exception of the 90-95 cm depth in SB-2 because of bedrock. These soils were air-dried, crushed, passed through a 2 mm sieve, and stored in plastic containers with sealed air-tight lids.

Ten-g air-dry soil samples from desert profiles were placed individually into 125 ml Warburg respirometer flasks and moistened with 2 ml of H₂O. One ml of 20% KOH

was placed in the center well and oxygen and gas exchange were measured at 37 C using standard Warburg respirometer techniques (Umbreit, Burris and Stauffer, 1964).

Fifty-g samples of air dry soil were placed in calibrated 125 ml Erlenmeyer flasks containing 2 ml of saturated KOH in wells. The samples were moistened with 10 ml solutions containing 4.9 g of $\text{NO}_3\text{-N}$ in water or in 0.25 M glucose solution. The $\text{NO}_3\text{-N}$ added was enriched with 33 atom percent ^{15}N . The flasks were closed with rubber septum caps, flushed for 10 min with argon gas, then incubated for 18 days at 36 C. Gas samples were taken from the air in each flask with a gas tight syringe at varying time intervals and analyzed by mass spectrometry. Calculations were made for gaseous composition, ^{15}N in the N_2 and N_2O components, and N_2 to N_2O ratios. Samples of the initial soil before treatment and after incubation were analyzed for $\text{NH}_4^+\text{-N}$, $\text{NO}_2^- + \text{NO}_3^- \text{-N}$, and organic N fraction by micro-Kjeldahl procedure (Bremner, 1965). Atom percent ^{15}N in each fraction was determined by mass spectrometry and percent loss of added $\text{NO}_3\text{-N}$ was calculated.

Detection of the presence of denitrifying organisms in soil profiles was accomplished using standard techniques (Alexander, 1965a). One hundred ml of sterile water was added to 10-g soil samples in 150 ml bottles which were shaken horizontally in a mechanical shaker for 10 min. Samples were removed from the shaker and were shaken again by hand just prior to removing a 10 ml aliquot with a sterile pipette from the center of the suspension. The aliquot was added to 90 ml of sterile water. One ml aliquots from the above dilution were added to each of five sterile tubes containing the sterile liquid denitrifican medium. The tubes were plugged and incubated for 5 days at 37 C. Presence of denitrifiers was determined in this specific medium by a pH indicator color change from green to blue plus the presence of gas (Alexander, 1965a). It was difficult to identify denitrifiers by this procedure and a more sensitive procedure was adopted. A nitrate nutrient agar was inoculated and sulfanilic acid and α -naphthylamine was used to detect the presence of nitrite (Difco, 1953). Denitrifiers were detected by a pink color, specific for nitrite, and presence of gas bubbles in the agar.

Most probable numbers of denitrifying organisms were measured at 37 C using procedures outlined by Alexander (1965b) in a specific liquid denitrifican broth. The liquid broth contained succinic acid, K_2HPO_4 , $\text{MgSO}_3 \cdot 7\text{H}_2\text{O}$, KNO_3 , CaCO_3 , yeast extract and tap water, respectively, in the following g/l: 2.0, 1.0, 0.5, 10.0, 2.0, 1.0, with tap water used to make to final volume.

Soils were sterilized using standard steam sterilization procedures (Alexander, 1965a) and a methyl bromide gas treatment developed in this laboratory. Ten-g soil samples were spread thinly over a 9 cm petri dish and steam sterilized in an autoclave

2.3.4.3.-4

for 30 min at 121 C and 15 psi. For methyl bromide sterilization, 10-g samples of soil were placed in tubular glass and separated by cotton. The gas was diffused through the soil slowly for 24 hr using an alcohol absorbent trap to catch the CH_3Br gas passing through the column. Following the methyl bromide gassing the soils were scrubbed for 8 hr with compressed air that had been passed through dilute sulfuric acid and deionized water baths. This scrubbing procedure was adopted to remove CH_3Br adsorbed to clay surface areas.

After sterilization by steam or by methyl bromide, the soils were placed aseptically in sterile glass petri dishes and allowed to de-gas for 24 hr. Then soils were placed into acetone-heat-treated Warburg flasks for oxygen consumption studies. Other soil samples were plated on denitrifican agar to check sterility.

RESULTS

Wetting dry desert soils increased the oxygen consumption, which showed in the initiation of biological and/or chemical activity (Table 1, DSCODE A3UTH04). No consistent pattern was evident for differences between soils or in profile depths. However, oxygen consumption tended to increase with increasing organic matter in the profile. For example, the Anthony sandy loam (SR-2) has a buried A horizon at approximately 60 cm and is higher in organic matter (0.39%) and consumed more oxygen ($0.15 \mu\text{l/g/hr}$) when moistened than the overlying sandy material which was lower in organic matter (0.17%) and consumed less oxygen ($0.03 \mu\text{l/g/hr}$).

Table 1. Organic matter and oxygen consumption in Sonoran Desert profile soil samples after wetting DSCODE—A3UTH04

Soil	SR-1		SR-2		SB-1		SB-2	
	$\mu\text{l O}_2/\text{g/hr}$	%O.M.	$\mu\text{l O}_2/\text{g/hr}$	%O.M.	$\mu\text{l O}_2/\text{g/hr}$	%O.M.	$\mu\text{l O}_2/\text{g/hr}$	%O.M.
Depth, cm								
0-5	0.16	0.46	0.09	0.27	0.14	0.32	0.17	0.54
15-20	0.17	0.37	0.04	0.16	0.09	0.28	0.13	0.53
30-35	0.11	0.26	0.03	0.17	0.10	0.34	0.12	0.39
60-65	0.05	0.23	0.15	0.39	0.12	0.29	0.18	0.35
90-95	0.11	0.18	0.15	0.35	0.05	0.24	- bedrock -	

Percentages of N_2 , O_2 , N_2O and the N_2/N_2O ratio in the gas phase above soils incubated anaerobically are shown in Table 2. In soils amended with nitrate, the percentage of N_2 and O_2 increased with time in practically all depths of the three soil profiles. There were only slight changes in the percentage of N_2O , regardless of time, depth or soil profile. The N_2/N_2O ratios ranged from 138 to 6773 in the soils that were amended with nitrogen. In soils amended with nitrate plus glucose, the percentages of N_2 in the atmosphere above incubating soils generally were higher than observed in soils amended with only nitrate, and tended to increase with time. Percent oxygen tended to be lower at the 355 hr time of sampling than was observed at previous sampling times. The N_2/N_2O ratios were much smaller than in the soil amended with only nitrate, indicating a larger percentage of the gas was in the form of N_2O . The presence of the organic energy source apparently stimulated loss of nitrogen in the form of N_2O and increased the amount of N_2 gas in the atmosphere above the incubating soils.

Table 2. Composition of gas above Sonoran Desert soil profile samples incubated under argon atmosphere and amended with nitrate and nitrate plus glucose
DSCODE—A3UTH01

Depth (cm)	Time (hr)	N_2	O_2 %	N_2O	N_2/N_2O
Anthony sandy loam (SR-2) - Nitrate					
0- 5	18	7.37	1.131	0.012	640
	91	14.86	2.460	0.039	383
	187	14.38	2.381	0.024	609
	355	14.45	2.473	0.015	971
15-20	18	0.94	0.198	0.001	1238
	91	5.49	1.066	0.006	959
	187	8.06	1.588	0.004	1873
	355	15.87	3.014	0.005	3051
30-35	18	2.90	0.481	0.003	899
	91	3.07	0.609	0.017	180
	187	5.25	1.136	0.013	400
	355	7.01	1.739	0.010	680
60-65	18	8.03	1.155	0.015	535
	91	13.42	1.995	0.038	355
	187	9.92	1.187	0.005	2031
	355	12.99	1.250	0.012	1086
90-95	18	11.05	1.697	0.024	456
	91	15.86	2.460	0.115	138
	187	16.60	2.481	0.037	500
	355	12.02	1.387	0.016	758

Continued

2.3.4.3.-6

Table 2. Continued

Depth (cm)	Time (hr)	N ₂	O ₂ %	N ₂ O	N ₂ /N ₂ O
Anthony sandy loam (SR-2) - nitrate + glucose					
0- 5	20	2.71	0.288	0.051	53
	91	21.05	2.193	0.277	76
	188	3.38	0.314	0.039	86
	355	29.48	0.372	0.564	52
15-20	20	1.06	0.055	0.031	34
	91	13.77	1.886	0.098	140
	188	16.20	0.406	0.077	211
	355	26.30	0.419	0.126	210
30-35	20	1.49	0.170	0.071	21
	91	13.49	1.433	0.028	478
	188	16.69	1.570	1.848	9
	355	22.04	0.588	0.048	457
60-65	20	10.10	1.234	0.059	171
	91	25.24	2.508	0.041	612
	188	38.31	3.048	2.970	13
	355	39.61	0.611	8.733	5
90-95	20	10.64	0.919	0.021	508
	91	32.58	3.141	0.094	348
	188	41.92	3.089	1.895	22
	355	47.54	1.581	8.520	6
Rillito loam (SB-1) - nitrate					
0- 5	18	10.47	1.574	0.034	312
	91	20.60	2.989	0.067	309
	187	25.19	3.232	0.013	1894
	355	25.05	3.062	0.006	4464
15-20	18	2.79	0.405	0.004	676
	91	15.75	2.584	0.055	286
	187	17.80	2.838	0.021	842
	355	14.10	2.012	0.005	2801
30-35	18	2.51	0.304	0.006	388
	91	13.40	2.011	0.036	375
	187	24.40	3.679	0.026	932
	355	24.42	3.430	0.010	2489
60-65	18	9.66	1.405	0.016	596
	91	25.17	3.756	0.024	1030
	187	35.24	5.068	0.013	2743
	355	44.16	6.326	0.007	6773
90-95	18	1.11	0.116	0.003	396
	91	10.18	1.580	0.042	241
	187	6.96	1.026	0.004	1691
	355	18.75	2.911	0.006	3023

Continued

Table 2. Continued

Depth (cm)	Time (hr)	N ₂	O ₂ %	N ₂ O	N ₂ /N ₂ O
Rillito loam (SB-1) - nitrate + glucose					
0- 5	20	7.12	0.890	0.098	72
	91	17.11	6.640	0.079	217
	188	32.65	3.370	0.458	67
	355	31.04	1.099	4.813	6
15-20	20	7.10	0.702	0.123	58
	91	17.97	1.067	0.013	1370
	188	32.55	2.273	0.149	219
	355	42.21	0.808	5.276	8
30-35	20	4.29	0.289	0.210	20
	91	27.40	2.858	0.035	794
	188	31.76	1.827	0.027	1194
	355	22.02	0.229	0.012	1775
60-65	20	7.84	0.952	0.283	28
	91	31.59	3.658	0.085	371
	188	21.46	0.063	0.454	47
	355	36.50	0.801	4.587	8
90-95	20	36.70	0.150	0.166	22
	91	26.58	2.114	0.031	860
	188	31.15	0.091	0.003	10383
	355	51.50	0.641	0.536	96
Rillito loam, eroded(SB-2) - nitrate					
0- 5	18	8.51	1.098	0.036	234
	91	20.58	2.586	0.044	465
	187	26.05	2.354	0.015	1728
	355	38.40	3.981	0.017	2305
15-20	18	1.32	0.119	0.006	209
	91	17.93	2.498	0.084	213
	187	20.12	2.041	0.010	1971
	355	29.50	2.414	0.008	3508
30-35	18	1.40	0.136	0.008	173
	91	7.30	0.983	0.018	404
	187	12.08	1.531	0.009	1324
	355	13.07	1.204	0.005	2558
60-65	18	0.82	0.051	0.004	188
	91	13.62	2.047	0.025	605
	187	16.82	2.378	0.013	1281
	355	12.03	1.229	0.003	3965

Continued

Table 2. Continued

Depth (cm)	Time (hr)	N ₂	O ₂ %	N ₂ O	N ₂ /N ₂ O
Rillito loam, eroded (SB-2) - nitrate + glucose					
0- 5	20	7.08	0.668	0.147	48
	91	26.76	1.915	0.023	1154
	188	27.35	0.154	0.028	980
	355	43.88	0.555	3.109	14
15-20	20	6.82	0.507	0.018	377
	91	13.70	0.122	0.016	869
	188	30.20	0.328	0.085	356
	355	46.99	1.265	4.039	12
30-35	20	11.21	0.460	0.012	969
	91	25.56	0.342	0.007	3695
	188	34.98	0.243	0.036	976
	355				
60-65	20	2.61	0.032	0.007	351
	91	8.98	0.017	0.044	204
	188	22.47	0.124	0.771	29
	355	51.52	0.262	6.118	8

Data in Table 3 illustrate the amounts of nitrogen in different forms in initial profile samples and after 18 days of incubation following the addition of $^{15}\text{NO}_3\text{-N}$ either with or without glucose. Initial inorganic N fractions generally were low in all samples except the surface of SB-2 and depth samples of SB-1. These samples were higher in $\text{NH}_4^+\text{-N}$ than has been found for most desert soils. A large amount of $\text{NO}_3\text{-N}$ remained in all samples following incubation when only nitrate was added. However, the addition of the organic carbon source, glucose, resulted in almost complete disappearance of nitrate in all samples but the Anthony (SR-2) sandy surface soil. The result of adding nitrate was increased organic N in many but not all samples. The $\text{NH}_4^+\text{-N}$ fraction increased in the Rillito (SB-2) soil, and to a greater extent with glucose.

The calculated loss of $^{15}\text{NO}_3\text{-N}$ during incubation is given in Table 4. Losses without glucose ranged from approximately one-tenth of added nitrate to more than one-half from different soils and depths. With glucose addition losses increased until two-fifths to more than two-thirds of added nitrate could not be recovered.

The surface 0-5 cm depths of all the soil profiles were checked for the presence of denitrifying organisms (Table 5). Denitrifying organisms were positively identified in all soils using procedures outlined by Alexander (1965a).

Table 3. Soil nitrogen forms in Sonoran desert profiles — DSCODE A 3UTH03

Soil N Forms										
		NH ₄ ⁺ - N			NO ₂ ⁻ + NO ₃ ⁻ - N			Organic - N		
		Amended*			Amended			Amended		
		NO ₃ ⁺ + Glucose			NO ₃ ⁺ + Glucose			NO ₃ ⁺ + Glucose		
Soil	Depth(cm)	Initial	NO ₃		Initial	NO ₃		Initial	NO ₃	
- µg of N/g of soil -										
Sonoita sandy loam (SR-1)	---	---	---	---				---	---	---
	0-5	0.7	1.2	0.0	0.5	52.1	0.6	265.0	243.2	274.2
	15-20	1.2	2.4	1.6	1.1	99.5	2.0	256.7	218.1	293.1
	30-35	0.7	1.4	0.3	0.2	90.0	1.8	169.1	207.2	269.9
	60-65	0.6	0.3	1.1	0.8	89.3	1.7	152.3	128.8	274.8
	90-95	0.6	0.9	2.1	0.4	88.4	0.2	65.2	114.6	205.5
Anthony sandy loam (SR-2)										
	0-5	1.1	0.3	1.2	0.6	87.4	53.9	151.3	168.0	165.6
	15-20	0.7	0.4	2.0	1.3	91.7	2.1	59.6	112.6	160.4
	30-35	0.6	0.6	0.0	0.4	86.5	0.0	79.3	226.0	158.8
	60-65	0.9	3.1	0.3	1.7	83.4	1.0	244.7	419.6	392.6
	90-95	1.0	1.2	0.8	1.6	83.4	0.3	244.9	290.0	315.3
Rillito loam (SB-1)										
	0-5	2.2	0.7	0.8	2.1	70.9	0.8	191.2	209.9	242.0
	15-20	0.8	2.8	0.0	0.2	87.2	0.3	146.5	126.3	216.5
	30-35	4.6	2.7	3.6	1.0	89.2	0.9	171.7	248.1	253.6
	60-65	3.4	1.8	2.6	0.4	89.2	0.0	209.1	310.5	278.7
	90-95	2.6	0.8	0.3	0.6	93.9	0.2	194.9	215.1	217.4
Rillito loam, eroded (SB-2)										
	0-5	9.1	1.7	6.6	1.2	71.4	0.0	354.9	460.3	407.3
	15-20	1.6	8.1	16.4	0.3	96.3	0.0	407.0	447.0	543.2
	30-35	0.5	6.2	5.9	0.1	88.6	0.3	362.7	374.9	474.3
	60-65	0.6	2.8	9.4	2.0	93.0	0.1	262.8	360.0	450.4

*Amended with NO_3^- or $\text{NO}_3^- + \text{glucose}$ and incubated 18 days @ 36 C under argon atmosphere.

2.3.4.3.-10

Table 4. Calculated loss of added $^{15}\text{NO}_3$ in soil samples incubated under argon for 18 days at 36 C — DSCODE A3UTH01

Depth(cm)	SR-1		SR-2		SB-1		SB-2	
	$\text{NO}_3 +$		$\text{NO}_3 +$		$\text{NO}_3 +$		$\text{NO}_3 +$	
	NO_3	Glucose	NO_3	Glucose	NO_3	Glucose	NO_3	Glucose
	----- % loss -----				-----			
0-5	52.8	66.9	13.5	62.7	36.3	66.2	17.9	60.3
15-20	19.8	57.1	36.2	48.6	32.9	65.0	11.8	39.1
30-35	21.8	41.6	28.0	55.0	23.7	69.5	20.3	47.1
60-65	27.7	39.2	25.3	49.7	22.5	52.4	16.4	42.1
90-95	36.1	45.9	23.9	46.6	13.6	60.0	-	-

Table 5. Detection of denitrifying organisms in the 0-5 cm depth of Sonoran desert soils

Soil Condition	SR-1	SR-2	SB-1	SB-2
Dry	+	+	+	+
Wet	+	+	+	+

+ indicates presence of denitrifiers

In order to differentiate between biological and non-biological gaseous losses of N, a soil sterilization procedure had to be employed that would not destroy the physical structure or the chemical constituents of the soil. Standard steam sterilization procedures were inadequate because of the gross destruction of the clay minerals and changes in chemical constituents that occur when soils are subjected to high temperatures and pressures. A sterilization procedure using methyl bromide has been adopted and compared with steam sterilization and unsterilized soils for the presence of viable organisms on specific denitrifican agar plates. Data of a portion of the study are shown in Table 6. Agar plates inoculated with methyl bromide sterilized soil remained sterile for five days and longer. It is interesting

to note that steam sterilization of soil samples for 30 min at 121 C and 15 psi did not reduce the viable denitrifiers. The methyl bromide procedure is being used to differentiate between biological and non-biological gaseous losses of nitrogen.

Table 6. Detection of denitrifiers in steam sterilized and methyl bromide sterilized soils from the 0-5 cm depth of an eroded Rillito loam (SB-2)

	Unsterilized Days					Steam sterilized Days					CH ₃ Br Days				
	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5
Wet soil	+	+	+	-	+	+	+	+	+	-	no wet soil				
Dry soil	+	+	+	+	+	+	+	+	+	+	-	-	-	-	-
Wet soil extract 10:100	+	+	-	-	-	+	+	+	+	+	no wet soil				
Dry soil extract 10:100	+	+	+	+	+	+	+	+	+	-	-	-	-	-	-
Blank	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
+ indicates presence of denitrifiers															

Data for a detailed oxygen exchange study with time at all depths of two soils from Santa Rita and two soils from Silverbell are reported in Table 7. It is interesting to note that in the lower depths of the Sonoita sandy loam (SR-1) and the upper depths of the Anthony sandy loam (SR-2) gases are evolved during the first 5 hr rather than oxygen being consumed. However, oxygen was consumed in all depths of all profiles except the Anthony sandy loam (SR-2) which has a buried A horizon at approximately 60 cm.

Oxygen exchange data in a Sonoita sandy loam (site 2, different location than SR-1) that had been steam or methyl bromide sterilized are reported in Table 8. Oxygen consumption increased with time in the unsterilized soil with the highest amount of oxygen being consumed in the surface soil. Both steam and methyl bromide sterilization resulted in gaseous evolution. In the case of steam sterilized soils, the oxygen evolution probably resulted from broken chemical bonds and clay lattices that were collapsed during the heating with pressure in the autoclave. Only the lower depths of the soil showed oxygen consumption at 4 and 24 hr. Methyl bromide sterilization resulted in gaseous evolution from all depths with time. The gas evolved was thought to be CH₃Br adsorbed to clay surfaces which was released upon wetting and/or oxygen as a result of bromination of chemical constituents in the soil.

Table 7. Oxygen exchange in four Sonoran Desert soil profiles after wetting DSCODE--A3UTH04

Depth, cm	Sonoita sandy loam (SR-1) hours			Anthony sandy loam (SR-2) hours			Rillito loam (SB-1) hours			Rillito loam-eroded (SB-2) hours		
	1.0	3.0	5.0	1.0	3.0	5.0	1.0	3.0	5.0	1.0	3.0	5.0
pH O ₂ /10g of soil												
0-5	52.2	76.4	35.8	414.3	+8.0	+11.7	+19.5	160.5	19.8	59.9	88.1	402.1
15-20	43.4	71.3	35.5	340.3	+3.9	+27.8	+47.8	71.5	4.0	23.9	21.8	119.2
30-35	+8.0	+19.8	+4.0	175.1	+11.9	12.3	40.4	92.0	4.0	44.1	80.0	204.6
60-65	+7.7	+11.9	+12.1	127.7	0.2	31.7	47.5	198.0	+11.9	11.9	43.7	182.9
90-95	+11.9	+39.8	+71.6	107.6	0.0	18.8	39.6	266.4	15.7	3.7	+0.2	111.7
										--	--	--

+ indicates oxygen released from the soil.

Table 8. Oxygen exchange in a Sonoita sandy loam after steam sterilization and methyl bromide treatment — DSCODE A3UTH04

Depth(cm)	Unsterilized hours			Steam sterilized hours			CH ₃ Br hours		
	0.5	6.0	26.0	1.0	4.0	24.0	1.0	6.0	24.0
	----- $\mu\text{l O}_2/\text{10g of soil}$ -----								
0-5	15.9	131.1	401.2	+ 11.6	+ 7.8	+244.5	+43.5	+63.4	+126.7
10-15	11.8	70.9	201.0	+104.5	+128.7	+101.4	+35.3	+58.7	+ 93.7
25-30	4.0	23.9	91.7	+ 87.4	+119.3	+135.5	+19.6	+27.3	+ 43.0
50-55	4.1	20.3	32.4	+ 43.1	15.8	82.6	+39.3	+39.2	+ 35.4
75-80	+11.9	11.9	127.2	+ 24.0	12.1	88.0	+58.8	+58.8	+ 46.6

+ indicates gas released from the soil

Most probable numbers (MPN) of denitrifying organisms in the initial air-dry soil and soils saturated and partially saturated that were incubated 5, 10, and 15 days at 37 C are shown in Table 9. The MPN of denitrifiers in the initial air-dry samples were low but increased with depth. A cholla cactus root was decaying in the 25-30 cm depth and the organic carbon energy source was the apparent reason for the increased MPN of denitrifiers. The MPN of denitrifiers in the unsaturated soils were always less than the MPN of denitrifiers in the saturated soils. In unsaturated soils MPN of denitrifiers increased in 10-day incubation but decreased with 15-day incubation. In saturated soils MPN of denitrifiers increased with depth and time in all cases except in the 15-day, 25-30 cm depth incubation. With the large number of denitrifiers, energy may have been limiting.

Table 9. Number of denitrifiers in a Sonoita sandy loam (site-2) incubated at 37 C aerobically under partially saturated and saturated conditions — DSCODE A3UTH03

Depth(cm)		Days			
		t0	t5	t10	t15
		----- denitrifiers/g of soil -----			
0-5	Air Dry	0.2	---	---	---
	53% Sat.	---	4.9	11.0	17.0
	Sat.	---	22.0	220.0	790.0
10-15	Air Dry	0.6	---	---	---
	53% Sat.	---	7.9	79.9	46.0
	Sat.	---	140.0	280.0	1,100.0
25-30	Air Dry	42.0	---	---	---
	53% Sat.	---	17.0	35.0	13.0
	Sat.	---	490.0	2800.0	2,200.0

During the period October 14-24, 1972, we cooperated with and supported Dr. Roy Cameron (JPL and Utah State University) in a series of broadscale field experiments at the Silverbell site to gather data that would be representative of actual field conditions. Data pertaining to algae activity, gaseous composition of the soil atmosphere, fluxes in the microbial population, and nitrogen transformations were collected before, during, and after an intensive rainstorm. The nitrogen transformation data were processed in our laboratory and have been forwarded to Dr. Cameron to be included in his report.

DISCUSSION

Results of 1971 demonstrating the potential for gaseous N losses were expanded in 1972 to include three additional soil profiles. Gaseous loss of N occurred at all depths of all soil profiles and was enhanced by additions of nitrate and organic carbon. The total N loss can be appreciable when conditions are favorable, as indicated by the low amount of $\text{NO}_3\text{-N}$ remaining in the soils after incubation.

The oxygen consumption technique was useful in evaluating sterilization methods which will be used to distinguish between potential biological and non-biological N losses.

Methyl bromide and steam sterilization methods were compared and the methyl bromide technique was adopted for further study of biological vs. non-biological gaseous N losses. Methyl bromide treated soil samples were void of denitrifying organisms.

Studies on the rate of gaseous N loss have been initiated that include variables of moisture, temperature, soil depth, organic carbon, $\text{NO}_3\text{-N}$ concentration, and time. Other studies include methyl bromide sterilization in relation to several variables mentioned above as well as complete anaerobic incubation (Helium atmosphere).

Apparently not all of the denitrifying activity is confined to the upper surface of the desert soils, as indicated by the high number of denitrifying organisms in the lower depths of the profiles studied. The presence of organic material from decaying roots may have contributed to the higher number of denitrifiers in the lower depths of the observed profiles.

EXPECTATIONS

It is anticipated that the contribution of gaseous loss of N from non-biological and biological sources will be resolved in the immediate future, since adequate sterilization techniques have been developed. Preliminary indications are that non-biological contributions are negligible. Experiments have been initiated to determine rate of gaseous N loss as influenced by moisture, temperature, soil depth, organic carbon, and $\text{NO}_3\text{-N}$ concentration. Experiments are in progress and data for one profile are almost complete. After evaluation of these results, additional profiles will be studied with modifications of variables deemed appropriate.

In order to relate results obtained under laboratory conditions more closely to field conditions a series of field experiments will be conducted in 1973. Metal cylinders will be driven into the soil to various depths and known amounts of organic material with $^{15}\text{NO}_3$ will be incorporated in the soil. These cylinders will be closed at the top with plastic or metal foil. Acid and alkaline traps will be placed on the surface of the soil inside the cylinders to trap NH_3 and CO_2 gases evolved. Decomposition rates of organic carbon and nitrogen and the transfer of organic N to soil N as well as N loss will be measured at scheduled time intervals throughout the year.

Rates of gaseous loss of N as influenced by moisture, temperature, soil depth, organic carbon, and NO_3 concentration, in the laboratory studies as well as data pertaining to gaseous losses, decomposition of organic carbon and transfer of organic N to soil N under actual field conditions, will be very useful in the modelling of the ecosystems in semi-arid regions.

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1972 PROGRESS REPORT

GASEOUS LOSSES OF NITROGEN FROM THE SOIL OF SEMI-ARID REGIONS

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Research Memorandum, RM 73-37

MAY 1973

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A B S T R A C T

Soil profile samples were selected for laboratory studies of gaseous nitrogen (N) losses from two soil types at each Sonoran Desert Validation Site near Tucson. Oxygen consumption, gaseous evolution during anerobic incubation employing $^{15}\text{NO}_3$, changes in the N fractions, and most probable number (MPN) of denitrifying organisms were examined to determine N loss potential. The potential for gaseous loss of N was observed in all soils at all depths and resulted in $^{15}\text{N}_2$ and $^{15}\text{N}_2\text{O}$ evolution. The calculated loss in 18 days of added $^{15}\text{NO}_3$ ranged from approximately one-tenth to more than two-thirds of the total amendment. An organic carbon energy source was included in portions of these studies. Glucose additions increased N in the gaseous phase and increased the calculated loss based on ^{15}N remaining in the soil after incubation. Oxygen consumption increased, indicating biological and/or chemical activity, when the soils were moistened. Although oxygen was consumed in soils from all profile depths within 24 hr, the rate of consumption was higher in the surface soils of all profiles except the one having the buried A horizon. The number of denitrifying organisms under saturated moisture increased with soil depth, incubation time, and additions of $\text{NO}_3\text{-N}$ and organic carbon.

INTRODUCTION

This study was conducted to determine the potential for gaseous losses of nitrogen (N) from native desert soils and to quantify these losses in relation to the various parameters of the system. The previous work was concerned with the potential for gaseous loss and the identity of the gaseous products evolved, as well as techniques for the study. Some of this work was continued during 1972. The biological and non-biological contributions to gaseous N losses were studied and satisfactory techniques have been developed to differentiate between these two processes. Initial studies on rates of gaseous N loss as a function of temperature, moisture, nitrate concentrations, and organic carbon have been initiated and will be continued.

OBJECTIVES

The objectives for 1972 were:

1. To complete the study of denitrification potential on soil samples from various profile depths of two soils from each Sonoran Validation Site -- Santa Rita and Silverbell.
2. To determine the relative contributions of non-biological and biological gaseous losses.
3. To initiate rate studies of the gaseous loss process in relation to moisture, temperature, nitrate concentration and organic carbon source. This phase of the study will be continued and completed in 1973.

METHODS

Soil profile samples (DSCODE A3UTH-) were taken from two locations on the Santa Rita site (Sonoita sandy loam - SR-1, Anthony sandy loam - SR-2), and two from the Silverbell site (Rillito loam - SB-1, Rillito loam, eroded - SB-2). Sampling depths were 0-5, 15-20, 30-35, 60-65, and 90-95 cm, with exception of the 90-95 cm depth in SB-2 because of bedrock. These soils were air-dried, crushed, passed through a 2 mm sieve, and stored in plastic containers with sealed air-tight lids.

Ten-g air-dry soil samples from desert profiles were placed individually into 125 ml Warburg respirometer flasks and moistened with 2 ml of H₂O. One ml of 20% KOH

was placed in the center well and oxygen and gas exchange were measured at 37 C using standard Warburg respirometer techniques (Umbreit, Burris and Stauffer, 1964).

Fifty-g samples of air dry soil were placed in calibrated 125 ml Erlenmeyer flasks containing 2 ml of saturated KOH in wells. The samples were moistened with 10 ml solutions containing 4.9 g of $\text{NO}_3\text{-N}$ in water or in 0.25 M glucose solution. The $\text{NO}_3\text{-N}$ added was enriched with 33 atom percent ^{15}N . The flasks were closed with rubber septum caps, flushed for 10 min with argon gas, then incubated for 18 days at 36 C. Gas samples were taken from the air in each flask with a gas tight syringe at varying time intervals and analyzed by mass spectrometry. Calculations were made for gaseous composition, ^{15}N in the N_2 and N_2O components, and N_2 to N_2O ratios. Samples of the initial soil before treatment and after incubation were analyzed for $\text{NH}_4^+\text{-N}$, $\text{NO}_2^- + \text{NO}_3^- \text{-N}$, and organic N fraction by micro-Kjeldahl procedure (Bremner, 1965). Atom percent ^{15}N in each fraction was determined by mass spectrometry and percent loss of added $\text{NO}_3\text{-N}$ was calculated.

Detection of the presence of denitrifying organisms in soil profiles was accomplished using standard techniques (Alexander, 1965a). One hundred ml of sterile water was added to 10-g soil samples in 150 ml bottles which were shaken horizontally in a mechanical shaker for 10 min. Samples were removed from the shaker and were shaken again by hand just prior to removing a 10 ml aliquot with a sterile pipette from the center of the suspension. The aliquot was added to 90 ml of sterile water. One ml aliquots from the above dilution were added to each of five sterile tubes containing the sterile liquid denitrifican medium. The tubes were plugged and incubated for 5 days at 37 C. Presence of denitrifiers was determined in this specific medium by a pH indicator color change from green to blue plus the presence of gas (Alexander, 1965a). It was difficult to identify denitrifiers by this procedure and a more sensitive procedure was adopted. A nitrate nutrient agar was inoculated and sulfanilic acid and α -naphthylamine was used to detect the presence of nitrite (Difco, 1953). Denitrifiers were detected by a pink color, specific for nitrite, and presence of gas bubbles in the agar.

Most probable numbers of denitrifying organisms were measured at 37 C using procedures outlined by Alexander (1965b) in a specific liquid denitrifican broth. The liquid broth contained succinic acid, K_2HPO_4 , $\text{MgSO}_3 \cdot 7\text{H}_2\text{O}$, KNO_3 , CaCO_3 , yeast extract and tap water, respectively, in the following g/l: 2.0, 1.0, 0.5, 10.0, 2.0, 1.0, with tap water used to make to final volume.

Soils were sterilized using standard steam sterilization procedures (Alexander, 1965a) and a methyl bromide gas treatment developed in this laboratory. Ten-g soil samples were spread thinly over a 9 cm petri dish and steam sterilized in an autoclave

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for 30 min at 121 C and 15 psi. For methyl bromide sterilization, 10-g samples of soil were placed in tubular glass and separated by cotton. The gas was diffused through the soil slowly for 24 hr using an alcohol absorbent trap to catch the CH_3Br gas passing through the column. Following the methyl bromide gassing the soils were scrubbed for 8 hr with compressed air that had been passed through dilute sulfuric acid and deionized water baths. This scrubbing procedure was adopted to remove CH_3Br adsorbed to clay surface areas.

After sterilization by steam or by methyl bromide, the soils were placed aseptically in sterile glass petri dishes and allowed to de-gas for 24 hr. Then soils were placed into acetone-heat-treated Warburg flasks for oxygen consumption studies. Other soil samples were plated on denitrifican agar to check sterility.

RESULTS

Wetting dry desert soils increased the oxygen consumption, which showed in the initiation of biological and/or chemical activity (Table 1, DSCODE A3UTH04). No consistent pattern was evident for differences between soils or in profile depths. However, oxygen consumption tended to increase with increasing organic matter in the profile. For example, the Anthony sandy loam (SR-2) has a buried A horizon at approximately 60 cm and is higher in organic matter (0.39%) and consumed more oxygen ($0.15 \mu\text{l/g/hr}$) when moistened than the overlying sandy material which was lower in organic matter (0.17%) and consumed less oxygen ($0.03 \mu\text{l/g/hr}$).

Table 1. Organic matter and oxygen consumption in Sonoran Desert profile soil samples after wetting DSCODE—A3UTH04

Soil	SR-1		SR-2		SB-1		SB-2	
	$\mu\text{l O}_2/\text{g/hr}$	%O.M.	$\mu\text{l O}_2/\text{g/hr}$	%O.M.	$\mu\text{l O}_2/\text{g/hr}$	%O.M.	$\mu\text{l O}_2/\text{g/hr}$	%O.M.
Depth, cm								
0-5	0.16	0.46	0.09	0.27	0.14	0.32	0.17	0.54
15-20	0.17	0.37	0.04	0.16	0.09	0.28	0.13	0.53
30-35	0.11	0.26	0.03	0.17	0.10	0.34	0.12	0.39
60-65	0.05	0.23	0.15	0.39	0.12	0.29	0.18	0.35
90-95	0.11	0.18	0.15	0.35	0.05	0.24	- bedrock -	

Percentages of N_2 , O_2 , N_2O and the N_2/N_2O ratio in the gas phase above soils incubated anaerobically are shown in Table 2. In soils amended with nitrate, the percentage of N_2 and O_2 increased with time in practically all depths of the three soil profiles. There were only slight changes in the percentage of N_2O , regardless of time, depth or soil profile. The N_2/N_2O ratios ranged from 138 to 6773 in the soils that were amended with nitrogen. In soils amended with nitrate plus glucose, the percentages of N_2 in the atmosphere above incubating soils generally were higher than observed in soils amended with only nitrate, and tended to increase with time. Percent oxygen tended to be lower at the 355 hr time of sampling than was observed at previous sampling times. The N_2/N_2O ratios were much smaller than in the soil amended with only nitrate, indicating a larger percentage of the gas was in the form of N_2O . The presence of the organic energy source apparently stimulated loss of nitrogen in the form of N_2O and increased the amount of N_2 gas in the atmosphere above the incubating soils.

Table 2. Composition of gas above Sonoran Desert soil profile samples incubated under argon atmosphere and amended with nitrate and nitrate plus glucose
DSCODE—A3UTH01

Depth (cm)	Time (hr)	N_2	O_2	N_2O	N_2/N_2O
Anthony sandy loam (SR-2) - Nitrate					
0- 5	18	7.37	1.131	0.012	640
	91	14.86	2.460	0.039	383
	187	14.38	2.381	0.024	609
	355	14.45	2.473	0.015	971
15-20	18	0.94	0.198	0.001	1238
	91	5.49	1.066	0.006	959
	187	8.06	1.588	0.004	1873
	355	15.87	3.014	0.005	3051
30-35	18	2.90	0.481	0.003	899
	91	3.07	0.609	0.017	180
	187	5.25	1.136	0.013	400
	355	7.01	1.739	0.010	680
60-65	18	8.03	1.155	0.015	535
	91	13.42	1.995	0.038	355
	187	9.92	1.187	0.005	2031
	355	12.99	1.250	0.012	1086
90-95	18	11.05	1.697	0.024	456
	91	15.86	2.460	0.115	138
	187	16.60	2.481	0.037	500
	355	12.02	1.387	0.016	758

Continued

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Table 2. Continued

Depth (cm)	Time (hr)	N ₂	O ₂ %	N ₂ O	N ₂ /N ₂ O
Anthony sandy loam (SR-2) - nitrate + glucose					
0- 5	20	2.71	0.288	0.051	53
	91	21.05	2.193	0.277	76
	188	3.38	0.314	0.039	86
	355	29.48	0.372	0.564	52
15-20	20	1.06	0.055	0.031	34
	91	13.77	1.886	0.098	140
	188	16.20	0.406	0.077	211
	355	26.30	0.419	0.126	210
30-35	20	1.49	0.170	0.071	21
	91	13.49	1.433	0.028	478
	188	16.69	1.570	1.848	9
	355	22.04	0.588	0.048	457
60-65	20	10.10	1.234	0.059	171
	91	25.24	2.508	0.041	612
	188	38.31	3.048	2.970	13
	355	39.61	0.611	8.733	5
90-95	20	10.64	0.919	0.021	508
	91	32.58	3.141	0.094	348
	188	41.92	3.089	1.895	22
	355	47.54	1.581	8.520	6
Rillito loam (SB-1) - nitrate					
0- 5	18	10.47	1.574	0.034	312
	91	20.60	2.989	0.067	309
	187	25.19	3.232	0.013	1894
	355	25.05	3.062	0.006	4464
15-20	18	2.79	0.405	0.004	676
	91	15.75	2.584	0.055	286
	187	17.80	2.838	0.021	842
	355	14.10	2.012	0.005	2801
30-35	18	2.51	0.304	0.006	388
	91	13.40	2.011	0.036	375
	187	24.40	3.679	0.026	932
	355	24.42	3.430	0.010	2489
60-65	18	9.66	1.405	0.016	596
	91	25.17	3.756	0.024	1030
	187	35.24	5.068	0.013	2743
	355	44.16	6.326	0.007	6773
90-95	18	1.11	0.116	0.003	396
	91	10.18	1.580	0.042	241
	187	6.96	1.026	0.004	1691
	355	18.75	2.911	0.006	3023

Continued

Table 2. Continued

Depth (cm)	Time (hr)	N ₂	O ₂ %	N ₂ O	N ₂ /N ₂ O
Rillito loam (SB-1) - nitrate + glucose					
0- 5	20	7.12	0.890	0.098	72
	91	17.11	6.640	0.079	217
	188	32.65	3.370	0.458	67
	355	31.04	1.099	4.813	6
15-20	20	7.10	0.702	0.123	58
	91	17.97	1.067	0.013	1370
	188	32.55	2.273	0.149	219
	355	42.21	0.808	5.276	8
30-35	20	4.29	0.289	0.210	20
	91	27.40	2.858	0.035	794
	188	31.76	1.827	0.027	1194
	355	22.02	0.229	0.012	1775
60-65	20	7.84	0.952	0.283	28
	91	31.59	3.658	0.085	371
	188	21.46	0.063	0.454	47
	355	36.50	0.801	4.587	8
90-95	20	36.70	0.150	0.166	22
	91	26.58	2.114	0.031	860
	188	31.15	0.091	0.003	10383
	355	51.50	0.641	0.536	96
Rillito loam, eroded(SB-2) - nitrate					
0- 5	18	8.51	1.098	0.036	234
	91	20.58	2.586	0.044	465
	187	26.05	2.354	0.015	1728
	355	38.40	3.981	0.017	2305
15-20	18	1.32	0.119	0.006	209
	91	17.93	2.498	0.084	213
	187	20.12	2.041	0.010	1971
	355	29.50	2.414	0.008	3508
30-35	18	1.40	0.136	0.008	173
	91	7.30	0.983	0.018	404
	187	12.08	1.531	0.009	1324
	355	13.07	1.204	0.005	2558
60-65	18	0.82	0.051	0.004	188
	91	13.62	2.047	0.025	605
	187	16.82	2.378	0.013	1281
	355	12.03	1.229	0.003	3965

Continued

Table 2. Continued

Depth (cm)	Time (hr)	N ₂	O ₂ %	N ₂ O	N ₂ /N ₂ O
Rillito loam, eroded (SB-2) - nitrate + glucose					
0- 5	20	7.08	0.668	0.147	48
	91	26.76	1.915	0.023	1154
	188	27.35	0.154	0.028	980
	355	43.88	0.555	3.109	14
15-20	20	6.82	0.507	0.018	377
	91	13.70	0.122	0.016	869
	188	30.20	0.328	0.085	356
	355	46.99	1.265	4.039	12
30-35	20	11.21	0.460	0.012	969
	91	25.56	0.342	0.007	3695
	188	34.98	0.243	0.036	976
	355				
60-65	20	2.61	0.032	0.007	351
	91	8.98	0.017	0.044	204
	188	22.47	0.124	0.771	29
	355	51.52	0.262	6.118	8

Data in Table 3 illustrate the amounts of nitrogen in different forms in initial profile samples and after 18 days of incubation following the addition of $^{15}\text{NO}_3\text{-N}$ either with or without glucose. Initial inorganic N fractions generally were low in all samples except the surface of SB-2 and depth samples of SB-1. These samples were higher in $\text{NH}_4^+\text{-N}$ than has been found for most desert soils. A large amount of $\text{NO}_3\text{-N}$ remained in all samples following incubation when only nitrate was added. However, the addition of the organic carbon source, glucose, resulted in almost complete disappearance of nitrate in all samples but the Anthony (SR-2) sandy surface soil. The result of adding nitrate was increased organic N in many but not all samples. The $\text{NH}_4^+\text{-N}$ fraction increased in the Rillito (SB-2) soil, and to a greater extent with glucose.

The calculated loss of $^{15}\text{NO}_3\text{-N}$ during incubation is given in Table 4. Losses without glucose ranged from approximately one-tenth of added nitrate to more than one-half from different soils and depths. With glucose addition losses increased until two-fifths to more than two-thirds of added nitrate could not be recovered.

The surface 0-5 cm depths of all the soil profiles were checked for the presence of denitrifying organisms (Table 5). Denitrifying organisms were positively identified in all soils using procedures outlined by Alexander (1965a).

Table 3. Soil nitrogen forms in Sonoran desert profiles — DSCODE A 3UTH03

Soil N Forms										
		$\text{NH}_4^+ - \text{N}$			$\text{NO}_2^- + \text{NO}_3^- - \text{N}$			Organic - N		
		Amended*			Amended			Amended		
		$\text{NO}_3^- + \text{Glucose}$			$\text{NO}_3^- + \text{Glucose}$			$\text{NO}_3^- + \text{Glucose}$		
Soil	Depth(cm)	Initial	NO_3^-	Glucose	Initial	NO_3^-	Glucose	Initial	NO_3^-	Glucose
- μg of N/g of soil -										
Sonoita sandy loam (SR-1)	---	---	---	---				---	---	---
	0-5	0.7	1.2	0.0	0.5	52.1	0.6	265.0	243.2	274.2
	15-20	1.2	2.4	1.6	1.1	99.5	2.0	256.7	218.1	293.1
	30-35	0.7	1.4	0.3	0.2	90.0	1.8	169.1	207.2	269.9
	60-65	0.6	0.3	1.1	0.8	89.3	1.7	152.3	128.8	274.8
	90-95	0.6	0.9	2.1	0.4	88.4	0.2	65.2	114.6	205.5
Anthony sandy loam (SR-2)										
	0-5	1.1	0.3	1.2	0.6	87.4	53.9	151.3	168.0	165.6
	15-20	0.7	0.4	2.0	1.3	91.7	2.1	59.6	112.6	160.4
	30-35	0.6	0.6	0.0	0.4	86.5	0.0	79.3	226.0	158.8
	60-65	0.9	3.1	0.3	1.7	83.4	1.0	244.7	419.6	392.6
	90-95	1.0	1.2	0.8	1.6	83.4	0.3	244.9	290.0	315.3
Rillito loam (SB-1)										
	0-5	2.2	0.7	0.8	2.1	70.9	0.8	191.2	209.9	242.0
	15-20	0.8	2.8	0.0	0.2	87.2	0.3	146.5	126.3	216.5
	30-35	4.6	2.7	3.6	1.0	89.2	0.9	171.7	248.1	253.6
	60-65	3.4	1.8	2.6	0.4	89.2	0.0	209.1	310.5	278.7
	90-95	2.6	0.8	0.3	0.6	93.9	0.2	194.9	215.1	217.4
Rillito loam, eroded (SB-2)										
	0-5	9.1	1.7	6.6	1.2	71.4	0.0	354.9	460.3	407.3
	15-20	1.6	8.1	16.4	0.3	96.3	0.0	407.0	447.0	543.2
	30-35	0.5	6.2	5.9	0.1	88.6	0.3	362.7	374.9	474.3
	60-65	0.6	2.8	9.4	2.0	93.0	0.1	262.8	360.0	450.4

*Amended with NO_3^- or $\text{NO}_3^- + \text{glucose}$ and incubated 18 days @ 36 C under argon atmosphere.

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Table 4. Calculated loss of added $^{15}\text{NO}_3$ in soil samples incubated under argon for 18 days at 36 C — DSCODE A3UTH01

Depth(cm)	SR-1		SR-2		SB-1		SB-2	
	$\text{NO}_3 +$		$\text{NO}_3 +$		$\text{NO}_3 +$		$\text{NO}_3 +$	
	NO_3	Glucose	NO_3	Glucose	NO_3	Glucose	NO_3	Glucose
	----- % loss -----				-----			
0-5	52.8	66.9	13.5	62.7	36.3	66.2	17.9	60.3
15-20	19.8	57.1	36.2	48.6	32.9	65.0	11.8	39.1
30-35	21.8	41.6	28.0	55.0	23.7	69.5	20.3	47.1
60-65	27.7	39.2	25.3	49.7	22.5	52.4	16.4	42.1
90-95	36.1	45.9	23.9	46.6	13.6	60.0	-	-

Table 5. Detection of denitrifying organisms in the 0-5 cm depth of Sonoran desert soils

Soil Condition	SR-1	SR-2	SB-1	SB-2
Dry	+	+	+	+
Wet	+	+	+	+

+ indicates presence of denitrifiers

In order to differentiate between biological and non-biological gaseous losses of N, a soil sterilization procedure had to be employed that would not destroy the physical structure or the chemical constituents of the soil. Standard steam sterilization procedures were inadequate because of the gross destruction of the clay minerals and changes in chemical constituents that occur when soils are subjected to high temperatures and pressures. A sterilization procedure using methyl bromide has been adopted and compared with steam sterilization and unsterilized soils for the presence of viable organisms on specific denitrifican agar plates. Data of a portion of the study are shown in Table 6. Agar plates inoculated with methyl bromide sterilized soil remained sterile for five days and longer. It is interesting

to note that steam sterilization of soil samples for 30 min at 121 C and 15 psi did not reduce the viable denitrifiers. The methyl bromide procedure is being used to differentiate between biological and non-biological gaseous losses of nitrogen.

Table 6. Detection of denitrifiers in steam sterilized and methyl bromide sterilized soils from the 0-5 cm depth of an eroded Rillito loam (SB-2)

	Unsterilized Days					Steam sterilized Days					CH ₃ Br Days				
	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5
Wet soil	+	+	+	-	+	+	+	+	+	-	no wet soil				
Dry soil	+	+	+	+	+	+	+	+	+	+	-	-	-	-	-
Wet soil extract 10:100	+	+	-	-	-	+	+	+	+	+	no wet soil				
Dry soil extract 10:100	+	+	+	+	+	+	+	+	+	-	-	-	-	-	-
Blank	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
+ indicates presence of denitrifiers															

Data for a detailed oxygen exchange study with time at all depths of two soils from Santa Rita and two soils from Silverbell are reported in Table 7. It is interesting to note that in the lower depths of the Sonoita sandy loam (SR-1) and the upper depths of the Anthony sandy loam (SR-2) gases are evolved during the first 5 hr rather than oxygen being consumed. However, oxygen was consumed in all depths of all profiles except the Anthony sandy loam (SR-2) which has a buried A horizon at approximately 60 cm.

Oxygen exchange data in a Sonoita sandy loam (site 2, different location than SR-1) that had been steam or methyl bromide sterilized are reported in Table 8. Oxygen consumption increased with time in the unsterilized soil with the highest amount of oxygen being consumed in the surface soil. Both steam and methyl bromide sterilization resulted in gaseous evolution. In the case of steam sterilized soils, the oxygen evolution probably resulted from broken chemical bonds and clay lattices that were collapsed during the heating with pressure in the autoclave. Only the lower depths of the soil showed oxygen consumption at 4 and 24 hr. Methyl bromide sterilization resulted in gaseous evolution from all depths with time. The gas evolved was thought to be CH₃Br adsorbed to clay surfaces which was released upon wetting and/or oxygen as a result of bromination of chemical constituents in the soil.

Table 7. Oxygen exchange in four Sonoran Desert soil profiles after wetting DSCODE--A3UTH04

Depth, cm	Sonoita sandy loam (SR-1) hours			Anthony sandy loam (SR-2) hours			Rillito loam (SB-1) hours			Rillito loam-eroded (SB-2) hours		
	1.0	3.0	5.0	1.0	3.0	5.0	1.0	3.0	5.0	1.0	3.0	5.0
pH O ₂ /10g of soil												
0-5	52.2	76.4	35.8	414.3	+8.0	+11.7	+19.5	160.5	19.8	59.9	88.1	402.1
15-20	43.4	71.3	35.5	340.3	+3.9	+27.8	+47.8	71.5	4.0	23.9	21.8	119.2
30-35	+8.0	+19.8	+4.0	175.1	+11.9	12.3	40.4	92.0	4.0	44.1	80.0	204.6
60-65	+7.7	+11.9	+12.1	127.7	0.2	31.7	47.5	198.0	+11.9	11.9	43.7	182.9
90-95	+11.9	+39.8	+71.6	107.6	0.0	18.8	39.6	266.4	15.7	3.7	+0.2	111.7
										--	--	--

+ indicates oxygen released from the soil.

Table 8. Oxygen exchange in a Sonoita sandy loam after steam sterilization and methyl bromide treatment — DSCODE A3UTH04

Depth(cm)	Unsterilized hours			Steam sterilized hours			CH ₃ Br hours		
	0.5	6.0	26.0	1.0	4.0	24.0	1.0	6.0	24.0
	----- $\mu\text{l O}_2/\text{10g of soil}$ -----								
0-5	15.9	131.1	401.2	+ 11.6	+ 7.8	+244.5	+43.5	+63.4	+126.7
10-15	11.8	70.9	201.0	+104.5	+128.7	+101.4	+35.3	+58.7	+ 93.7
25-30	4.0	23.9	91.7	+ 87.4	+119.3	+135.5	+19.6	+27.3	+ 43.0
50-55	4.1	20.3	32.4	+ 43.1	15.8	82.6	+39.3	+39.2	+ 35.4
75-80	+11.9	11.9	127.2	+ 24.0	12.1	88.0	+58.8	+58.8	+ 46.6

+ indicates gas released from the soil

Most probable numbers (MPN) of denitrifying organisms in the initial air-dry soil and soils saturated and partially saturated that were incubated 5, 10, and 15 days at 37 C are shown in Table 9. The MPN of denitrifiers in the initial air-dry samples were low but increased with depth. A cholla cactus root was decaying in the 25-30 cm depth and the organic carbon energy source was the apparent reason for the increased MPN of denitrifiers. The MPN of denitrifiers in the unsaturated soils were always less than the MPN of denitrifiers in the saturated soils. In unsaturated soils MPN of denitrifiers increased in 10-day incubation but decreased with 15-day incubation. In saturated soils MPN of denitrifiers increased with depth and time in all cases except in the 15-day, 25-30 cm depth incubation. With the large number of denitrifiers, energy may have been limiting.

Table 9. Number of denitrifiers in a Sonoita sandy loam (site-2) incubated at 37 C aerobically under partially saturated and saturated conditions — DSCODE A3UTH03

Depth(cm)		Days			
		t0	t5	t10	t15
		----- denitrifiers/g of soil -----			
0-5	Air Dry	0.2	---	---	---
	53% Sat.	---	4.9	11.0	17.0
	Sat.	---	22.0	220.0	790.0
10-15	Air Dry	0.6	---	---	---
	53% Sat.	---	7.9	79.9	46.0
	Sat.	---	140.0	280.0	1,100.0
25-30	Air Dry	42.0	---	---	---
	53% Sat.	---	17.0	35.0	13.0
	Sat.	---	490.0	2800.0	2,200.0

During the period October 14-24, 1972, we cooperated with and supported Dr. Roy Cameron (JPL and Utah State University) in a series of broadscale field experiments at the Silverbell site to gather data that would be representative of actual field conditions. Data pertaining to algae activity, gaseous composition of the soil atmosphere, fluxes in the microbial population, and nitrogen transformations were collected before, during, and after an intensive rainstorm. The nitrogen transformation data were processed in our laboratory and have been forwarded to Dr. Cameron to be included in his report.

DISCUSSION

Results of 1971 demonstrating the potential for gaseous N losses were expanded in 1972 to include three additional soil profiles. Gaseous loss of N occurred at all depths of all soil profiles and was enhanced by additions of nitrate and organic carbon. The total N loss can be appreciable when conditions are favorable, as indicated by the low amount of $\text{NO}_3\text{-N}$ remaining in the soils after incubation.

The oxygen consumption technique was useful in evaluating sterilization methods which will be used to distinguish between potential biological and non-biological N losses.

Methyl bromide and steam sterilization methods were compared and the methyl bromide technique was adopted for further study of biological vs. non-biological gaseous N losses. Methyl bromide treated soil samples were void of denitrifying organisms.

Studies on the rate of gaseous N loss have been initiated that include variables of moisture, temperature, soil depth, organic carbon, $\text{NO}_3\text{-N}$ concentration, and time. Other studies include methyl bromide sterilization in relation to several variables mentioned above as well as complete anaerobic incubation (Helium atmosphere).

Apparently not all of the denitrifying activity is confined to the upper surface of the desert soils, as indicated by the high number of denitrifying organisms in the lower depths of the profiles studied. The presence of organic material from decaying roots may have contributed to the higher number of denitrifiers in the lower depths of the observed profiles.

EXPECTATIONS

It is anticipated that the contribution of gaseous loss of N from non-biological and biological sources will be resolved in the immediate future, since adequate sterilization techniques have been developed. Preliminary indications are that non-biological contributions are negligible. Experiments have been initiated to determine rate of gaseous N loss as influenced by moisture, temperature, soil depth, organic carbon, and $\text{NO}_3\text{-N}$ concentration. Experiments are in progress and data for one profile are almost complete. After evaluation of these results, additional profiles will be studied with modifications of variables deemed appropriate.

In order to relate results obtained under laboratory conditions more closely to field conditions a series of field experiments will be conducted in 1973. Metal cylinders will be driven into the soil to various depths and known amounts of organic material with $^{15}\text{NO}_3$ will be incorporated in the soil. These cylinders will be closed at the top with plastic or metal foil. Acid and alkaline traps will be placed on the surface of the soil inside the cylinders to trap NH_3 and CO_2 gases evolved. Decomposition rates of organic carbon and nitrogen and the transfer of organic N to soil N as well as N loss will be measured at scheduled time intervals throughout the year.

Rates of gaseous loss of N as influenced by moisture, temperature, soil depth, organic carbon, and NO_3 concentration, in the laboratory studies as well as data pertaining to gaseous losses, decomposition of organic carbon and transfer of organic N to soil N under actual field conditions, will be very useful in the modelling of the ecosystems in semi-arid regions.

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1972 PROGRESS REPORT

PROTEOLYTIC ACTIVITY OF SOIL MICROORGANISMS

Robert T. O'Brien
New Mexico State University

Research Memorandum, RM 73-38

MAY 1973

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It is subject to revision and reinterpretation. The author
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A B S T R A C T

Deaminase activities and ammonia volatilization were studied under laboratory and field conditions.

Ammonia loss to the atmosphere was shown to be related to water evaporation. During dry periods the ammonia volatilization rate was $0.7 \text{ mg/m}^2/\text{dry}$ while under wet conditions the rate was $2.3 \text{ mg/m}^2/\text{dry}$. Volatilization rates were an order of magnitude higher under mesquite canopies than over bare ground.

Deaminase activities of soil microorganisms in bajada soil decreased sharply with depth whereas the vertical profile in playa soils was constant. Activities in both soils increased after summer rains and remained at the higher levels throughout the summer.

Deaminase activity was determined by suspending 1 g of soil in 9 ml of 1% vitamin-free casamino acid at pH 6.5. The soil suspensions were incubated at 25 C for 26 hr in screw cap tubes and ammonia was determined as described above.

Field determinations of soil moisture were determined from gypsum soil block readings (Data Sets A3UWJ05 and A3UMJ61) and were supplied by Dr. J. Ludwig.

RESULTS AND DISCUSSION

The effects of moisture on ammonia formation were determined by amending composite soil samples with water and in most cases casein. Results of these experiments are summarized in Figure 1. It is evident that the rates of ammonia formation were nearly the same at 20 to 80% soil water content. It would appear then that protein decomposition and ammonification of amino nitrogen were not limited by moisture availability within the range tested. Additional experiments were done with moisture amendments between 0 and 20%; however, the results were extremely variable and are not presented. The variable results were apparently due to difficulties in obtaining uniform distribution of small amounts of water in the soils.

The effects of temperature were studied at 40% soil moisture since at this level the system was not moisture limited. Results are shown in Figure 2. Optimal ammonia formation was obtained at 30 C with natural soils and with protein-amended soils.

Results of field studies on ammonification in playa and bajada soils are summarized in Figures 3 and 4. For purposes of clarity the ammonia volatilization data were superimposed on soil moisture profiles. Taken alone there was little about the rates of ammonia evolution which can be related to anything approaching a meaningful rate calculation. However, when data were plotted as in Figures 3 and 4, a pattern emerged which related the rate of ammonia loss to the atmosphere to soil moisture content or, more properly, water loss to the atmosphere. Immediately following precipitation the rates of ammonia fell to low levels. During subsequent evaporation the rates of ammonia evolution increased until the soil moisture tension reached about -130 bars. Ammonia volatilization rates then fell back to levels characteristic of dry conditions ($0.7 \text{ mg NH}_4/\text{m}^2/\text{day}$). During periods when soil moisture levels were adequate (-20 bars), the characteristic rate of ammonia loss to atmosphere was $2.3 \text{ mg}/\text{m}^2/\text{day}$. This rate was also observed for the water air interface during the time when the playa was flooded.

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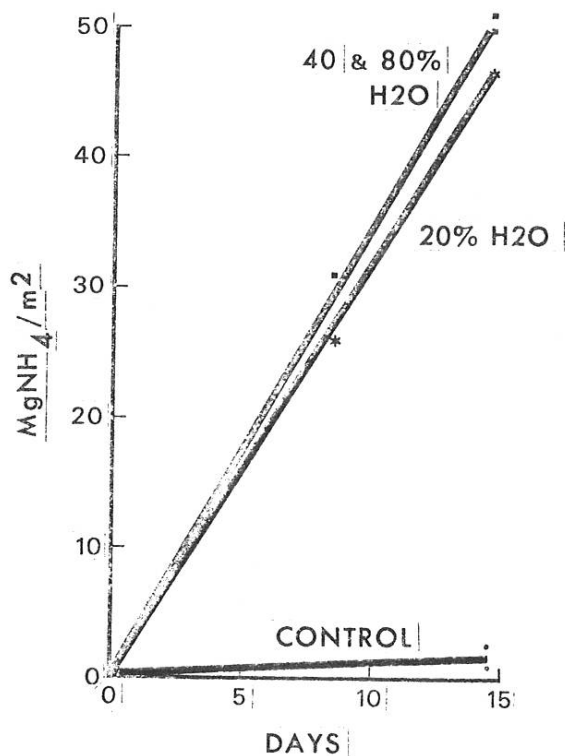


Figure 1. Effects of moisture on ammonia formation in bajada soil. Samples were amended with indicated amounts of water (V:W) and casein (1% final concentration W:W). Temperature 25 C. (DSCODE A3U0A02)

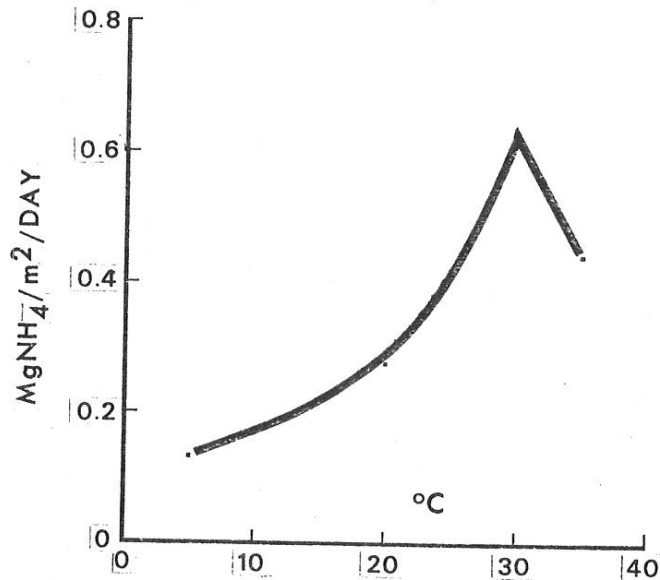


Figure 2. Effect of temperature on ammonia formations in bajada soil. Water amendment was 20% (V:W). (DSCODE A3U0A02)

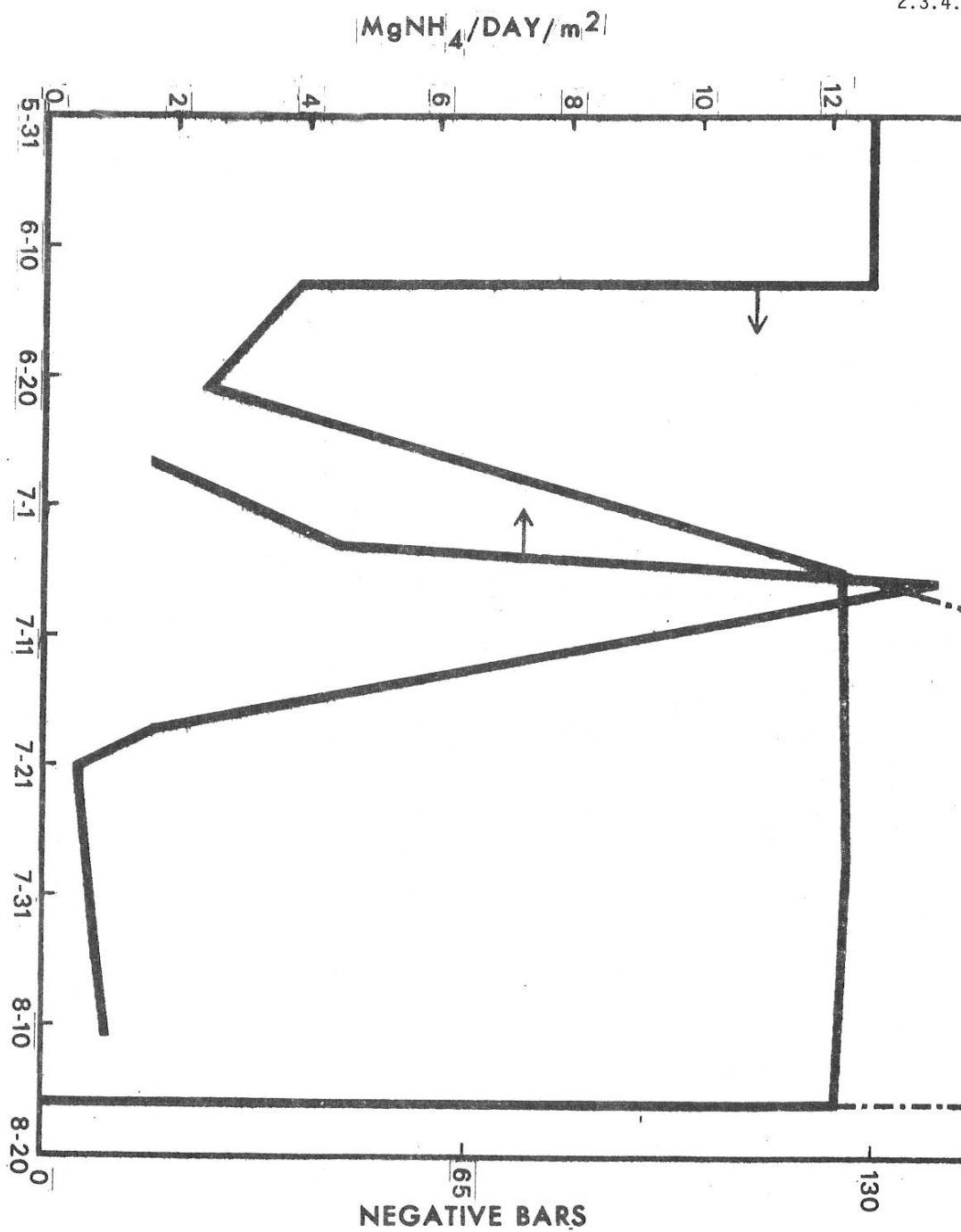


Figure 3. Ammonia evolution from Jornada bajada area. (DSCODE A3U0A02)

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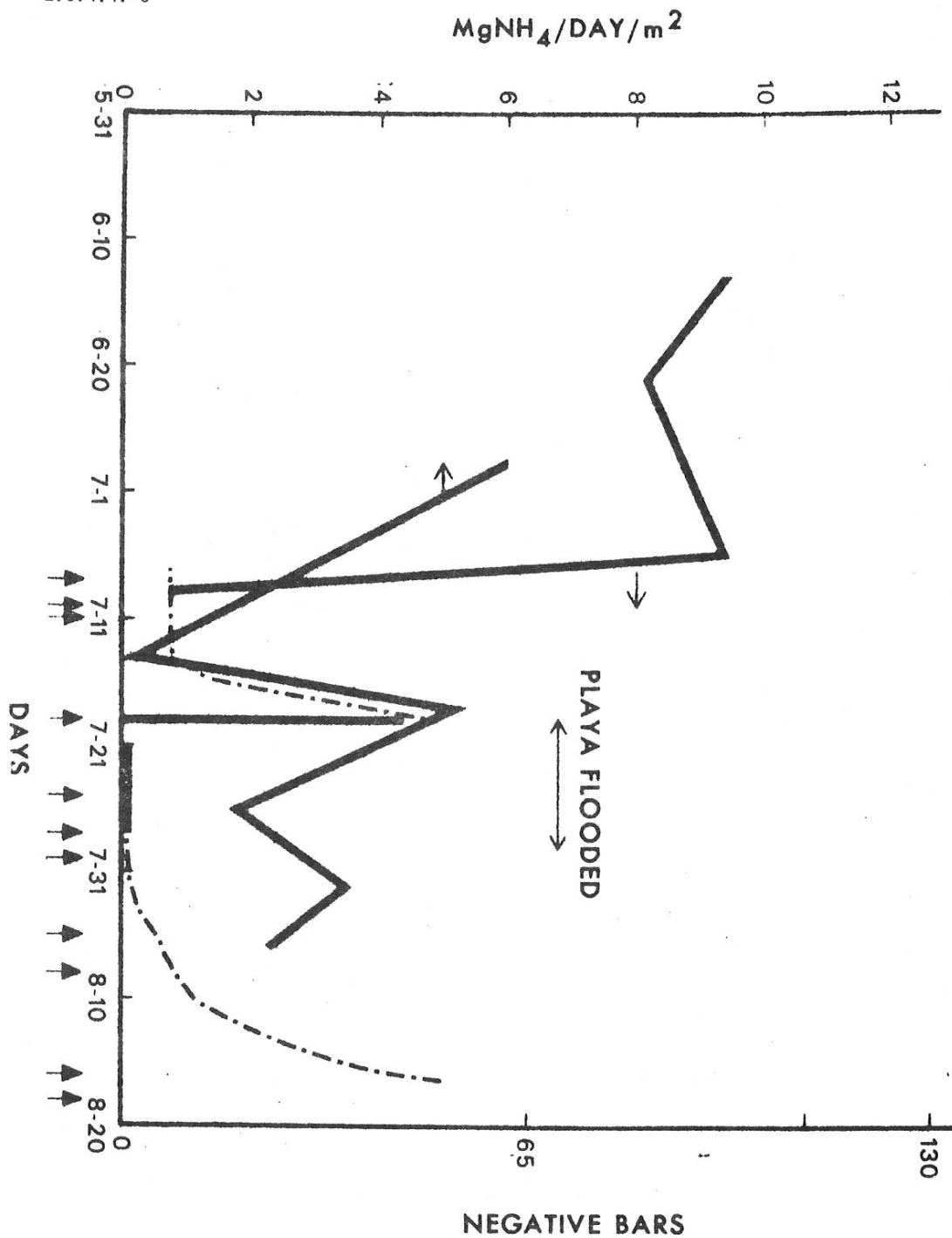


Figure 4. Ammonia evolution from Jornada playa site (DSCODE A3U0A02).

Ammonia volatilization was also influenced by the nature of the ground cover. As shown in Figure 5, the rate of ammonia loss from soil under mesquite canopy was 10 times the rate for adjacent bare ground.

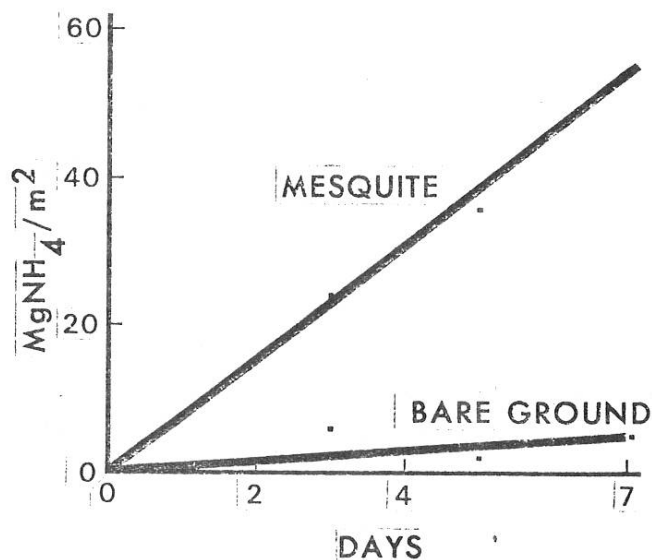


Figure 5. Comparison of rates of ammonia evolution from soil under mesquite canopy and bareground. (DSCODE A3U0A02)

Deaminase activities were also determined during the sampling period. Representative data are shown in Tables 1 and 2. The first samples taken prior to the onset of summer rains and after a prolonged drought had similar activities. However, after soil moisture increased, deaminase activities increased 3 to 4 times and remained at the higher levels throughout the sampling period (Tables 1 and 2). Deaminase activity in playa water samples were comparable to activities observed in wet soils from bajada and playa sites (Table 3).

Table 1. Deaminase activities in bajada soil

Date	Sample Site*					Soil Moisture
	A	B	C	D	Mean	
6-27	50**	60	60	63	58	92 †
7-8	240	70	220	85	154	20
8-1	242	198	198	162	200	0

* Sites were on a north-south transect.

** $\mu\text{g NH}_4$ produced in 24 hr (DSCODE A3U0A02).

† Soil moisture in negative bars.

2.3.4.4.-8

Table 2. Deaminase activities in playa soils

Date	Sample Site*					Mean	Soil Moisture
	A	B	C	D	E		
6-7	72**	58	72	69	86	71	92 †
7-17	190	250	250	190	190	412	0
7-20	142	162			192	165	0
7-28	122	162	252	172		177	0
8-1	262	322	222	182	142	226	0
8-8		198	142	122	198	165	10

* Sites were on a north-south transect.

** $\mu\text{g NH}_4$ produced in 24 hr (DSCODE A3U0A02).

† Soil moisture in negative bars.

Table 3. Deaminase activities on playa water samples

Date	$\mu\text{g NH}_4$
7-21	42*
7-22	179
7-23	262
7-24	262
7-25	398

* $\mu\text{g NH}_4$ produced in 24 hr (DSCODE A3U0A02).

Although deaminase activity was relatively uniform with respect to horizontal distribution in playa and bajada soils, there were differences in vertical distribution. In Table 4 it can be seen that in bajada soil activity decreased sharply between 5 and 20 cm whereas activity in playa soils was constant over the same depth. The reasons for the difference in vertical distribution of activity are not known.

Amino acids were deaminated immediately when added to soil. As shown by typical results in Figure 6, there was no lag in ammonia formation and the rate of ammonia formation was linear over the 24 hr incubation period. Apparently the potential for deamination is maintained in soils for long periods of time since the data shown in Figure 6 were taken with soil samples which had moisture potentials of less than -130 bars.

Table 4. Vertical distribution of deaminase activity in desert soils

Location	Depth in cm		
	5	10	20
Bajada	34*	20	13
Playa	130	140	140

* $\mu\text{g NH}_4$ formed in 24 hr (DSCODE A3U0A02).

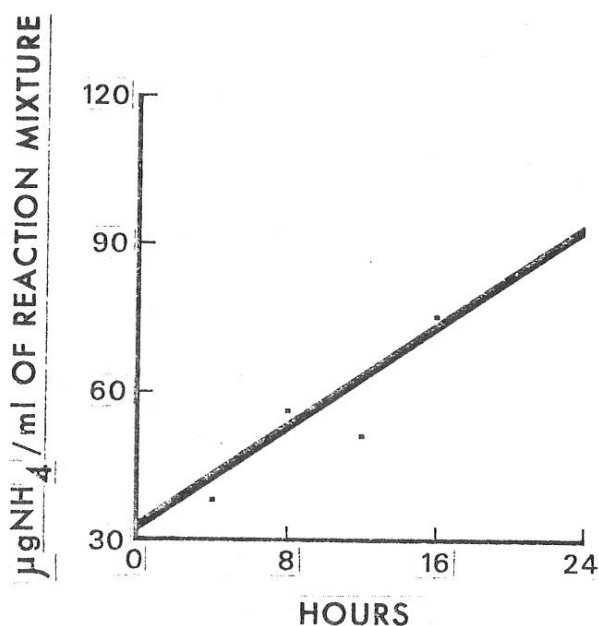


Figure 6. Rate of deaminase activity in bajada soil. (DSCODE A3U0A02)

The current results clearly show the necessity of obtaining adequate field data to corroborate laboratory results. Most laboratory work is done under controlled conditions in which temperature, moisture, etc., are maintained at constant levels, whereas such conditions are rarely met in the field. The necessity for field data is most clearly shown by the fluctuations in ammonia volatilization observed during the past year. From laboratory work and the deaminase activity experiments it would be expected that ammonification of amino nitrogen is fairly constant under a given

2.3.4.4.-10

set of moisture and temperature regimes. However, the release of ammonia to the atmosphere is closely tied to the direction of soil water movement. That is, during periods of evaporation the rates of ammonia loss will be one or two orders of magnitude greater than during dry periods or during and immediately after rainfall. Apparently ammonia evolution is enhanced by evaporation.

Evidence was also obtained which shows that nitrogen loss is influenced by vegetation. Although only data comparing soils from under mesquite canopy and bare ground were obtained, the differences are sufficiently great that plant density and possibly identity should be considered in attempting to incorporate ammonia loss to the atmosphere in the nitrogen model. This is an area which should be investigated further at the various Desert Biome sites.

L I T E R A T U R E C I T E D

O'Brien, R. T. 1972. Proteolytic activity of soil microorganisms. US/IBP Desert Biome Res. Memo. RM 72-18.

1972 PROGRESS REPORT

DECOMPOSITION AND MINERALIZATION IN AN *Artemesia tridentata*
COMMUNITY IN NORTHERN NEVADA

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Research Memorandum, RM 73-39

MAY 1973

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A B S T R A C T

Litter fungal analysis through July, 1972, produced a list of 37 isolates. Identification was made to species when possible. *Aureobasidium pullulans* occurred with the greatest frequency in the spring. Preliminary observations revealed the presence of a successional pattern of fungi on the litter. Preliminary growth studies revealed the potential for understanding of the role of fungi in the decomposition of sagebrush litter.

During major decomposition activity there appeared to be a correlated increase in leaf nitrogen content. The rates of increase were similar regardless of the sample age. Several possible explanations for this increase are discussed briefly.

Carbon dioxide production showed a direct correlation with weekly rainfall. Higher rainfall resulted in greater CO_2 evolution until the onset of cold temperature, which presumably restricts microorganism activity. Maximum evolution recorded was on October 18 at $4500 \text{ mg CO}_2/\text{m}^2/24 \text{ hr}$.

Weight loss of bagged litter samples showed variable results. There was an initial loss of weight of all 2 g subsamples after placement in the field. The greatest weight loss occurred in those samples placed in the field from July to September. Monthly weight loss was greatest for all samples during the August-October period, in some cases being about 0.4 g.

INTRODUCTION

The purpose of this project was to provide data on rates of decomposition and mineralization of *Artemisia tridentata* Nutt. under field and laboratory conditions in order to establish mineral cycling rates through the leaf litter compartment by microbial decomposition and leaching. Rates of turnover of N, P, K, Ca, lignin and cellulose, were to be determined in an attempt to correlate them with decomposition. Fungi isolated from the litter were to be used to establish successional patterns, unifungal decomposition rates, and rates of growth under a range of environmental conditions representative of field conditions. In mid-1972, at the request of the microbiological studies Coordinator, the objectives of the study were altered to better fit into the research objectives of the Biome. The continuation of the project into 1973 will emphasize the rate of organic matter breakdown expressed in terms of controlled variables, as well as the rate of C and N release from organic matter, chiefly *A. tridentata* material.

OBJECTIVES

The primary objectives of the original proposal were:

1. Analysis of fresh litter for N, P, K, Ca, lignin and cellulose content.
2. Analysis of decomposing litter of known age for N, P, K, Ca, lignin and cellulose content.
3. Rates of release of minerals from leaf litter under controlled laboratory conditions.
4. Weight loss of decomposing leaf litter on a monthly basis.
5. Isolation and identification of fungi from fresh and decomposing leaf litter.
6. Determination of fungal succession on decomposing leaf litter.
7. Rates of decomposition of leaf litter by mixed and unifungal cultures under controlled laboratory conditions.

In July, 1972, the project direction was changed to eliminate the analysis of P, K, Ca, lignin and cellulose and the isolation of fungi for further laboratory work. The primary objectives for 1972/1973 became:

1. Determination of the rate of litter break-down of *Artemisia tridentata* as a function of the time of initial placement in the field and meteorological variables.
2. Determination of rates of transfer of carbon and nitrogen from litter to ammonia, carbon dioxide, organic nitrogen and organic carbon, and, when possible, their disposition into the several compartments or pools of the system including soil, atmosphere and decomposer accumulation.

3. The rate of organic matter break-down in terms of controlled variables, as well as the rate of C and N release from organic matter, chiefly *Artemisia tridentata*.

The three objectives above constitute continuing ones for the duration of the project. The types of litter analyzed during 1973 will be expanded.

METHODS

Experimental design

Artemisia tridentata is an evergreen shrub which loses leaves throughout the year (Mack, 1970). The experimental design incorporates a monthly collection of leaves to be bagged, returned to the field, and retrieved at monthly intervals for analysis.

A site was selected upon the recommendation of USDA personnel as being very typical of the big-sage habitat. The site was 24 miles north of the University of Nevada at the junction of Highways US 395 and California State Route 70 at Hallelujah Junction, Plumas County, California, elevation 4950 ft. The site is adjacent to an ARS enclosure, providing access to some long-range meteorological data as well as better security for field equipment, in an area classed as sagebrush steppe (Kuchler, 1964).

A plot 12 x 12 m was arbitrarily selected and staked into meter squares for ease of placement and recovery of randomly-placed litter samples (Fig. 1). Adjacent areas provided 3 secondary or auxiliary plots used for additional studies (i.e. soil pits, litter traps, monitoring of soil and litter relative humidity, etc.).

Once a month a 12-channel YSI telethermometer was used to monitor soil and litter conditions hourly over a 24-hour period in identified micro-habitats in the main plot, the data located on Data Set A3UCHO2. Additionally, 2 max/min thermometers, 2 hygro-thermographs (of the latter, one was placed under a shrub, the other in a standard weather shelter) and rain gauge were installed in adjacent areas.

Monthly collections of fresh leaves were made, encompassing collection and placement for 12 consecutive months and retrieval lasting for 24 months. Short terminal branches were the source of the leaves. These are cut from shrubs in the area adjacent to the research plots and taken to the laboratory for drying, weighing and bagging.

In an adjacent plot 4 litter traps were constructed, 2 with open tops and 2 completely enclosing shrubs. Monthly collections are being made of litter either by hand or using a 12-volt automotive vacuum.

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Fresh litter collected in the field was air-dried at room temperature, weighed into 2 g units (sub-samples) and sewn into 1 dm² polyester bags with 1 mm² mesh. The bags were placed in the research plot in groups of 4 (a sample) in randomly-selected locations, except that areas without shrubs were avoided. Each month a suite (12 samples consisting of 48 subsamples) was placed in the field and a sample from each previously-placed suite was returned to the laboratory for analysis.

During the first part of the study 1 subsample from each sample returned to the laboratory was placed into a sterile container and used for fungal isolation and identification. Leaves from these bags were placed on 2 types of agar, Water Agar (H₂O) and fortified Corn Meal Agar (CM+). During the earlier months of the year they were incubated at both 12 C and 23 C. As colonies appeared on the agar they were isolated and, where possible, identified, then maintained as a pure culture for further work. Some indication was made of their frequency on the leaves; however, no attempt was made to make plate counts, etc. This portion of the study was discontinued in July, 1972.

The 3 remaining subsamples were kept separate and treated as follows. Each bag was weighed as it was brought into the laboratory (bag plus leaves and any foreign material). Leaves were then removed from the bag and, as much as possible, all foreign material removed, and fresh weight of the leaves recorded. The leaves were then allowed to air dry at room temperature and weighed, after which they were oven-dried at 45 C for 48 hr and reweighed. The weight data are on Data Set A3UCH01.

Total nitrogen content of the leaf litter was determined by the micro-Kjeldahl method as presented by Jackson (1958) and Bremner (1965), with modifications being made for plant material. Oven-dried (45 C) leaves were ground sufficiently to pass a 0.4 mm screen and weighed into approximately 0.5 g portions, then wrapped in cigarette paper. After drying a minimum of 2 days these samples were digested using copper (Cal-Pak Powder #2-Gunning Method) and a selenium catalyst (Hengar Selenized Granules). Distillation was carried out using a boric acid trap with the distillate being titrated with a 0.01 N sulfuric acid standard using N-point indicator.

Litter respiration in the field was monitored using bagged samples in order that respiration could be correlated with litter weight loss. The bags were placed in sealed plastic containers along with a vial containing a static 20 ml NaOH trap. Six samples (24 bags) and 12 controls were monitored for a 1-2 day period each week. Laboratory analysis of the NaOH uses titration with standard HCl after fixing with BaCl₂ and using thymolphthalein as the indicator (Coleman, 1971).

RESULTS

Figure 1 shows the distribution of the cover within the main 12 x 12 m plot. Most cover is provided by big sagebrush with some *Tetradymia canescens* DC (gray horsebrush). Several grasses are also present, but not mapped.

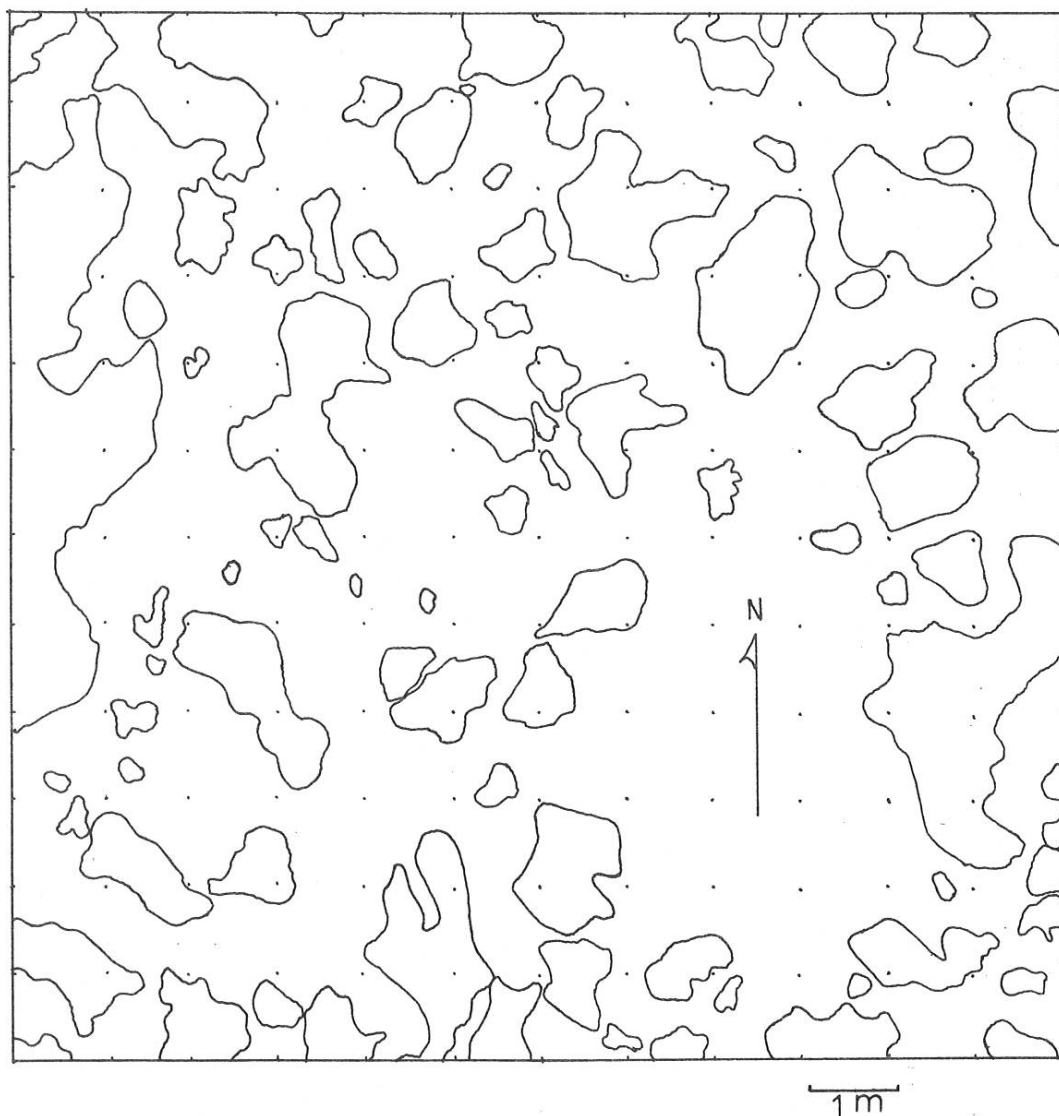


Figure 1. Map of the main 12 x 12 m plot showing shrub crown outlines plus the location of grid stakes.

Fungal analysis

Following is a list of the fungi isolated up to June, 1972, when the primary objectives of the project were modified.

Division Mycota

Subdivision Eymycotina

Class Zygomycetes

Order Mucorales

Family Mucoraceae

Mucor sp.

Family Thamnidiaeeae

Thamnidium anomalum Hess & Ander.

Class Ascomycetes

Order Spaaeriales

Melanomma subcatum Ell.

Unknown 1 sp

Class Basidiomycetes

Order Uredinales

Family Pucciniaceae

Puccinia absinthii (Hedwig.) DC

Fungi Imperfecti

Order Sphaeropsidales

Chaetodiplodia sp.*Diplodina tridentatae* Cooke & Shaw*Phoma* sp. (2 isolates)

Order Moniliales

Family Moniliaceae

Beauvaria sp. (2 isloates)*Penicillium* sp. (6 isolates)*Trichoderma viride* Pers.

Family Dematiaceae

Alternaria sp. (5 isolates)*Aureobasidium pullulans* (de Bary) Arnaud*Cladosporium* sp. (6 isolates)*Humicola* sp.*Nigrospora* sp.*Paecilomyces* sp.*Stemphylium* sp.

Family Tuberculariaceae

Epicoccum nigrum Link*Fusarium* sp. (2 isolates)

Although no attempt was made to quantify the numbers of each species present, notes were kept on the number of leaves on which each appeared. The most obvious change involved *Aureobasidium pullulans*. Every leaf plated from the April collection of the March suite produced 1-several colonies of *A. pullulans*. The May retrieval of the March suite showed about 50% of the leaves with *A. pullulans*. The June retrieval showed no colonies of this fungus, but no other species seemed to be dominant. Cursory examination of the July retrieval of the March sample showed a different, unidentified species appearing more frequently on all leaves. This pattern was also noted in the collections of the samples of other suites brought in during May, June and July.

Preliminary growth studies were undertaken on some of the fungal isolates utilizing a small incubator lacking adequate light, lighting control and temperature control. Variations in colony growth, production of reproductive structures, and by-products of metabolism appearing in the agar were observed.

During the study the presence of other fungi in or near the research plot were noted. The following fungi were recorded and collected for more positive identification:

Class Basidiomycetes
 Subclass Heterobasidiomycetidae
 Order Ustilaginales
 Family Ustilaginaceae
Ustilago gayophyti Hark on *Gayophytum ramosissimum* T & G
 Subclass Homobasidiomycetidae
 Order Agaricales
 Unidentified sp. 2
 Order Lycoperdales
Geastrum sp.
Tulostoma sp.
 Unidentified sp. 2
 Order Nidulariales
 Family Nidulariaceae
 Unidentified sp. 1
 Family Sphaerobolaceae
Sphaerobolus sp.

Sagebrush litter weight loss

Figure 2 presents the weight loss of bagged *Artemisia tridentata* leaves during the study period; Data Set A3UCH01. In all cases there was an initial loss of weight of the 2 g subsamples after they were placed in the field plot. The slopes of weight loss during the first month in the field were variable; the loss ranged from 2-16% of the initial weight. The slopes were lowest for the March and April samples, and greatest for the samples placed in the field from July-September. Weight losses for the second and following months were also variable.

The slopes of the curves may also be considered by monthly time intervals during the year. The May-June period shows greater weight loss than either of the adjacent monthly periods. The most consistently large weight loss, for all bags regardless of time of placement, occurs during the August-October period. For the August and September (fresh) samples this loss exceeded 0.3 g. For those samples which had been in the field for some time the loss was variable; two "older" samples also showed a weight loss equal to those placed in the field in the August-September period. Anomalous weight gains are evident for some of the samples.

Figure 3 presents the bagged litter weight loss during the study period on an oven-dried weight basis; Data Set A3UCH01. Weight losses during the first month in the field (calculated on this basis) are highly variable, showing an anomalous weight increase in several instances. Consistent weight losses are evident for all samples

2.3.4.5.-8

during the May-June period. With one exception, the greatest weight loss occurred during the August-October period. Weight loss on a fresh weight basis (Fig. 2) was the greatest during that period also. Weight losses were greatest for those samples which had been in the field for some time. Oven-dried weight equivalents of the 2 g air dry bagged litter ranged from 1.72 - 1.82 g.

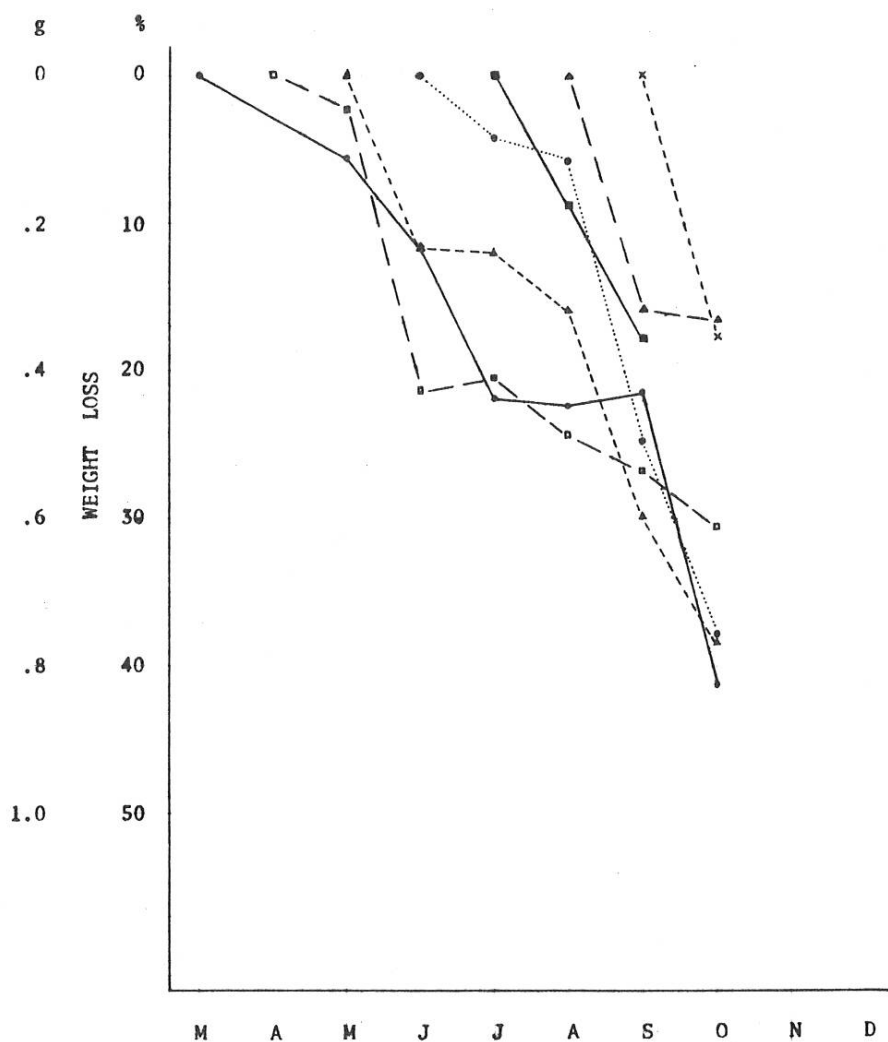


Figure 2. Weight loss of bagged *Artemisia tridentata* leaves on the soil surface as a function of time. Weight loss is expressed in grams and as a percent. Starting points for each curve represent initial placement of sample in field. Data based on initial air-dry weights of 2 g/sample. DSCODE A3UCH01

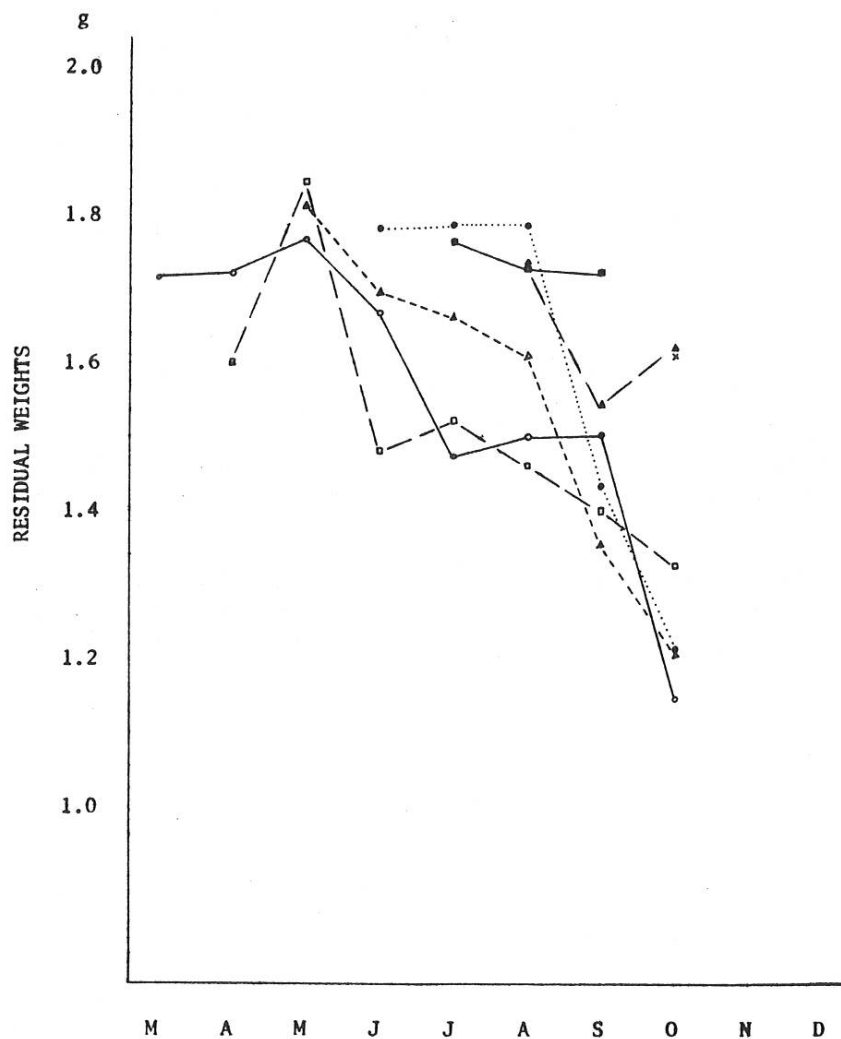


Figure 3. Residual weights of bagged *Artemisia tridentata* leaves on the soil surface as a function of time. Starting point for each curve represents initial placement of sample in field. Data based on oven-dry weight calculations. DSCODE A3UCH01

Litter nitrogen content

Although fluctuating, there was little variation in nitrogen content of the samples until the August-September period, when a sharp increase took place (Fig. 4). Samples placed in August and September show an immediate increase in N content. The increase in N content in this period corresponds with the increase in weight loss of the bagged litter (Fig. 2). The slopes of the curves of N content are very similar during this period, regardless of the time of placement of the samples into the field.

Carbon dioxide evolution from bagged litter

As shown in Fig. 5, weekly carbon dioxide evolution during the months of October and November, 1972, correlates directly with weekly precipitation, which was measured for the previous week on the date the CO₂ monitoring apparatus was set up. The week prior to the 18 October sampling period had the highest rainfall of the study period and also showed the greatest 24-hr CO₂ evolution from the bagged *Artemisia* leaves. The following two weeks the rainfall was only a trace and the CO₂ evolution was markedly reduced. In the week prior to 8 November an increase in rainfall again related directly to an increase in CO₂ evolution. Although precipitation the week prior to the 15 November sampling period was higher, it was in the form of snow, with associated lower temperatures. Low CO₂ evolution was recorded on 30 November corresponding with very little precipitation and below freezing temperatures.

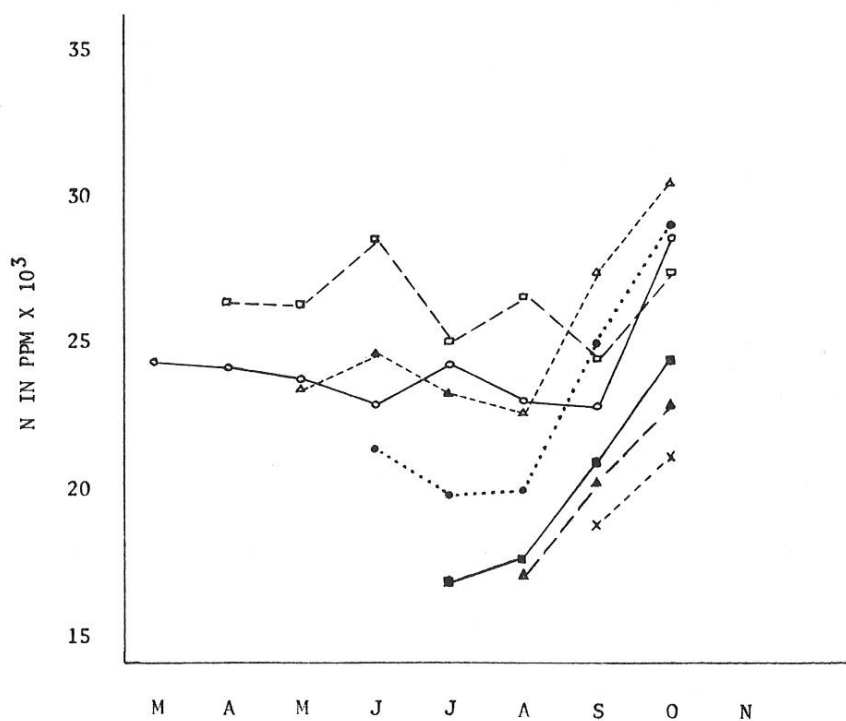


Figure 4. Total N content of bagged *Artemisia tridentata* leaves on the soil surface as a function of time.

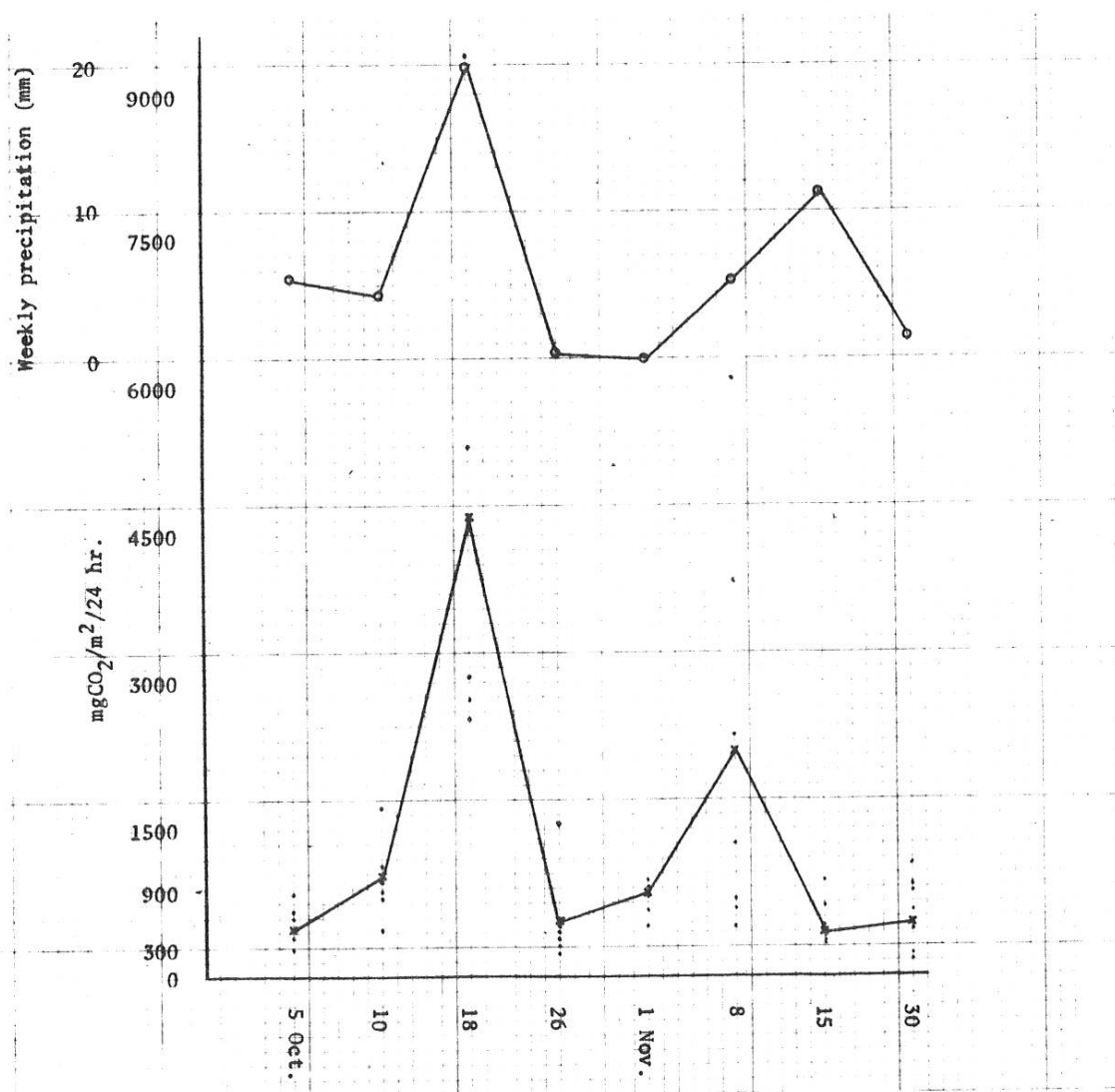


Figure 5. CO_2 evolution from bagged *Artemisia tridentata* leaves on the soil surface plotted against total weekly precipitation.

DISCUSSION

Fungal analysis

The study of successional patterns of fungi on decomposing leaves, and those fungi responsible for decomposition, was terminated in the early stage of the project. The results available are not sufficient to warrant the formation of any conclusions or lead to any meaningful discussion.

The preliminary growth studies showed the necessity of utilizing an incubator equipped with adequate light and diurnal controls for both light and temperature, should this portion of the study be resumed at a later time.

Litter weight loss, nitrogen content, and CO₂ evolution

It appears that during periods of major decomposition activity there is a correlated increase in leaf N content. Possibly, rather than being deposited into the soil or atmosphere during decomposition some of the N is being retained in association with the leaves. It is possible that as the decomposer organisms break down the leaves, this N is being concentrated by fungal action (and possibly the bacterial cells) so that when nitrogen analysis is carried out it is being detected in both leaves and decomposer organisms. Also, if relatively little nitrogen is utilized by the microorganisms or converted to other products (i.e., gas) a relatively high amount of N may still be present in the leaf tissue even though the weight of the remaining leaf has been reduced. Thus, the nitrogen content of a 0.5 g sample of decomposed litter would be higher than in a 0.5 g sample of fresh litter. Only additional study of both microorganism utilization of nitrogen and products of decomposition would help to provide the answer to the increase in N. The role of leaching still has to be investigated since the increase in nitrogen takes place during major moisture periods, indicating that leaching may not have too much of an effect.

EXPECTATIONS

The experimental design establishes the pattern of placement of samples for 1 year and retrieval for a 2-year period. The analysis of litter weight loss, N content and CO₂ evolution will continue for that period. It is hoped that some of the variations and unexpected phenomena will be explained as the picture of year-round decomposition becomes clearer.

Bagged litter samples will be expanded to include both root and stem litter, with the root samples being monitored *in situ*. Also, bagged litter will be buried to investigate the rate of decomposition in that type of environment.

Plans include the development of automatic micrometeorological recording instrumentation. The key emphasis will be on combining the results of detailed micrometeorological measurements with weight loss, C loss, N transformation, etc. Correlations obtained will be very specific. As an example, identified sub-samples are monitored weekly in the field for CO₂ evolution. These samples will be analyzed afterwards for weight loss and total carbon content.

Limitations to the decomposition process will also be studied and will involve the monitoring of decomposition in the incubator as well as the field, controlling the variables of temperature, relative humidity, substrate, and microorganism composition, which should allow a better understanding of the role of climatic conditions and the microorganisms in the overall decomposition process.

ACKNOWLEDGEMENTS

The authors would like to acknowledge their debt to Dr. Richard Gifford for his assistance with the micrometeorological work, and to Dr. Nellie Stark for her assistance with the nitrogen analyses.

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1972 PROGRESS REPORT

THE ROLE OF ALGAE IN CRUST FORMATION AND NITROGEN
CYCLING IN DESERT SOILS

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Research Memorandum, RM 73-40

MAY 1973

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Report Volume 3

Page 2.3.4.6.

A B S T R A C T

Algal-lichen crusts are shown to constitute a significant biomass component of the Curlew Valley region of northern Utah. Such crusts, even during minimum periods of productivity, represent up to 239 kg/ha biomass and cover approximately 70% of the desert soil surface. These crusts seem to contribute significantly to the total carbon fixation of the area and are capable of very rapid initiation of growth and carbon fixation when provided with moisture, even following an extended period of desiccation. Lag time for resumption of measurable photosynthetic activity is shown to be less than 30 minutes and may be as low as five minutes. Growth of the algal component of these desiccated soil crusts, following rewetting, is so rapid as to produce a doubling of biomass within a 24 hr period under conditions of continuous illumination and optimum temperature.

Revegetation of areas whose soil crust flora has been killed appears to be very rapid even during relatively dry periods of the year. Monitoring of manipulated and control areas *in situ* indicated a rapid response to moisture in regard to growth and carbon fixation of algal crusts.

In areas disturbed by cultivation the reestablishment of the algal-lichen crust is slow although the algal component, in free-living condition, rapidly establishes itself preceding the appearance of any recognizable lichen component.

The distribution and quantity of algal crust appears to be totally independent of vascular plant distribution.

INTRODUCTION

Soil crusts are prominent features in many desert areas, especially those where distribution of higher plants is sparse. In the majority of cases, soil crusts are composed of a tightly-packed community of microorganisms which are physically held together by the proliferating trichomes of blue-green algae and fungal hyphae. Algae are present wherever moisture is available during a part of their life cycle. Light, temperature, nutrients, pH, and other physical, physiochemical, and biotic factors are generally suitable for growth throughout the year if adequate moisture is present.

Soil algae may form extensive photosynthesizing areas in hot, cold and polar desert areas or in other extreme environments with respect to salinity or pH where no other chlorophyllous plants are evident. In arid and semi-arid areas, their importance has been noted in soil stabilization as well as protection against erosion, restriction of water penetration, evaporation, reclamation of salty land, and as primary colonizers of denuded, eroded or barren ground. Their resistance to desiccation and prolonged drought, and to extreme soil temperatures including diurnal freeze-thaw cycles, plays an important role. They are noteworthy forerunners to subsequent soil-surface establishment of mosses and seed-plants (Booth, 1941; Lynn and Brock, 1969).

A recent review has indicated that desert soil crusts and associated diaphanous materials provide ecological niches where environmental factors are much less restrictive than in the surrounding soil, and the algal abundance is increased (Cameron and Blank, 1966). The abundance and diversity of populations built up in these microniches and their algal components are an important source of organic matter (e.g., Fletcher and Martin, 1948; Lund, 1962; Shields and Durrell, 1964). It has been found that some soil crusts and some of the algal isolates from arid regions have the ability to fix atmospheric nitrogen (Cameron and Fuller, 1960; Mayland et al., 1966).

Since the investigation is primarily concerned with the algae of the area and since algae constitute a significant portion of the biomass of the lichen association, both free-living algae and lichen masses were recorded as cryptogamic crusts. This was required due to the virtual impossibility of effectively, quantitatively separating the free-living algal material from the lichen association and higher plant debris. In addition, the technique of estimating algal biomass is dependent on chlorophyll per unit surface area and does not distinguish between chlorophyll of algal-fungal associations and free-living algae.

OBJECTIVES

Objectives for the 1972 study are those appearing in the 1972 interim report of the Coordinator for Microbial Process Studies, Dr. Eugene Staffeldt. Those objectives specifically assigned to the current study are indicated below:

1. Determination of biomass of algal crusts.
2. Evaluation of the contribution of algal crusts to the nitrogen content of desert soils.
3. Determination of the percent of soil coverage by algae and algal crusts in relation to types of higher vegetation present.

Objectives 1 and 3 have either been fully accomplished or are currently in a state of on-going research. Objective 2 is currently being pursued but fulfillment has been hampered by technical difficulties. These are currently being overcome and data will be forthcoming during the next investigative period. Samples to determine the variation of soil-nitrogen content in response to algal activity have been collected but are currently pending laboratory analysis. Work will continue in all above areas to ascertain relative seasonal activities of the algal crusts with regard to the listed objectives as suggested by the project Coordinator.

Other objectives being pursued, and to some extent accomplished, during the 1972 research period include the following:

4. Establishment of recovery rates of algal crusts when surface organisms are killed *in situ*.
5. Establishment of the effect of soil moisture on the growth and decomposition of algal crusts.
6. Establishment of the time period required between rainfall events and resumption of photosynthetic (carbon fixing) activity by the algae of desert soils.
7. Establishment of the time period required between a rainfall event and resumption of growth by algal crusts.
8. Establishment of the relationship between soil moisture and algal productivity, carbon fixation and nitrogen fixation.
9. Determination of the contribution by the algal crusts to the carbon and nitrogen content of desert soils via leaching of these crusts during high moisture periods.
10. Determination of the parameters (pH, temperature, salinity, and nutrient availability) governing growth, carbon fixation and nitrogen fixation of the algal crusts.

2.3.4.6.-4

Data are presented in the following report indicating progress in the above-mentioned categories. Objectives four through eight have yielded significant data at the time of report submission, while work dealing with objectives nine and ten has only recently been initiated.

METHODS

Sampling procedures

Samples were removed from the investigative sites for subsequent laboratory experimentation or evaluation. Such samples were taken from the interspace areas between vascular vegetation. When experimentation or evaluation was in regard to quantification of values on an area basis, samples were harvested by means of a stainless steel cork borer of known diameter and the surface area of the sample calculated. All data gathered were from samples of the upper 1 cm of soil surface unless otherwise indicated.

Selection of investigative sites

These sites were selected to emphasize those areas exhibiting the most common dominant vascular vegetation of the region. One exception to this was the selection of a site characterized by crested wheatgrass, a commonly introduced forage plant of cold desert winter ranges. The locations of the intensive study sites are illustrated in Figure 1. Four investigative sites were established in southern Curlew Valley on the basis of vascular vegetation types present (two sagebrush, one grease wood and one crested wheatgrass site).

Determination of biomass

Samples of known algal surface area were homogenized in 90% acetone and extracted in the dark for 24 hr. Following extraction, the supernatant was cleared of debris by centrifugation or by filtration through glass-fiber filters. The supernatant was then decanted to a spectrophotometer tube and read at 665 m μ before and after acidifying with one drop of conc. HCl. The 750 m μ readings were subtracted from the 665 m μ readings in both pre- and post-acidified solutions to account for turbidity. In every case in which samples were filtered the 750 m μ readings were found to be stable before and after acidification. This portion of the technique will be omitted in the future. The corrected 665 m μ readings were used to calculate the concentration of chlorophyll in the sample according to the following equation:

$$C = \frac{26.73 (665_b - 750_b) \times (665_a - 750_a) \times V}{A}$$

Where 665_a and 665_b and 750_a and 750_b = O.D. of the acetone extract at the indicated wave lengths before and after acidification; V = volume in liters of extracting solution; and A = the area in m^2 represented by the sample. C = chlorophyll *a* in mg/m^2 .

The above method is discussed in more detail in the 1971 progress report (Lynn, 1972). The method itself is a modification of that presented in Standard Methods for the Examination of Water and Wastewater, 13th edition, 1971. All such extractions were performed in the laboratory whether on laboratory-grown or field-harvested crusts.

Previous work, also described in the 1971 progress report, indicated that the relationship between algal biomass and chlorophyll *a* content is expressed by the following equation:

$$B = \frac{84.2 \times (665_b - 665_a) \times V}{A}$$

Where B = algal biomass in kg/ha. The O.D., V and A were previously described.

Seasonal changes of algal crust biomass were monitored on a weekly or near-weekly basis along with rainfall and soil moisture. Samples to provide data regarding carbon and nitrogen variation were collected concurrently and a number of the carbon samples have been analyzed at this time. Other samples are awaiting analysis.

Since rates of productivity and decomposition were assumed to be of approximately equal magnitude in undisturbed cold desert communities, it was deemed necessary to manipulate selected study areas in such a manner as to provide an opportunity to observe these phenomena in other than a steady state system.

Experimental plots were selected for manipulation which were approximately $9 m^2$ in area. Once selected, these plots were gassed with methyl bromide (Dowfume MC-2) to kill all vascular vegetation and to radically reduce the numbers of viable algae, bacteria and fungi in the upper 5 cm of soil. The gassing procedure involved trenching the plot perimeter, covering with plastic sheeting and subsequent application of the gas from aerosol cans. The plastic coverings were left in place for 8 to 10 hr to insure penetration of the gas to subsurface levels (Figure 2). Prior to application of the gas, samples for microbial analysis were removed, and a second set sampled following the gassing process. These samples served as controls to determine numbers of microorganisms present immediately prior to and immediately following the gas application. An additional set of samples from an area in the immediate vicinity of the experimental plots was taken to insure that the experimental plots themselves were truly representative of the microbial populations of the selected sites. Samples from the untreated areas were designated as controls and appear in Table 2. Such samples were used to provide a base-line value to determine recovery rate and establishment of normal standing crop levels of both bacterial and algal populations.

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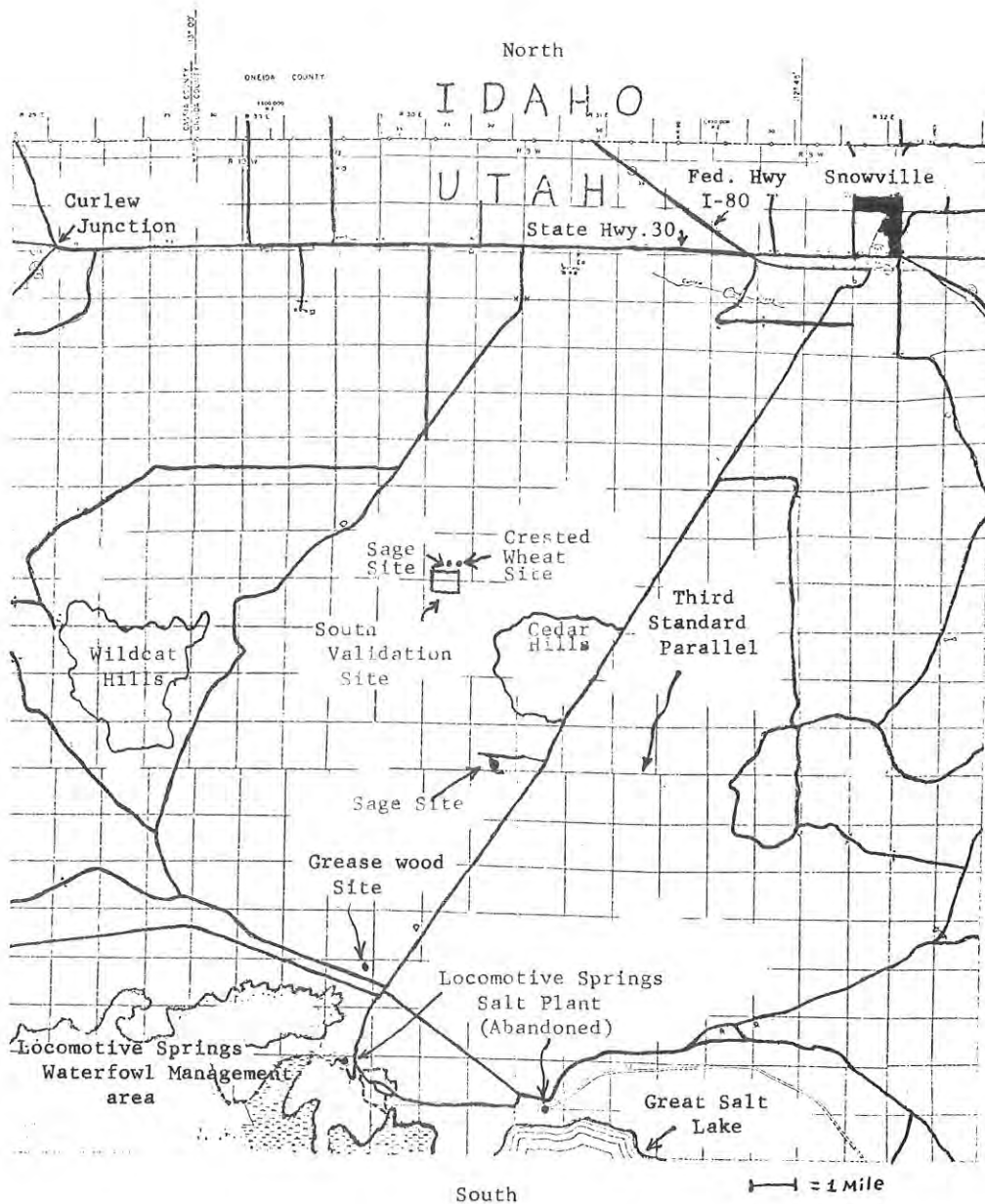


Figure 1. Approximate locations of intensive study sites of the southern Curlew Valley area.

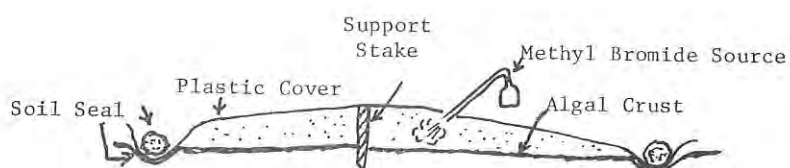


Figure 2. Illustration of methyl bromide gassing procedure.

Samples were analyzed for bacterial and fungal populations by plating on appropriate media. Algal numbers were established using dilution tubes prepared by addition of known weights of pre- and post-treatment soils. All determinations of algal numbers were made using a soil extract medium prepared by extracting one part soil from the investigative site with five parts glass-distilled water at 5 C for 48 hr and subsequently clearing of any microorganisms and particulate matter by filtration through a type HA 0.45 μ Millipore membrane filter. Dilutions were carried out on a ten-fold basis and the greatest dilution which yielded algal material was used to establish the number of algae present in the soil sample. All samples were taken from the upper 1 cm of surface crust.

Fixation of labeled carbon dioxide by algal crusts

Algal crusts were incubated in a vessel containing labeled carbon dioxide for selected time intervals. The reaction was halted by killing the algal material. Algal material and attendant soil were then dried and homogenized and subsamples of the homogenate suspended in counting cocktail and counted on a liquid scintillation counter. Results are reported in terms of counts/min/mg of chlorophyll. Determination of chlorophyll content is as previously described. A detailed presentation of the experimental procedure is provided in conjunction with the experimental design. All such experiments were conducted in the laboratory.

Determination of carbon content of soil-algal crusts

Algal crust samples collected as previously described were homogenized and assayed for carbon content by the Sawyer and McCarty modification of the method of Walkley (Sawyer and McCarty, 1967; Walkley, 1935).

Determination of surface cover by algal crusts

Line transects of 100 m were used to determine surface cover. Samples and/or observations were taken in the field as well as in the laboratory. Observation and sample intervals along the transect were at 1 m intervals.

Soil moisture determinations

Determination of soil moisture was conducted in the field at each of the sampling sites on a weekly basis during the summer months and at somewhat greater intervals during the late fall period. Determination was by means of a self-contained unit measuring the pressure of gas generated by the interaction of moisture in soil samples of known weight and a known weight of calcium carbide. Pressure readings were directly converted to wt % moisture readings by the unit at the time of sampling.

Precipitation

Precipitation data were supplied by Drs. Porcella and Fletcher, whose investigative sites were located within a few meters of those of the author.

Identification of algal genera

Identification of algal material was by microscopic examination of samples at the Utah State University Phycology Laboratory.

Resumption of growth by dry algal crusts

Resumption of growth of algal crusts was determined by placing crust material, which had been air-dried in the laboratory at 28 ± 5 C for a period of one year, in petri dishes lined with filter paper and rewetting with glass-distilled water (Figure 3).

Samples were removed at selected time intervals on an area basis by means of a stainless steel corkborer. Biomass was determined as previously described.

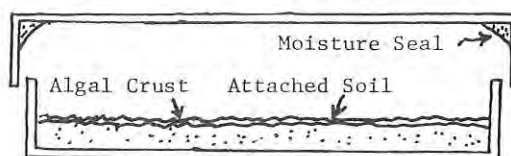


Figure 3. Incubation system used to measure resumption of growth of algal crusts following rewetting.

Resumption of photosynthetic activity of rewet algal crusts

Algal crust material was placed in a small (5 cm diameter), open, plastic petri dish which was in turn housed in a larger glass petri dish containing 0.1N HCl. The larger dish was covered with a suitable lid which had been ringed with silicone sealing compound to provide a gas-tight seal. Just prior to sealing of the larger dish the experiment was initiated by moistening the crust with glass-distilled water and the addition of 1 ml of (2 mc/ml) $\text{NaH}^{14}\text{CO}_3$ to the external acid solution to generate $^{14}\text{CO}_2$ (Figure 4). Lag time between addition of label and sealing of the vessel was less than two seconds.

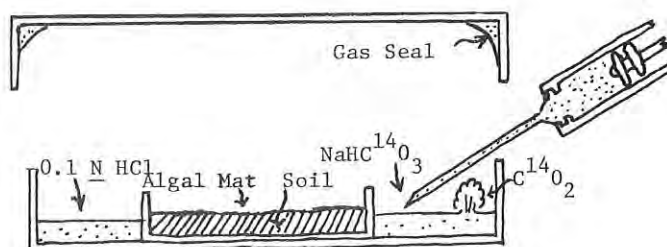


Figure 4. Incubation system used to measure photosynthetic activity of algal crusts following rewetting.

At the end of each incubation period the samples were killed by addition of 40% formalin to stop isotope incorporation and allowed to air-dry at 37 C to constant weight, usually about 24 hr. The material was then homogenized using a mortar and pestle. One g of the soil-algal homogenate was assayed for chlorophyll and duplicate 1 g sub-samples suspended in counting cocktail (15 ml Aquasol; 5 ml H₂O) and counted on a liquid scintillation counter for 10,000 counts or 10 min.

RESULTS

Estimation of algal cover and biomass *in situ*

One of the major objectives of the 1972 project was to establish the extent to which the surface soil of the Curlew Valley area is covered by algal soil crusts, and to determine the standing crop of these organisms in terms of kg/ha.

The most extensive of the surveys was conducted at the southern validation site. Using vascular vegetation maps prepared by Karl E. Holte of Idaho State University (Holte and Adamson, 1972) as a guide, the sites were surveyed by means of multiple 100 m line transects. Observations were made and samples removed at 1 m intervals along each transect. Presence or absence of visible algal crust was recorded in the field and samples were returned to the laboratory for microscopic examination and determination of biomass.

Figures 5 and 6 illustrate the location of the transects within the validation site and Table 1 presents the information collected.

Analysis of the data indicates that no correlation exists between the type of vascular vegetation present and the extent or character of the cryptogamic crust. However, the cultivated crested wheatgrass areas surveyed yielded a more homogeneous cover with regard to algal flora than did the sagebrush area which was rich in both algal and lichen cryptogams. Algal biomass in the crested wheatgrass areas was also much less variable than in the sage areas examined.

Visual examination in the field indicated an average of 71% algal cover for the sage area and 80% for the crested wheatgrass area. Biomass values for the sage area ranged from 95.7 kg/ha to 239 kg/ha and averaged 159 kg/ha. It should be pointed out that these data were collected in July, a period at which algal biomass values would be expected to approach their yearly minimum due to the very dry conditions which prevailed. A follow-up

analysis of standing crop of soil algae will be conducted in the winter and spring of 1973, periods during which it would be assumed that algal standing crop would be near maximum for these investigative areas.

Growth of algal crusts *in situ*

Studies of the growth rates of algal crusts were initiated in the early spring of 1972.

The percentage of kill for bacteria and fungi appeared to be in excess of 93% in all cases, with the majority of treatments resulting in kills of 98% or greater. Rate of kill for the algal component of the system was quite successful, yielding reductions of algal numbers in excess of 99% in all cases (Table 2).

In conjunction with this experiment the percent algal cover and algal biomass at each of the experimental sites were also determined and appear in Table 1.

Following treatment the sites were fenced and both the killed plot and an adjacent control plot were monitored on a weekly or near-weekly basis for algal biomass, soil moisture, carbon and nitrogen content. Soil moisture was determined for depths of 0-1, 2-3, and 4-5 cm. All other samples were removed from the upper 1 cm of soil on an area basis. Data presented for algal biomass and moisture content is current; however, a back-log of carbon and nitrogen samples exists at the time of submission of this report. Currently available data for each of the investigative sites are presented in Figures 7, 8, 9, and 10 (DSCODE A3ULA04).

Algal biomass appears to be at a minimum in Curlew Valley during the period extending from mid-July to mid-September. The onset of relatively regular and significant precipitation in late September and early October resulted in a distinct increase in algal biomass.

Data available at this time indicate that the algal biomass correlates with total carbon in the upper 1 cm. Figures 7-10 suggest that moisture content of the soil below 1 cm has little effect on algal production, compared to surface moisture. Algal biomass increased rapidly following any significant rainfall event during the period of this study.

Plots treated with methyl bromide showed little variation with respect to untreated control plots. This may be the result of several factors. First, it is possible that the techniques employed are not capable of resolving the variations which exist. This is not, however, thought to be the case since previous application of this method has

been successful. A second explanation is that the chlorophyll content of the killed algae, upon which our estimation of biomass hinges, may not have had sufficient time to degrade, perhaps due to lack of moisture required to support the activities of decomposers which are essential to the breakdown of the material. If this is the case it is expected that as moisture becomes more available and temperature rises with the onset of the spring of 1973, a divergence in algal biomass will be observed with regard to the treated and control plots. It should be mentioned that in recent field observations of control and treated plots following a rainfall event it was very apparent, even to several untrained observers in the party, that the untreated control areas quickly developed a bright green appearance while the adjacent treated plots remained a dull gray, characteristic of all plots prior to rewetting.

Initiation of growth by desert algal crusts following rewetting

Considerable controversy has existed among investigators regarding the rapidity with which desert algal soil crusts and lichen flora resume growth, photosynthesis and nitrogen fixation following a rainfall event.

These experiments were conducted to establish the lag time following rewetting and resumption of growth and to establish the lag time between rewetting and the onset of measurable photosynthetic activity.

All values are reported in terms of kg per ha (Figure 11). Pertinent controls were included in the experiments and are indicated in conjunction with the Figures supplied.

It should be pointed out that by using algal-lichen crusts which had been subjected to an extended period of dessication one must consider the values obtained for recovery times to represent minimum recovery rates of the organisms under what might be described as very adverse preconditioning treatment.

Controls which had not been rewet showed no change in biomass whether in light or darkness; however, the rewet control placed in the dark exhibited a decrease in algal biomass over the course of the experiment. This decrease has been attributed to death and decomposition of algal cells by heterotrophic organisms such as bacteria and fungi present in the samples which must be assumed to have resumed activity concurrently with the algal component under study.

Table 1. Transect Results

Zone Number	Vegetation Type	Quadrats Surveyed	Percent Algal Cover	Algal Biomass (Kg/ha)
1*	<i>Agr cri</i> ** <i>Atr con</i> <i>Sit hys</i>	12 14-15 33-34	80	96
2*	<i>Agr cri</i> <i>Atr con</i>	09 38-39 55-56 64-65	80	96
3*	<i>Agr cri</i>	58 72 77 84-85	80	97
4	<i>Agr cri</i>	01	80	97
5	<i>Art tri</i> <i>Atr con</i> <i>Chr vis</i> <i>Sit hys</i>	05-06	82	144
6	<i>Art tri</i> <i>Atr con</i> <i>Sit hys</i>	09-10 12-13 25-26	74	144
7	<i>Atr con</i> <i>Sit hys</i>	24-33	61	192
8	<i>Art tri</i> <i>Atr con</i> <i>Chr vis</i> <i>Sit hys</i>	29-30 47-48	73	191
9	<i>Art tri</i> (dead) <i>Sit hys</i>	41-51-52	73	96
10	<i>Art tri</i> <i>Atr con</i>	56-66-65	78	169
11	<i>Art tri</i> <i>Atr con</i> <i>Chr vis</i>	57-58 67-68	78	216
12	<i>Art tri</i> <i>Ely cin</i>	59-60	80	167
13	<i>Art tri</i> (dead) <i>Hal glo</i>	86-87 94-95	41	96
14	<i>Art tri</i> <i>Sit hys</i>	81-91	67	96
15	<i>Sit hys</i>	91-92	70	239

*Zones 1-3 are located in the Southern Validation Grass Area while zones 4-15 are located in the Southern Validation Sagebrush Area

**Abbreviations used as indicated below:

Agr cri = *Agropyron cristatum*
Art tri = *Artemisia tridentata*
Atr con = *Atriplex confertifolia*
Chr vis = *Chrysothamnus viscidiflorus*

Ely cin = *Elymus cinereus*
Hal glo = *Halogeton glomerata*
Sit hys = *Sitanion hystrix*

Table 2. Effect of methyl bromide treatment on microbial populations

Site	Average Total Number of Bacterial Colonies			
	Sage 1	Sage 2	Greasewood	Crested Wheat
Before	152×10^5	45×10^5	126×10^5	39×10^5
After	171	203×10^3	540	673×10^2
% Kill	99+	93	99+	98
Control	149×10^5	51×10^5	106×10^5	49×10^5
Medium used: Euglena Agar				
Before	71×10^5	40×10^5	32×10^5	51×10^5
After	329	75×10^2	24×10^2	94×10^3
% Kill	$\alpha 100$	99	99	98
Control	26×10^5	41×10^5	29×10^5	48×10^5
Medium used: Burk's N-free Agar				
Site	Average Total Number of Fungal Colonies			
	Sage 1	Sage 2	Greasewood	Crested Wheat
Before	17×10^5	64×10^5	30×10^4	37×10^5
After	86	21×10^2	86×10^1	42×10^2
% Kill	$\alpha 100$	$\alpha 100$	$\alpha 100$	$\alpha 100$
Control	6×10^5	7×10^5	51×10^5	29×10^5
Medium used: Euglena Agar				
Site	Average Total Number of Algae Per Gram Soil			
	Sage 1	Sage 2	Greasewood	Crested Wheat
Before	10^5	10^5	10^5	10^5
After	10^2	10^2	10^2	10^2
% Kill	99	99	99	99
Control	10^5	10^5	10^5	10^5
Medium used: Soil-water extract				

SOUTHERN VALIDATION SITE - SAGEBRUSH AREA

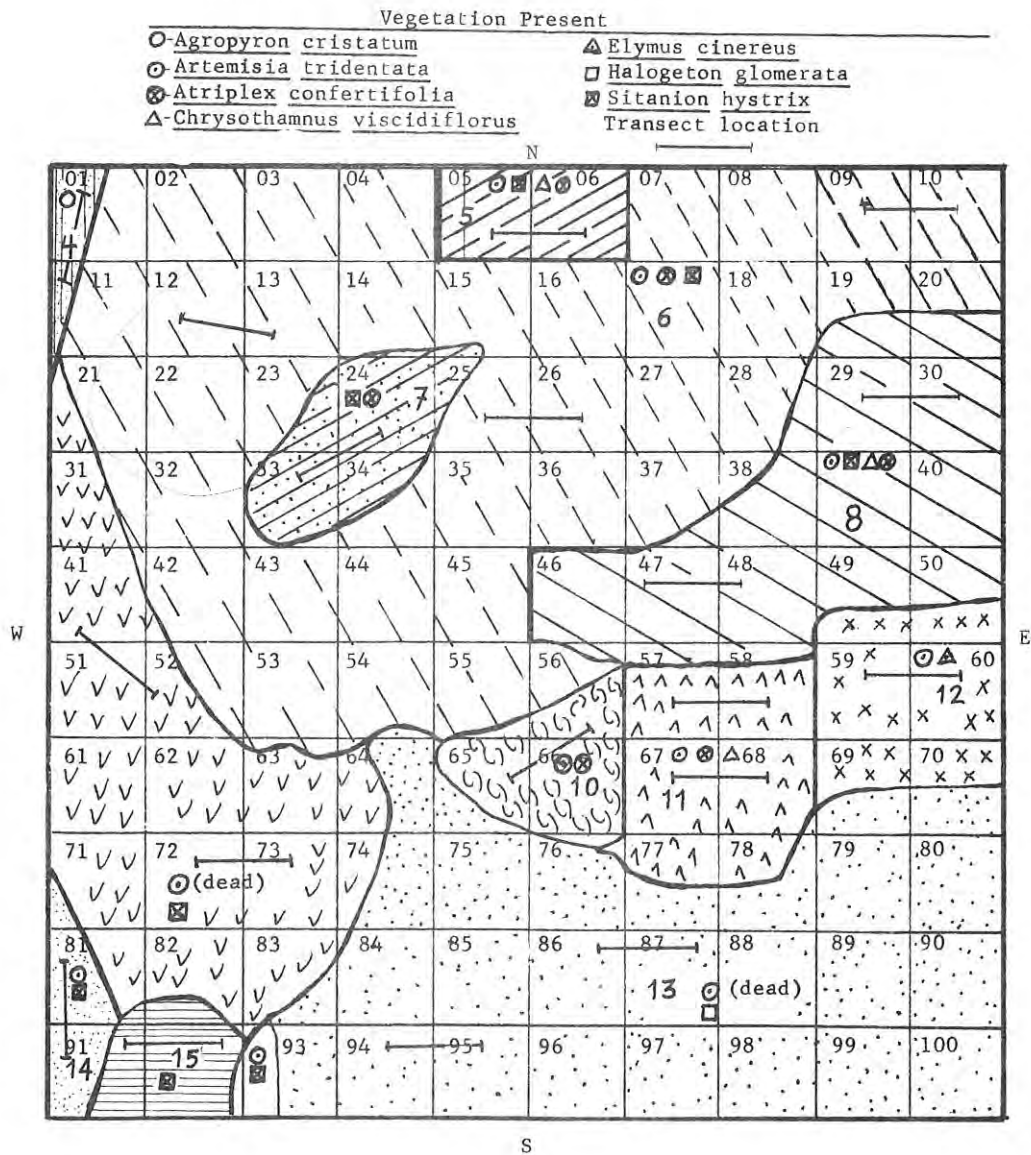


Figure 6. Transect locations in southern sage area.

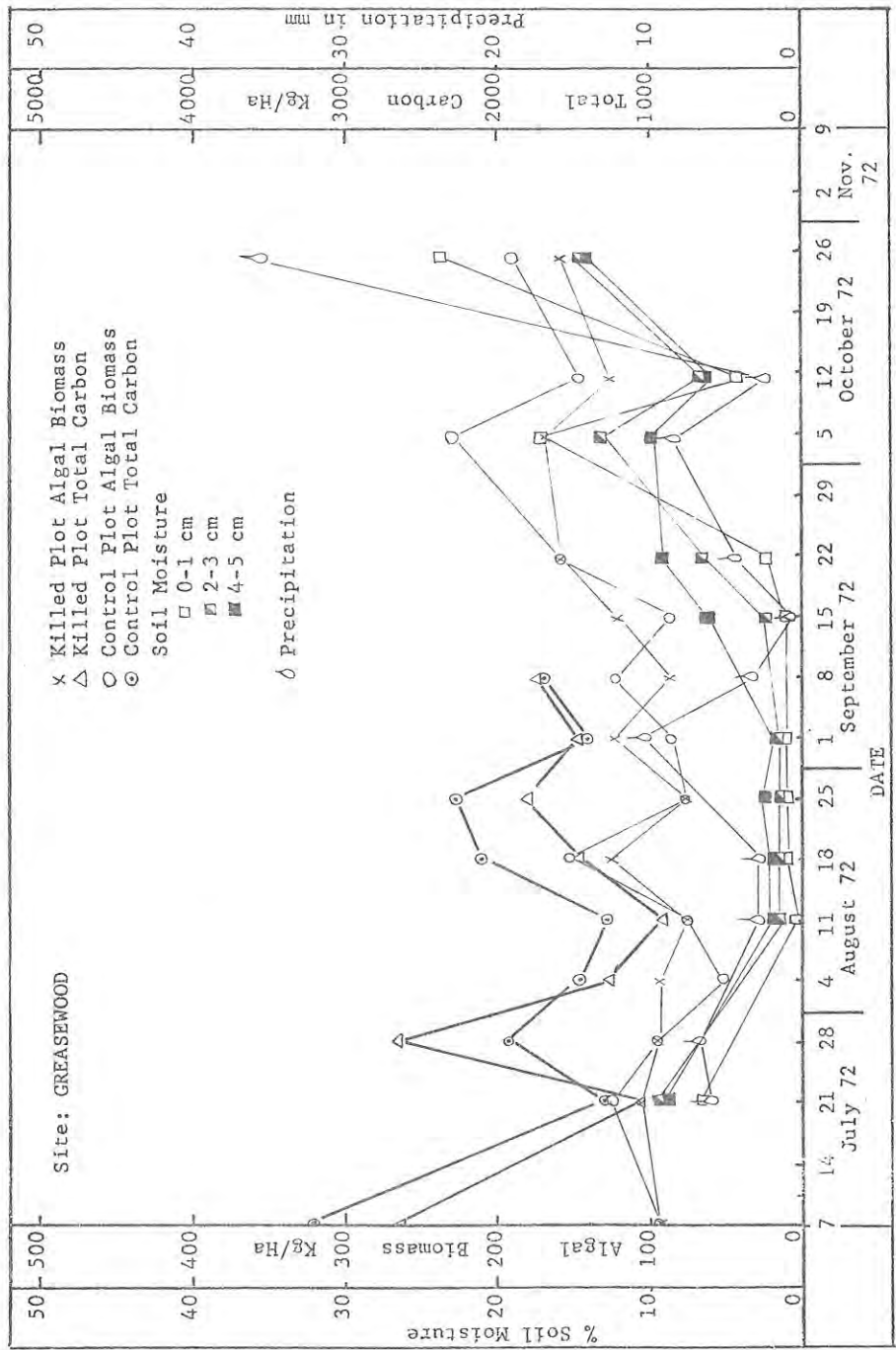


Figure 7. Biological and physical events recorded at the Greasewood intensive study site.

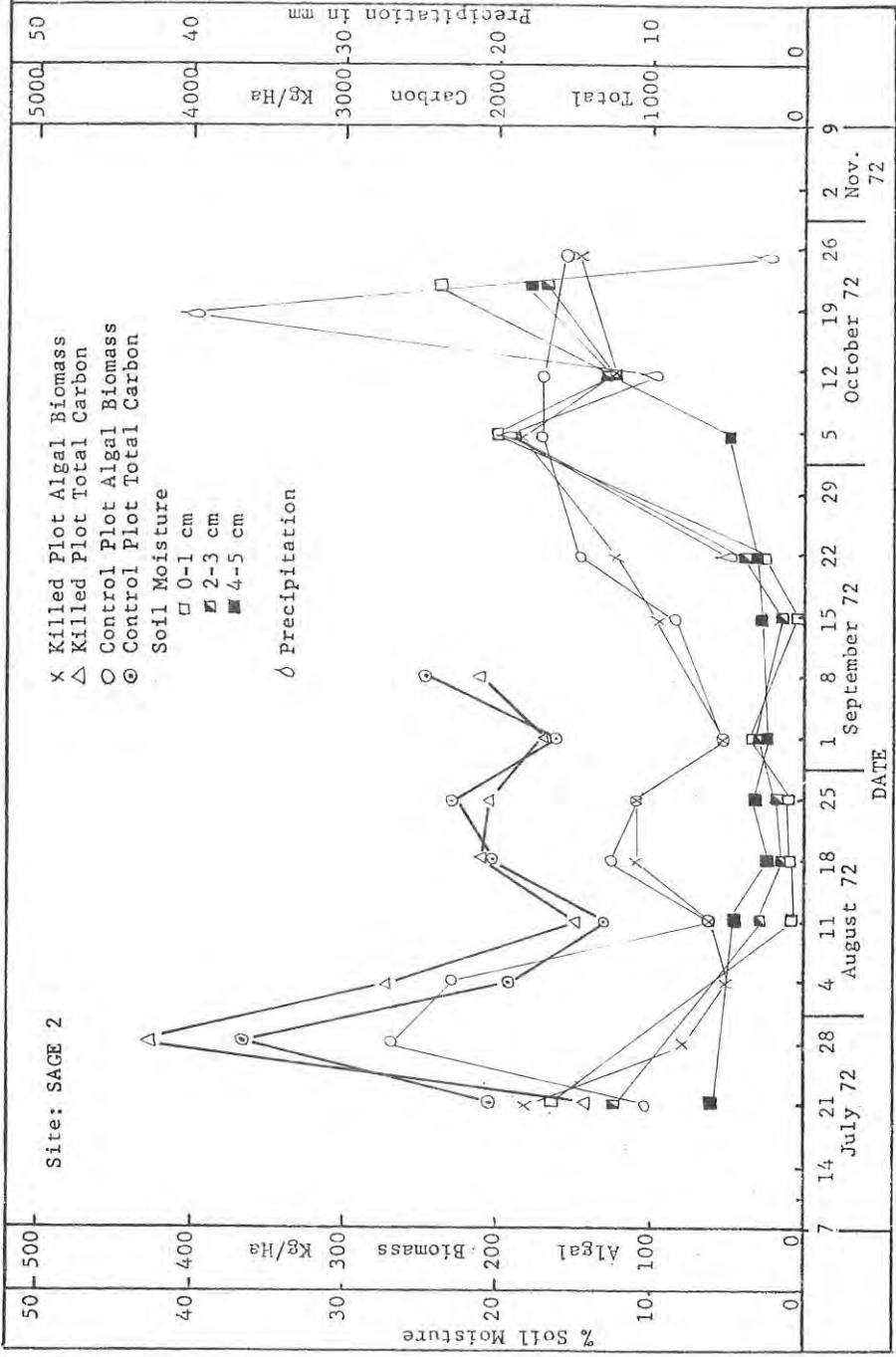


Figure 8. Biological and physical events recorded at the sage 2 intensive study site.

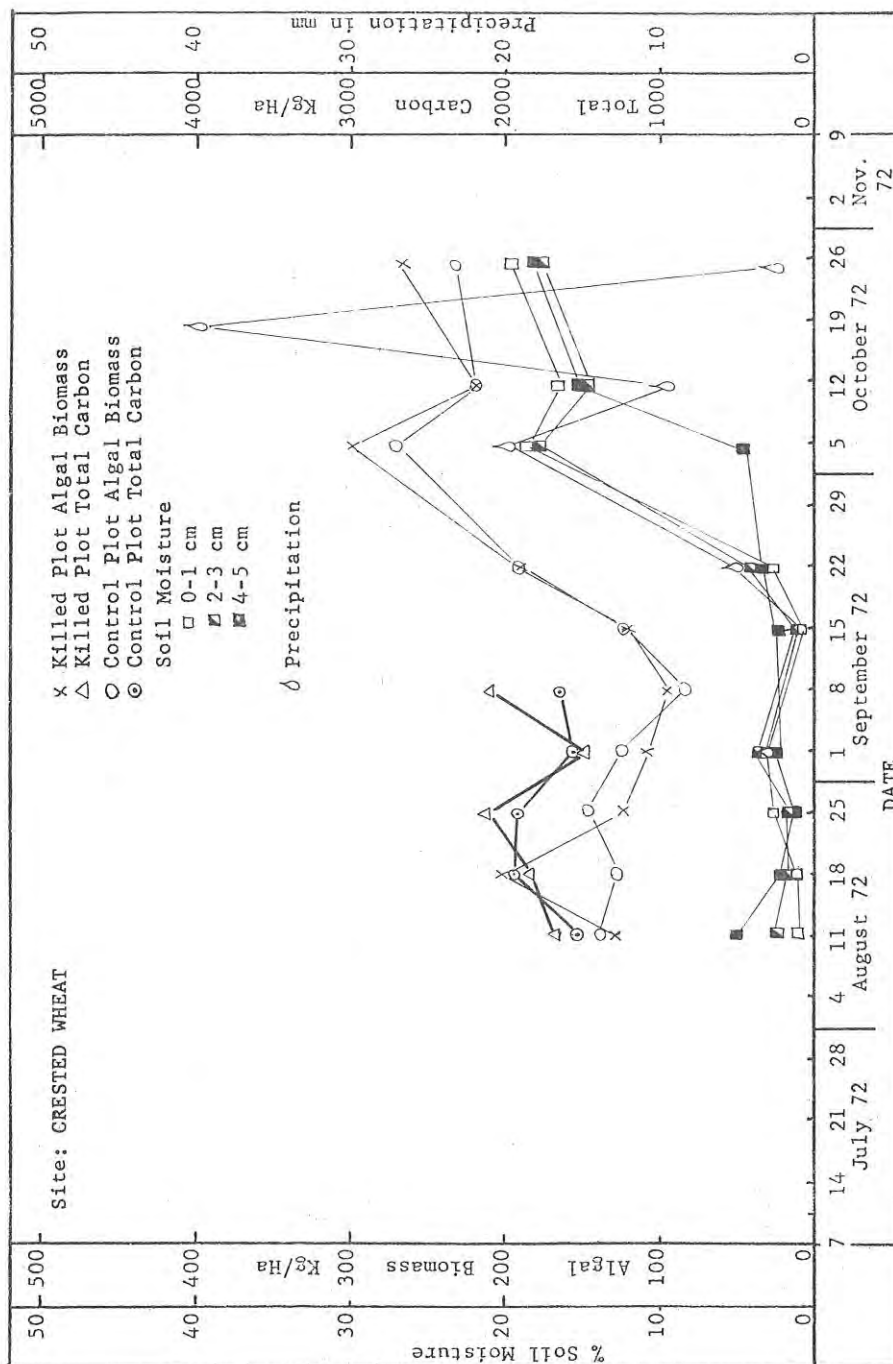


Figure 9. Biological and physical events recorded at the crested wheat study site.

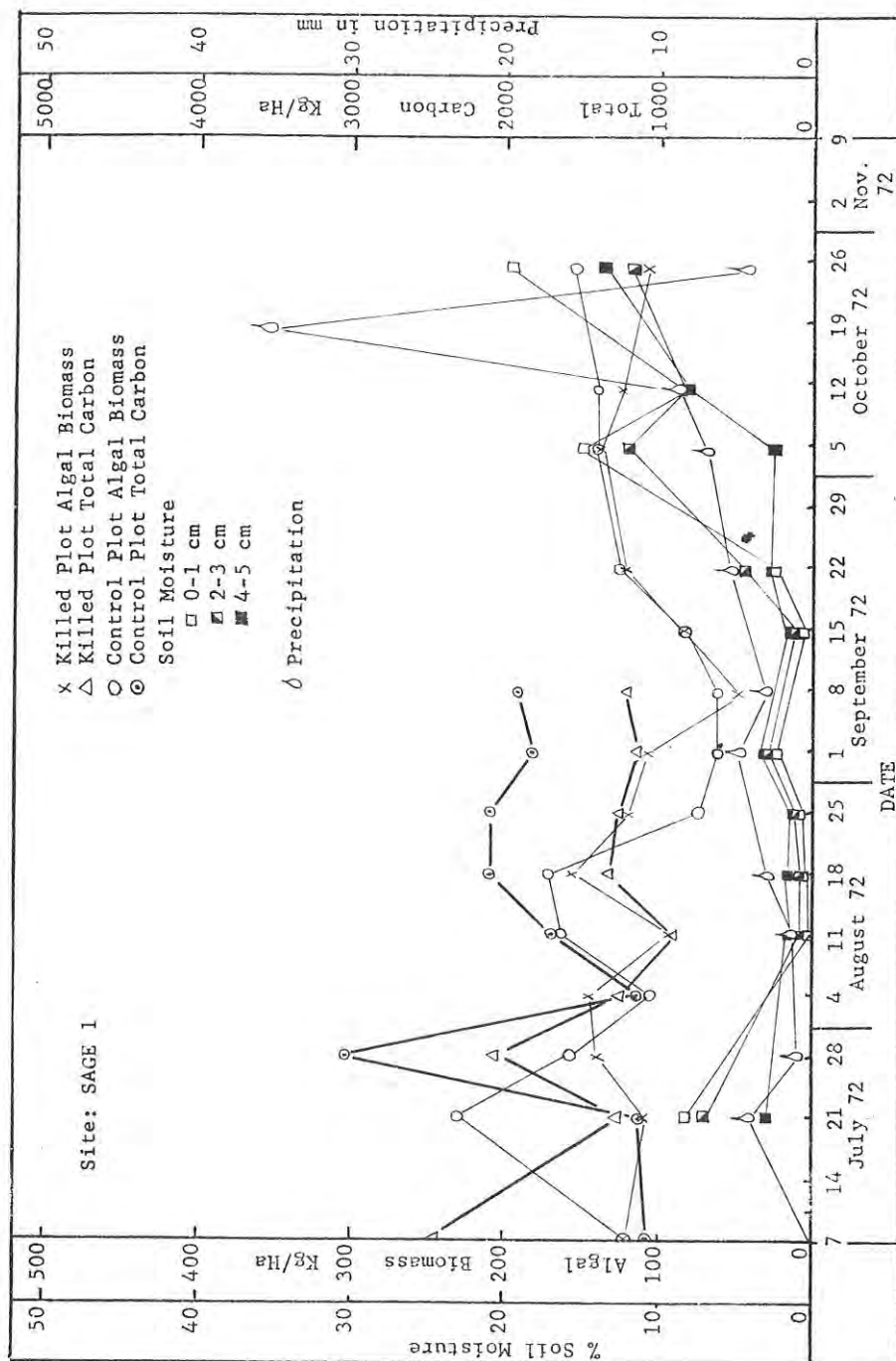


Figure 10. Biological and physical events recorded at the sage 1 intensive study site.

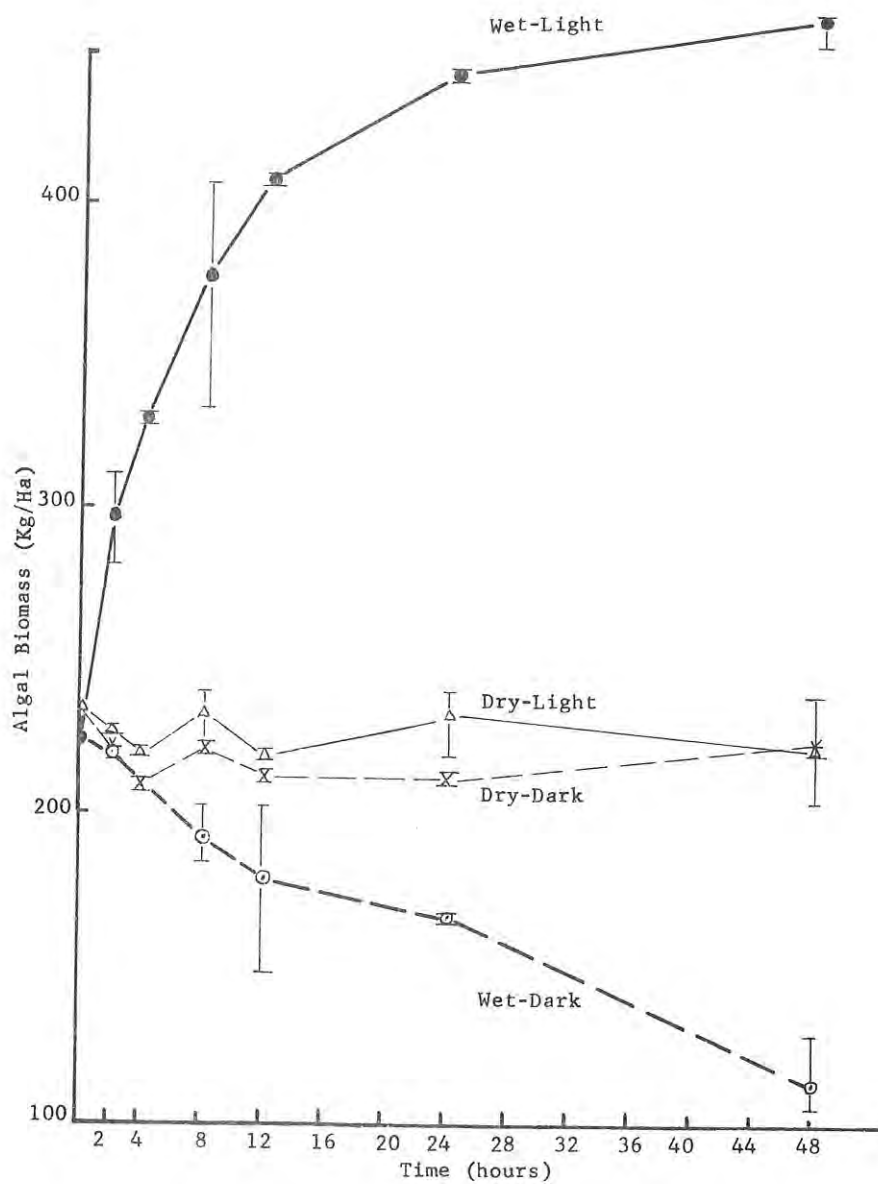


Figure 11. Increase in algal biomass following rewetting of algal crust.

The very rapid initial increase in algal biomass of the system tapered off sharply after 24 hr and virtually plateaued in 48 hr. This truncation of growth is not, however, thought to be the case under field conditions. The decreased growth rate apparently reflects a limitation of available carbon dioxide as a result of the experiment being carried out in a sealed vessel whose gas volume was quite restrictive relative to the rather large amount of algal material present. It is possible that some other, non-defined factor was responsible for early flattening of the curve. Other experiments are currently underway to resolve this question.

It is apparent that the rate of increase in primary producers in the light surpasses their rate of decomposition under conditions of either light or darkness. Under field conditions the time course of the experiments would represent four daylight periods of 12 hr each of four "natural" days, while the dark phase of the experiment would represent four consecutive natural nights.

It is apparent from the data that the increase in biomass of algal crust material occurs rapidly following rewetting and the obvious inference is that photosynthetic "tool-up time" for the algal crust is quite short, only a matter of minutes. This is not however, proven by the experiment.

Initiation of carbon fixation by algal crusts following rewetting

In order to examine the lag time between rewetting and the onset of carbon fixation (photosynthesis) by the algal crust the previously-described experimental design was altered to allow for addition of radioactive carbon dioxide to the system. Results were expressed in counts/min/mg chlorophyll to adjust for variation in algal content from reaction vessel to reaction vessel (Figure 12). See Figure 4 (page 9) for methodology.

No significant photosynthetic activity was observed during the first 10 min following rewetting, counts from light-incubated cultures being equivalent to those of controls. After 30 min of incubation, however, cultures incubated in the light showed marked uptake of label which continued for 24 hr. The initial, rapid uptake was followed by a decline in rate and probably reflects a limitation of label-enriched carbon dioxide in the reaction chamber during the course of the experiment. Nevertheless the experiment clearly indicates that a relatively short tool-up time is required for the initiation of photosynthetic activity and incorporation of carbon by the desert algal crusts examined.

Experiments employing these techniques are currently underway to establish the effect of pH, salinity, and temperature on carbon fixation by algal crusts.

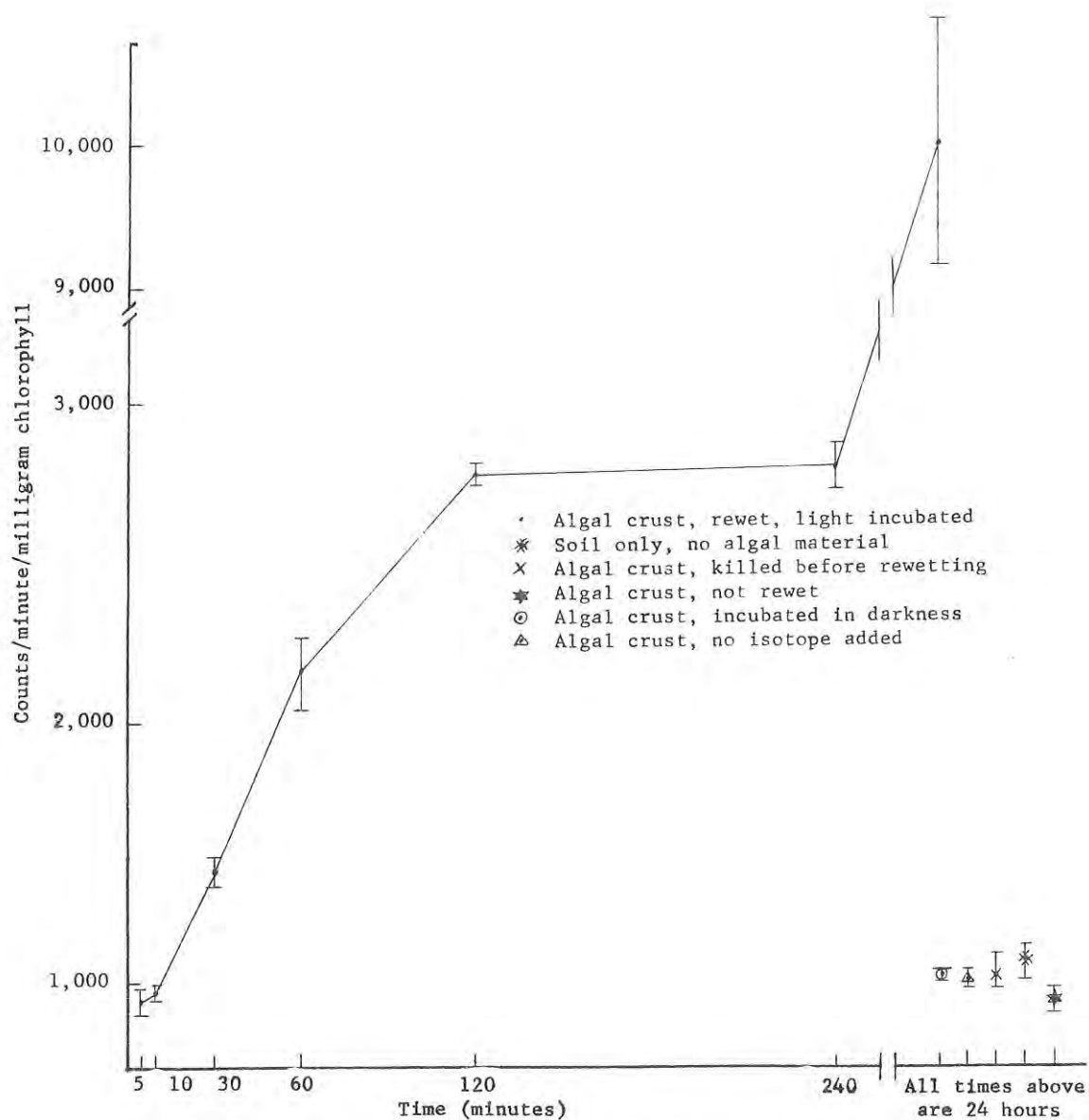


Figure 12. Initiation of carbon fixation by dried algal crusts following rewetting.

DISCUSSION

Techniques developed during the 1971 research period have been employed during the 1972 period with considerable success under both field and laboratory conditions. It is clear from observations during the current investigative period that algal crusts contribute significantly to the soil surface carbon content and overall biomass values of the cold desert ecosystem. Predictions from preliminary experimentation during 1971 have been verified by field and laboratory activity during the current research period.

Although not mentioned in this report, the investigators have developed the means by which the algal component of the soil crust system can be grown and harvested in quantity under laboratory conditions. This will greatly facilitate examination of the effects of pH, salinity, temperature and other environmental parameters governing growth of algal materials.

Establishment of the exceedingly short tool-up time required for initiation of photosynthetic activity and growth of the algal crust organisms suggests that they may be of great importance in terms of short-term carbon and nitrogen additions to the surface soils of cold desert regions.

The establishment of the rapid upsurge in carbon fixation following rewetting of dry algal crusts may account for the relatively high values for heterotrophic organisms, particularly bacteria and fungi, reported in the upper 1 cm of soil in the progress report of 1971 research (Lynn and Cameron, 1972).

While it has not yet been proven, it is to be expected that a similar rapid initiation of nitrogen fixing activity exists for the algal soil crust and this nitrogen production may prove very important in terms of degradation of higher plant litter on surface soils by way of providing a favorable C:N ratio for decomposer activity. It is noteworthy that the algal symbiont of *Collema tenax* is *Nostoc*, a known nitrogen fixing blue-green alga, and that most other gelatinous lichens, of which both *Dermatocarpon* and *Fulgensia* are representatives, are known nitrogen fixers (Henriksson, 1951, and Scott, 1956). *Nostoc* also exists as a free-living alga and by simple microscopic examination of the soil crusts appears to constitute roughly 0.5% of the algal soil crust component at the investigative sites.

EXPECTATIONS

Work will continue in the areas presented in this research report, especially in the area of nitrogen fixation by algal crusts. Facilities are now available for this research, and techniques employed by Dr. Don Porcella to measure nitrogen fixation under field conditions will be implemented as part of our program.

The monitoring of the manipulated investigative sites with regard to changes in algal biomass, nitrogen and carbon will be continued and additional work regarding the contribution by algal soil crusts to the nitrogen balance of the investigative sites is being initiated.

Several trips to other Biome sites to obtain suitable materials to establish the contributions of the algal soil crusts in these areas are anticipated.

The extent to which pH, salinity, nutrient availability and temperature affect the productivity of algal soil crusts will be established during the 1973 investigative period.

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1972 PROGRESS REPORT

PREDICTION OF PLANT-, SOIL- AND AIR-TEMPERATURE
ON A MICROSCALE IN THE DESERT

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Research Memorandum, RM 73-41

MAY 1973

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It is subject to revision and reinterpretation. The authors
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ABSTRACT

A micrometeorological station was set up in Curlew Valley. It consists of radiation sensors, air- and soil-temperature profiles, and surface temperature. After eliminating instrumental difficulties, two selected days of measurements were acquired. A scheme was developed to determine the daily variation of the heat exchange by using selected hours of recordings distributed over the day, taking one reading every second. The heat exchange under dry desert conditions for special cases is derived from these data, and temperature predictions can be developed. The bulk of the data will be taken with the improved equipment during the 1973 growing season.

INTRODUCTION

During 1972, measurements to determine the heat exchange at dry conditions in a sagebrush desert were carried out. These investigations followed a study during the previous year, which was directed towards the knowledge of the impact of radiative exchanges on the surface temperature (Dirmhirn, 1972). While these investigations were carried out mostly with mobile equipment, to concentrate on the horizontal and vertical radiation and temperature distribution around and in vegetation, this year's study involved equipment to record the heat exchange parameters. The goal during the 1972 study was to develop a feasible recording method to determine the components of the heat exchange; radiative exchange, heat exchange with the ground and with the air, all measured under "dry" desert conditions. The study is closely linked to that projected for 1973, in which an extension to "wet" conditions will be tried -- in other words, a determination of the entire heat exchange throughout the year, but with concentration on typical conditions.

Due to difficulties encountered in using the new equipment under desert conditions most of the measurements, also those for "dry" desert, will be taken during the 1973 period.

OBJECTIVES

1. To determine the radiative heat exchange above, around and in desert vegetation, and its impact on plant and soil surface temperature (1971).
2. To extend the study of the radiative measurement to develop a predictive model of soil- plant- and air-temperature in the desert (1972 and 1973).

METHODS

The goal in this study is to determine the heat exchange over desert ground, given by

$$R_n = G + H + LE$$

where:

R_n net radiation flux
 G heat flux into the ground
 H sensible heat flux in the air
 LE latent heat flux in the air

The environmental parameters measured are:

- incoming solar and scattered radiation
- net radiation
- a vertical temperature profile in the soil
- surface temperature
- a temperature profile in 6 heights above the surface
- a wind profile in 4 heights above the surface

Net radiation is measured, together with shortwave incoming (solar and scattered) radiation, with the intent to develop a relation between the two values for the area in question. Since the measurements of net radiation afford much attention, a relation with the easy-to-record solar and scattered radiation will provide a means to avoid net radiation measurements in the future and to conclude the latter from the former.

Surface temperature as well as the temperature profile in the ground is recorded by means of thermocouples. A reference junction was established in 125 cm depth; temperatures are further measured in 2 cm depths. The junctions are of normal 1 mm diameter gauge thermowire, except for the surface junction which was built from 0.1 mm Cu/0.12 mm Constantan wire to reduce the size. Thus the thermojunction could be placed on the soil surface, covered only by some dust.

The thermocouples for the temperature measurements in the air were also built from the thin wire. Tests and experiences during last year's study suggest a still finer wire for the measurement of air temperature. The thermometers were hence rebuilt by using 0.03 mm diameter Cu and Constantan wire. The heat dissipation from these thermocouples under natural environment is large enough that no over-heating by radiative processes can occur.

The thermometers are placed in the following heights:

5 cm (open spot)	1m
	2m
5 cm (in shade of plant)	4m
20 cm	8m

A triangular television mast is used to carry the thermometers.

Anemometers of the hot wire type are mounted in 4 heights on the mast: 1m, 2m, 4m, and 8m. Commercial hot wire anemometers (Hastings) were used during this year's study, but in-house built hot junction thermoelectric anemometers are being developed and will be used in the 1973 study to measure the vertical wind component (w).

A Metrodata Magnetic Tape Recorder was employed as a recording system. This digital recorder is designed for receiving data in time intervals from 1 sec to 1 hr. In our measurements short-term recordings are of importance, as explained in the next section.

RESULTS

During 1972, measurements to determine the heat exchange at dry conditions in a sagebrush desert were initiated. Efforts were focused on getting acquainted with the new recording system under desert conditions and developing appropriate sensors for heat flow measurements above the surface. The results established the possibilities for data collection appropriate to the heat exchange operation, provided a few adaptations of the equipment are performed.

Due to the late delivery of the Metrodata Magnetic Tape Recorder, measurements were not started until July. The process of receiving a computer-compatible tape from the Metrodata Tape recording for use on one of the USU computers was a slow process which took 2-3 weeks each time. Since this conversion is also relatively expensive, and considering our restricted funding, further measurements were postponed until the arrival of the first two days of measurements. Some special features of the recording system could be learned from these first two days of data, the most important being that high air temperatures, as they usually occur under desert conditions during the summer, offset the data record to a degree that reasonable results cannot be expected. Thus, the daytime values during these two sets of measurements were lost.

The nighttime values of the two days of recording, however, showed excellent reliability, so that we could continue measurements after having eliminated the hazards of high temperature errors.

After adaptation of the recording system in the light of the initial experience, three more sets of data were taken in September/October 1972. They proved to be without further errors and will be discussed here.

The scheme to accumulate sufficient data for a number of days throughout the warm season was determined as follows. Since one hour of short-term measurements (one second time interval) for eddy flux correlation computations needs one full tape, careful estimates had to be made for the absolute minimum amount of hours during the day which were necessary to interpolate a daily variation of the atmospheric parameters. We consider the absolute minimum of such hours to be five, distributed over the day as follows (starting time for one hour continuous recording):

1. during the warming period at mid-morning
2. at noon (maximum solar angle)
3. during decreasing solar radiation at mid-afternoon
4. one-half hour after sunset
5. one and one-half hour before sunrise

Thus, the increasing, maximum, and decreasing leg of the course of every atmospheric and ground parameter can be determined. The condition after sunset and throughout the night can be interpolated by using the two hours of measurements during the night (Figure 1).

In Figure 1 the hours of recording are shown for the shortwave solar and scattered radiation flux and for the net radiation flux. Thus a daily variation for the radiative parameters and all others following the course of the radiative flux can be easily interpolated.

This can be done also with the temperature measurements at the different depths and heights above the surface, as shown in Figure 2. Here 5 minute averages for selected temperature measurements are plotted and the daily variation interpolated.

An example for the temperature profile from the soil layers into the air is shown in Figure 3. Values are again 5 minute averages for each middle of hour recording. The active surface zone is apparent in this Figure, where, even as late in the year as October 3, temperatures of more than 40 C are reached during noon, while freezing temperatures occur close to sunrise. The temperature wave is dampened considerably in shallow soil layers, while the air up to 8 m follows the surface temperature wave more readily.

A history of the temperature profile of this type is to be recorded for selected days throughout the 1973 growing season, to provide environmental data for general use in biological studies. However, 1973 data will also be used to determine the heat exchange, including eddy transfer correlations.

A Fourier analysis is presently under way to determine if the time interval of one second is short enough to enter in the equations for the eddy flux method. Figures 4a and 4b show two short-term recordings of the temperature in different levels above the ground during day and night. Further studies are presently underway to determine the size of single eddies under daytime conditions. Frequency response analysis will be employed to analyze the data (Bendat and Piersol, 1971).

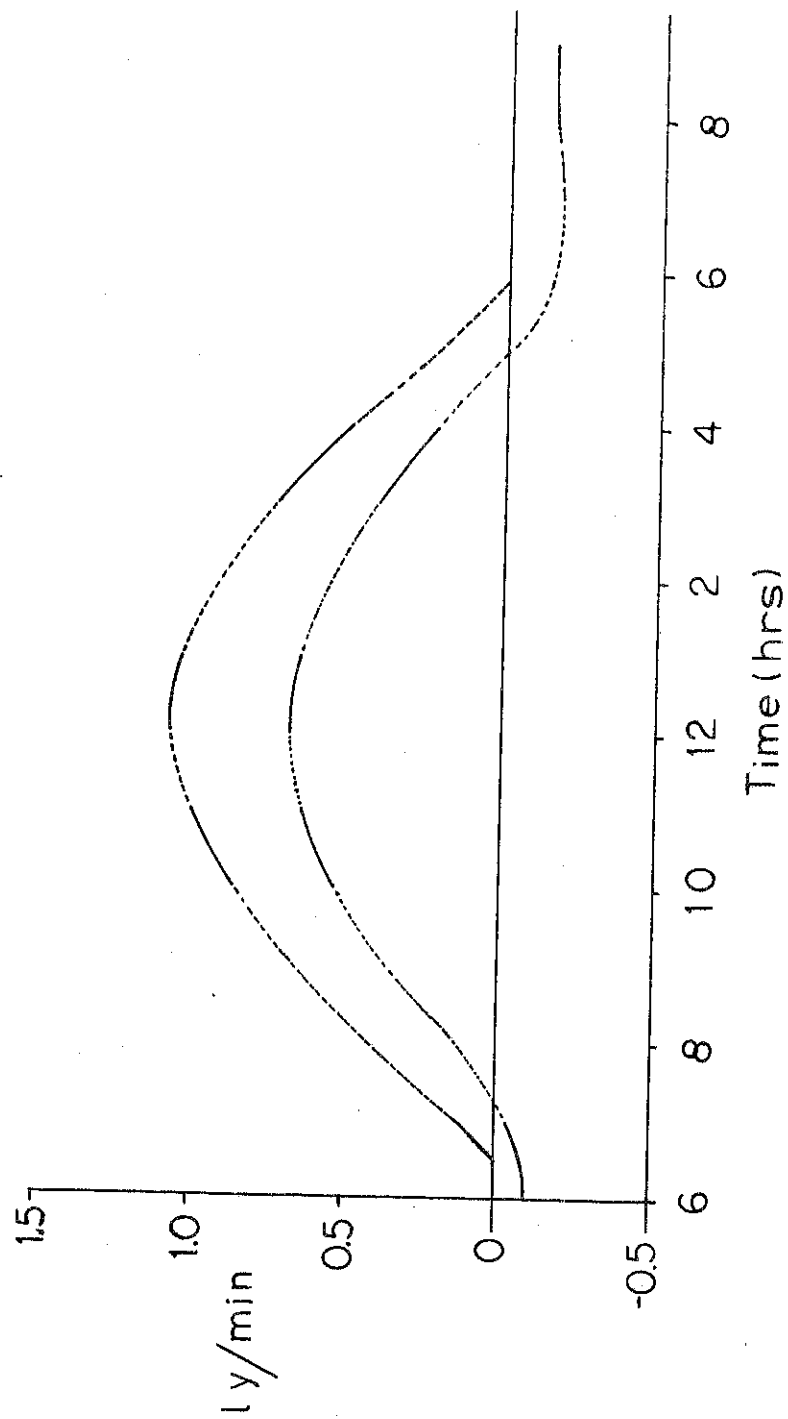


Figure 1. Hours chosen to construct daily variation.

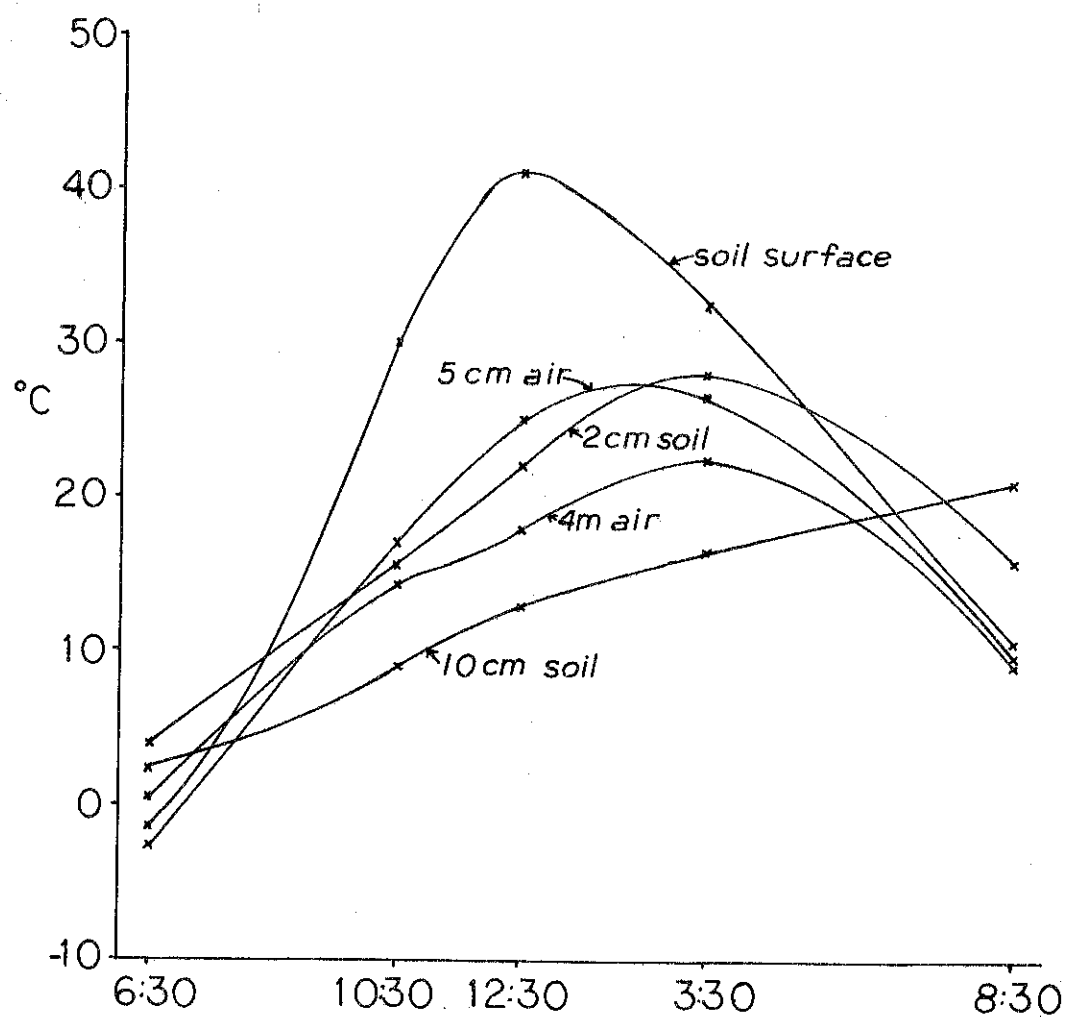


Figure 2. Daily variation of surface, soil and air temperature, October 3, 1972.

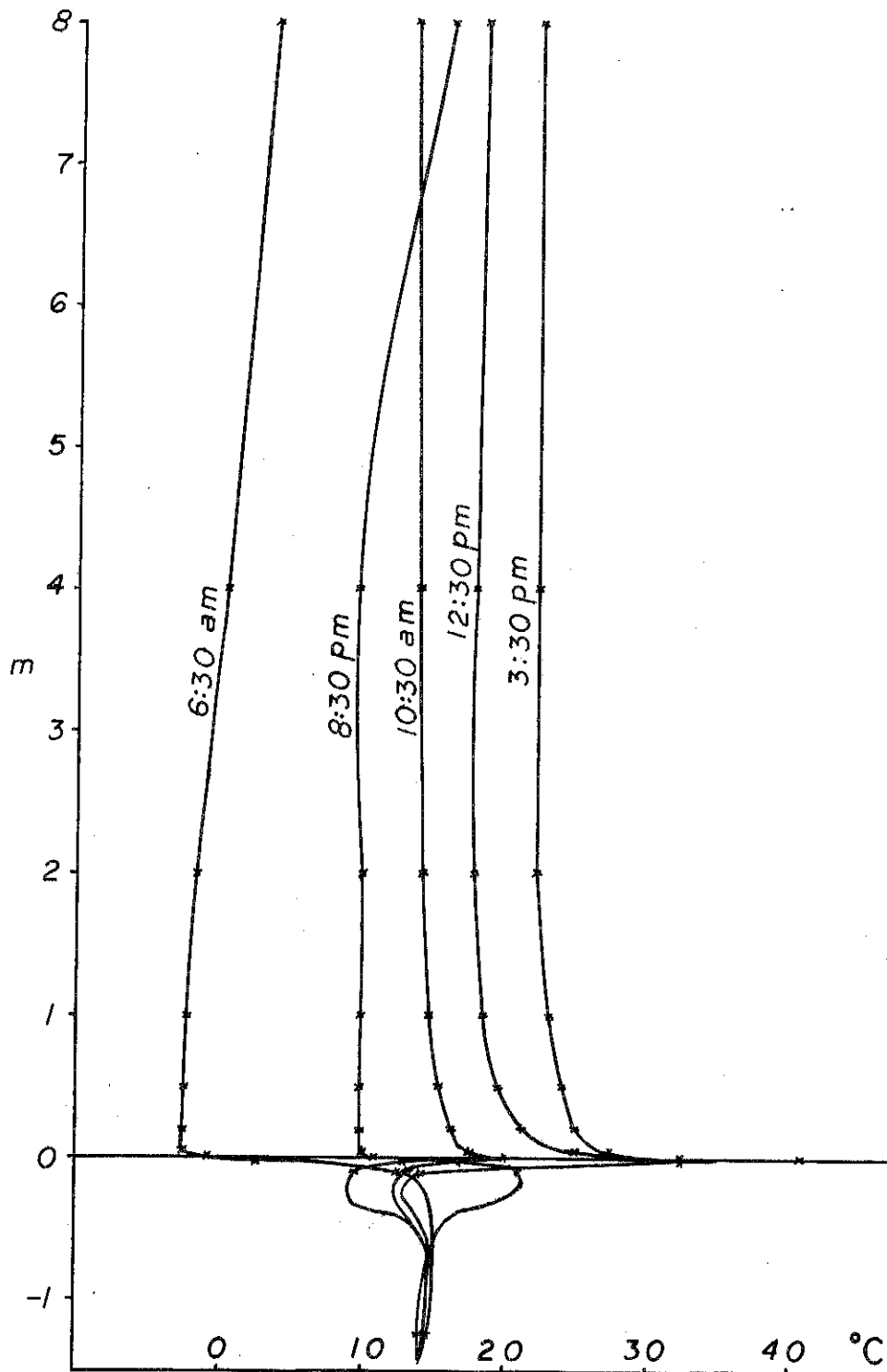


Figure 3. Profiles of soil and air temperature, October 3, 1972.

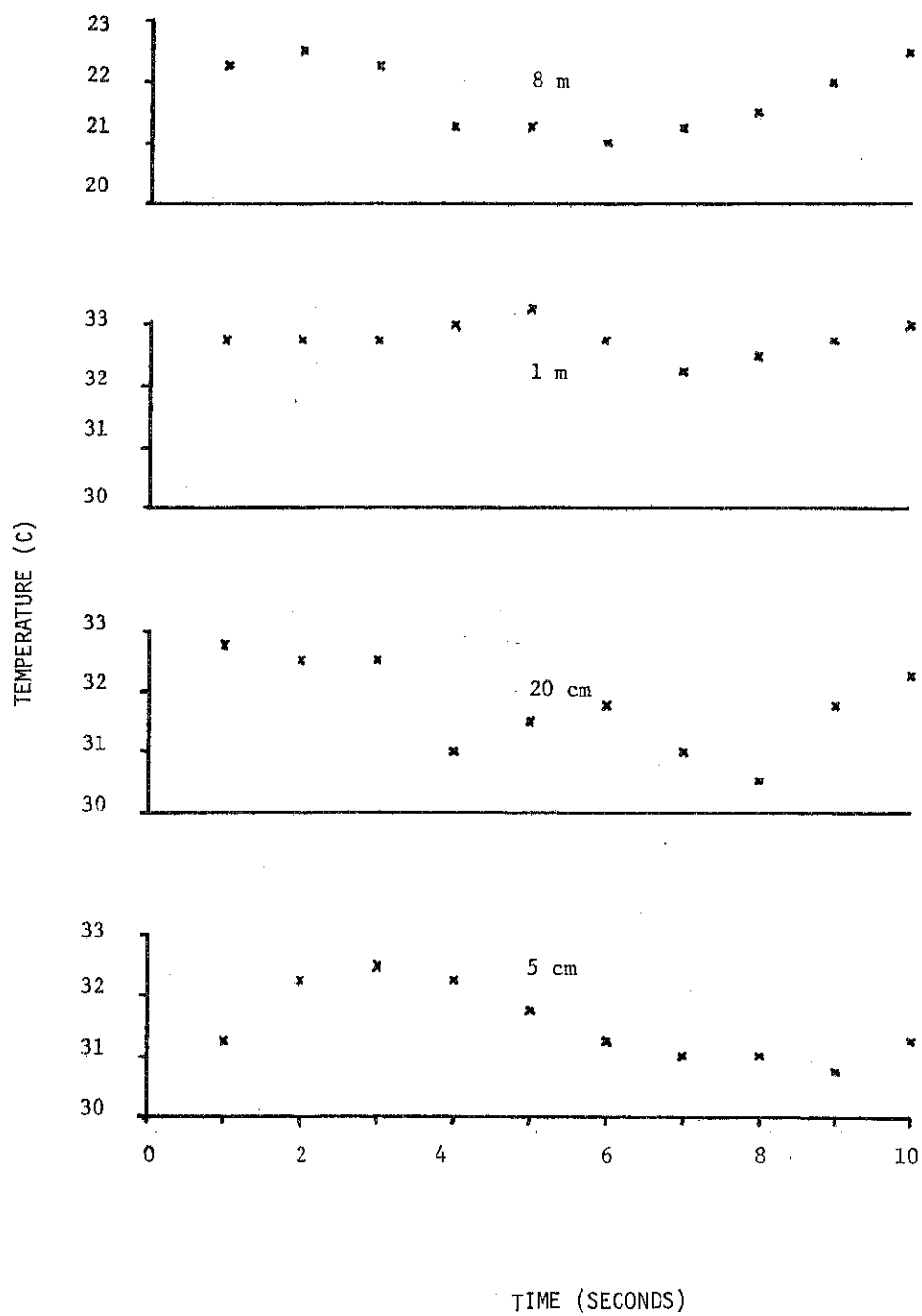


Figure 4a. Short term variation of air temperature in different levels at midday.

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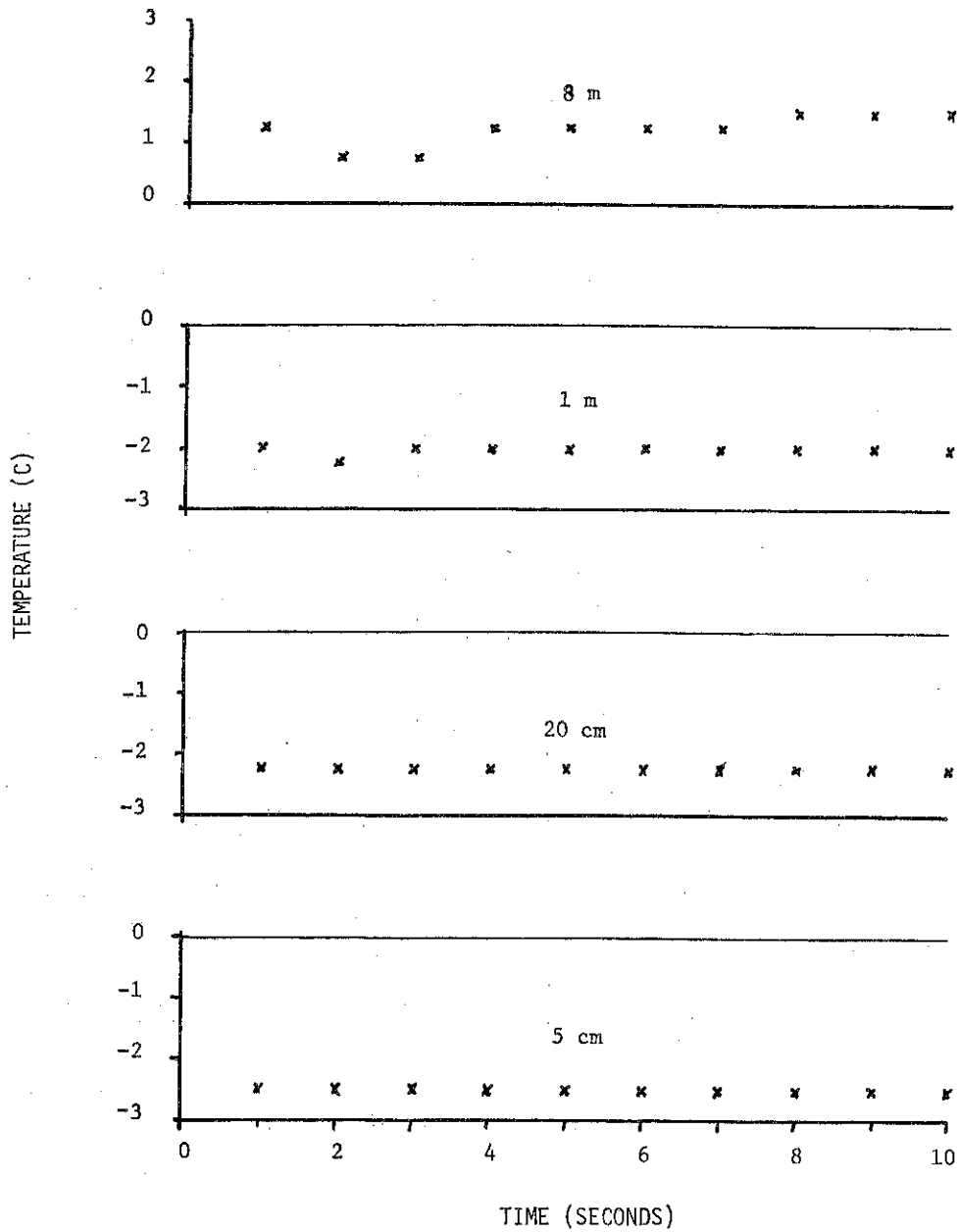


Figure 4b. Short term variation of air temperature in different levels at night.

DISCUSSION

The three days of recordings after adaptation of the equipment proved its capability of providing the data necessary for a broad history of the heat exchange during selected days, as well as for an intensive study of the individual parameters of the heat exchange. After eliminating the errors during this year's study, the main bulk of the data will be collected during the 1973 growing season.

EXPECTATIONS

With a series of selected days measured during 1973, an annual course of the heat exchange under desert conditions will be developed.

Models for the radiative exchange are presently being developed. An available soil model will be used, developed by Hanks, Austin, and Ondrechen (1971). The eddy flux will be measured, using the new sensors, and the heat exchange equation determined for dry and wet conditions.

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1972 PROGRESS REPORT

WATER UPTAKE BY PLANTS UNDER DESERT CONDITIONS

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Research Memorandum, RM 73-42

MAY 1973

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A B S T R A C T

Moisture transfer into and out of the root zone by abiotic processes is responsible for a significant portion of the observed soil moisture content variations adjacent to desert plants. In this study the relative magnitudes of these processes were investigated. Data were collected on variations in moisture content and soil moisture potential within vegetated and non-vegetated desert study plots. *In situ* methods were used to develop a moisture release curve for the soil within the root zone. Conductivity functions were obtained for moisture transfer due to thermal gradients and moisture content gradients.

The observed moisture content variations in the root zone were related to precipitation-evaporation processes at the study site. Rooting habits of *Celtis pallida* were examined, and related to moisture availability and soil structure. Data were collected on plant leaf potentials using pressure bomb techniques. The observed variations were related to both plant water use and to changes in the resistance to water flow through the plant. A model is described for analyzing the total resistance to water flow from the soil to the leaf.

INTRODUCTION

This study is a continuation of a 1971 investigation reported on by Qashu et al. (1972). Several processes were delineated as responsible for moisture movement within desert soils. The present investigation considers the relative magnitude of these several factors, and their effect upon water uptake by desert plants.

Traditionally, the investigation of natural ecosystems which do not offer any immediate substantive economic benefits to society has been constrained by limited budgets. The desert is such an ecosystem. There is a strong need for basic data collection in a fashion that will optimize the understanding gained from that data. It is the intent of this report to provide information on the factors most responsible for water use and movement in desert environments. This will aid in the structuring of future studies, and will provide insight into the types of data that should be collected.

OBJECTIVES

The generalized objective of this study was to determine the relative importance of various factors affecting water movement within the soil-plant-atmosphere system under desert conditions. Specifically the objectives were:

1. To measure spatial and temporal variations of water content, water potential and temperature within the root system of a desert plant species.
2. To determine moisture release curves and hydraulic conductivity relations characterizing the soil within the root zone of a desert plant species.
3. To describe water content changes within the root zone in terms of the several factors responsible for these changes.

METHODS

Plot description

This project was conducted at a field study site adjacent to the IBP Santa Rita study site (IBP, 1970). Several plots were selected, all but one containing specimens of the desert hackberry (*Celtis pallida*). Plot 1, with a single hackberry plant was the

same as that used in the 1971 study. Four additional plots were selected. Plot 3 has no vegetation. Plot 2, immediately adjacent to Plot 3, had over 15 individual plants, growing in close proximity. Plot 4, adjacent to Plot 2, had about 40 specimens of *Celtis pallida*, and occupied about three times the surface area. In order to have some control over the soil volume from which plant roots were extracting water, a trench approximately 1 m deep was dug around Plots 2 and 4. The insides of the trenches were located about 1.5 m from the edge of the plant canopies. The side of the trench adjacent to the plot was lined with 5 mm polyethylene, and the trench backfilled. This technique effectively confined the plant to obtaining water from soil within the plastic boundary. Some root penetration at the liner is likely over a long time period, but is not significant for the period of this study.

A fifth plot, number 5, was selected about 30 m from Plot 4. It had a clump of about 15 *Celtis* plants, being quite similar in size to Plot 2. It was left undisturbed as a control on the effect of the trenching on plant activity.

Plots 1, 2 and 3 were instrumented with thermocouple psychrometers at selected depths from 15 to 150 cm. Soil moisture potential values were recorded at about one-week intervals. Aluminum tubes 2 m in length were placed in the plots to serve as access tubes for neutron thermalization and gamma attenuation moisture probes. Moisture readings were taken with one or the other system at depths of 7.5, 15, 30.5, 61, 91.5 and 114 cm at about one-week intervals. On several occasions soil moisture values were recorded using both probes to permit cross-checking of the two methods. The locations of the psychrometers and access tubes are shown in Figure 1 and 2.

Continuous records were kept of atmospheric temperature and relative humidity at the field site. A standard 8-inch raingauge was used for recording precipitation, and a Class-A evaporation pan was maintained nearby. Measurements were made of cumulative evaporation and precipitation at about one-week intervals.

A Pressure bomb was utilized for measurement of leaf potential at intervals of about two weeks. Measurements were commonly made at midday, although several were made about 1 hr before sunrise.

Water potential measurements

Measurements of water potential during the 1971 study were obtained using standard Peltier cooling techniques. The instrumentation available at the start of this study for such measurements did not permit the measurement precision desired, and offered numerous measurement problems as discussed in the 1971 report (Qashu et al., 1972).

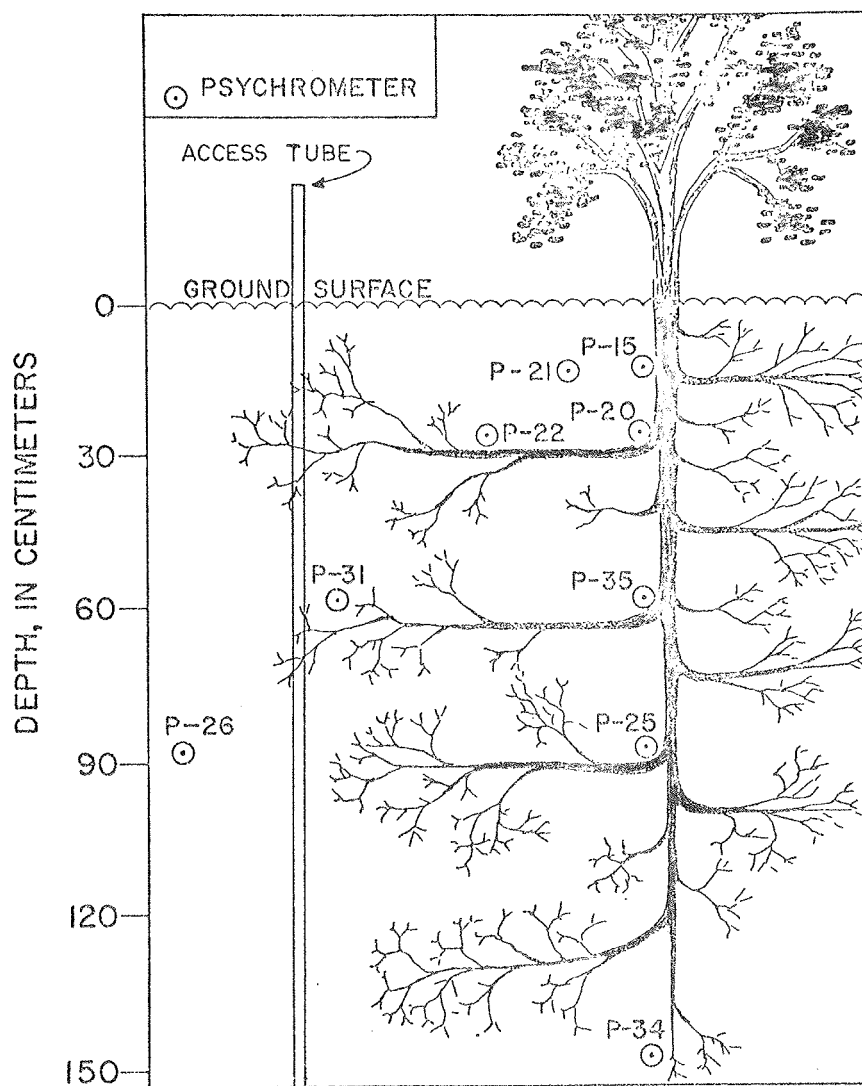


Figure 1. Psychrometer and access tube location within vegetated Plot No. 1.

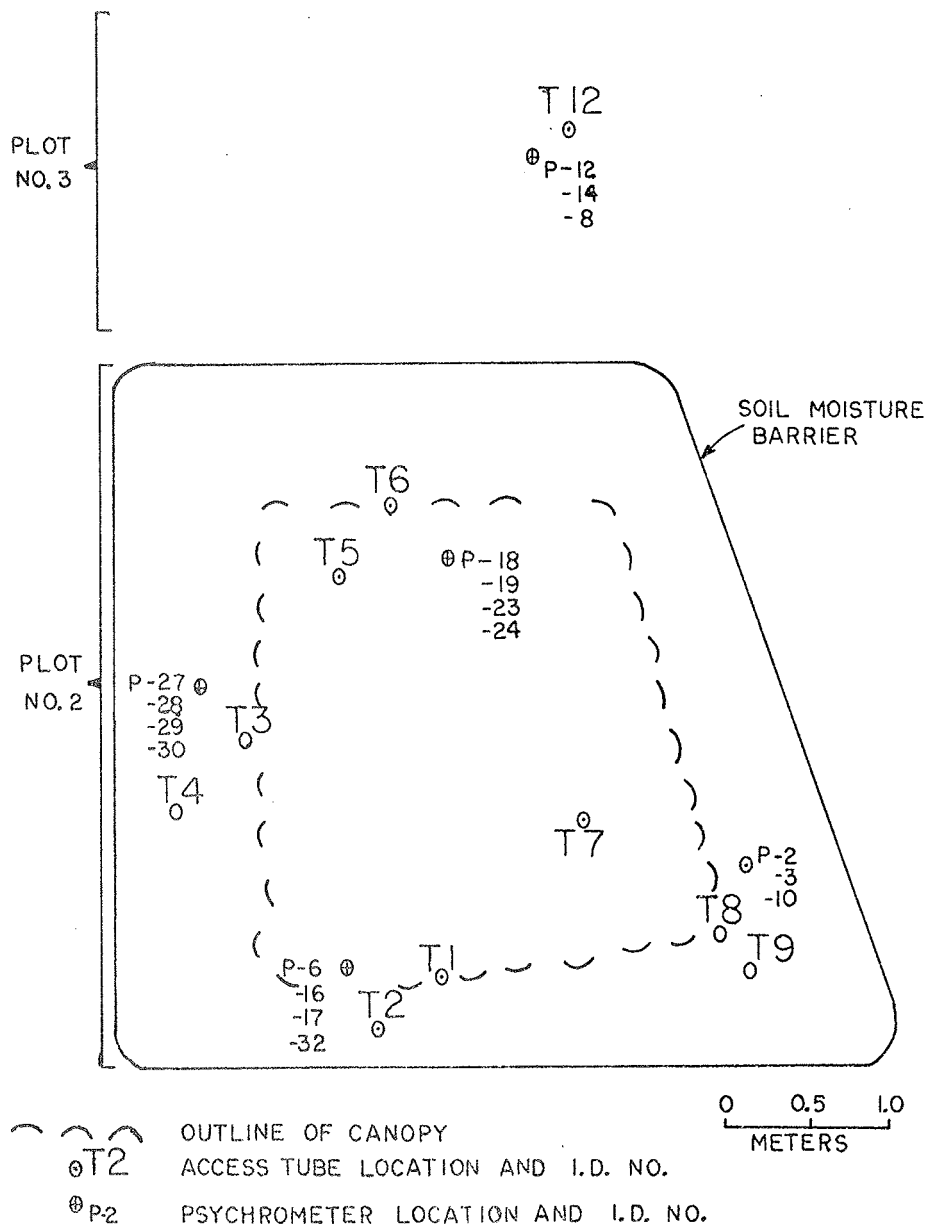


Figure 2. Psychrometer and access tube location within Plot 2 and Plot 3.

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Discussion with other investigators and with factory representatives led to the purchase of the HR-33 Dewpoint Microvoltmeter, manufactured by Wescor, Inc., of Logan, Utah. This meter utilizes a standard thermocouple psychrometer to obtain dewpoint temperature measurements of the soil atmosphere, which are then readily converted to water potential through a calibration curve. The measurement process utilizes a heat balance technique, balancing the heat loss or gain from a wet thermocouple junction by an input of energy through peltier heating or cooling. The technique is described in the HR-33 Instruction Manual:

Consider a hypothetical thermocouple junction whose temperature is determined exclusively by the heat transferred to it or away from it by condensing or evaporating water. Assume also that the junction has an initial temperature T , and that it is covered with a film of water. If T is above the dew point, water will evaporate from the junction, carrying with it the heat of vaporization until the temperature of the junction falls to the dew point, at which time evaporation will cease. If T is below the dew point, additional water will condense upon its surface, with the heat of condensation raising the temperature of the junction until it reaches the dew point, at which time condensation will cease. Therefore, given the aforesaid independence from other heat transfer mechanisms, the temperature of the wet junction will always converge upon the dew point.

In the real world, it is not possible for a thermocouple junction to be independent of heat transfer mechanisms which nature calls into play. Nevertheless, by considering the circumstances which will prevail whenever a measurement of water potential is to be made it is possible to simulate the above described hypothetical situation. During the measurement, the wet junction temperature will always be below the temperature of its surroundings. Therefore, heat will tend to flow from the surroundings to the junction. Using Peltier cooling, a counter flow can be created whose magnitude is adjusted electrically to exactly balance the heat inflow for a net transfer of zero. If this balanced conditions is set up on a dry thermocouple so to account for all heat transfer mechanisms other than condensing or evaporating water, then when the junction is wet, its temperature will be influenced only by the water, just as in the hypothetical example.

The dry junction heat balance is to be obtained for each psychrometer individually. The energy required to offset dry junction heat loss is translated into a voltage, referred to by the manufacturer as the DP Gain. This voltage is set into the meter for each individual psychrometer prior to all subsequent measurements.

The manufacturer of the meter has investigated the temperature dependence of the measurement technique, and reports a very low sensitivity, about 0.3% per degree from 10 to 50 C. Because of the low sensitivity the manufacturer feels that temperature measurement and/or compensation is unnecessary, and does not provide the circuitry for temperature measurement with the meter.

Laboratory calibration of psychrometers by the investigators revealed several serious problems with the use of the Dewpoint Microvoltmeter. First, the magnitude of the DP Gain was temperature dependent, varying about 2% per degree. Thus, a calibration curve was necessary for each psychrometer, relating the DP Gain to temperature, and requiring a temperature measurement prior to each potential measurement. Second, and of more concern, the DP Gain value was dependent on temperature gradients, which can be neither eliminated or effectively compensated for under field conditions. Unless the DP Gain for each psychrometer was set to compensate for the ambient temperature and the effect of temperature gradients at the time of measurement, no measurement could be obtained. Temperatures and temperature gradients change continually within field plots, particularly in the near surface soil layers. This continual change would produce conditions under which no reliable measurements could be obtained using the Dewpoint Microvoltmeter.

Third, the electronic sensitivity of the meter prevents measurements at potentials above -1 bar. Potential measurements can be made to approximately 0.5 bars using standard psychrometric techniques in the field, and to 0.1 or 0.2 bars in the laboratory. The limitations of the Dewpoint Microvoltmeter were considered sufficient to prevent its application to field problems.

Errors in potential measurement

The measurement errors inherent in the use of standard psychrometric measurement techniques were discussed in detail by Qashu et al. (1972). Briefly, the average accuracy in the range from -5 to -40 bars, for temperatures from 10 to 40 C, is approximately 0.5 bars. The accuracy ranges from about 0.3 bars at 10 C to about 0.6 bars at 40 C.

Potential measurements above 0.5 bars not only have a high error component, but are difficult to read on the meter. However, the measurement problems vary from psychrometer to psychrometer. Occasional units were sufficiently stable to permit measurement to values of 0.4 or 0.2 bars. When the investigator felt confident of such values they were recorded as read. For less stable units, or when the investigator was not confident of the reading, potentials above 0.5 bars were recorded as 0.0. These zero values serve only as an indication of the magnitude of the potentials, and should not be used for computational purposes when an error of ± 0.5 bars is important.

Soil moisture content

Soil moisture readings were made with probes manufactured by Troxler Electronic Laboratories, Inc. The calibration curves provided with the instruments were used for interpreting the recorded values. Measurements made with the gamma attenuation probe require that two access tubes be placed in the soil. The tubes must be parallel, with a 30 cm separation distance. The installation of such tubes in non-uniform dry desert soils is quite difficult, and it is somewhat fortuitous if the tubes are actually parallel when installation is completed. It was necessary to correct for the effect of the resultant skewness. Tubes were placed in a large container in the laboratory and surrounded by soil. Three different separation distances were used, and the apparent soil density recorded at each distance. It was found that the apparent density decreased as distance squared increased. The actual density can be obtained by the following relation:

$$\text{Actual Density} = \text{Apparent Density} \times \left(\frac{30 \text{ cm}}{\text{separation (cm)}} \right)^2 \quad (1)$$

It was necessary to obtain the separation distance at selected depths for the tubes at the field site. The source and detector probes which are used with the gamma attenuation procedure are attached to rigid steel rods. The rods are centered at the top of the tubes by special aluminum caps.

The probes themselves fit snugly within the access tubes. The steel rods are then parallel to the tube in which they are located. The probes were lowered part way into each tube and the distance between the rods was measured at several points above the ground surface. This permitted the calculation of the tube separation distance at desired depths below the ground surface. These distances were then used in the relation given by Equation (1) to correct the recorded soil densities.

The gamma attenuation probe provides measurements of the soil density within a horizontal soil layer 1 cm thick. Determination of the actual soil moisture content requires either a measurement of the soil bulk density, or independent measurements of the moisture content by another procedure. However, changes in soil moisture content can be readily determined without knowing the original moisture content, as the only factor responsible for density changes in this soil is the change in water content. Determination of the soil bulk density would require considerable destructive sampling of the plot, and was deemed undesirable. For depths below 30 cm moisture values recorded with the neutron thermalization probe were used to define the initial moisture content. At shallower depths the neutron procedure is less reliable, and only moisture changes were determined from the gamma data.

Leaf potential

A pressure bomb technique, as described by Scholander et al. (1966), was used to obtain measurements of plant leaf potential. The potential is taken as equivalent to the pressure required to force vascular sap back to the surface of a cut stem end. This method ignores the osmotic potential of the vascular sap, generally smaller than -2 bars. Recorded pressures were uniformly larger than 12 bars, and generally larger than 20 bars. A measurement error of ± 0.5 bars is considered applicable. The additional error caused by ignoring the osmotic potential is not considered significant in view of other limitations on the measurement technique.

RESULTS

Soil structure and root distribution

The construction of the trenches around two of the vegetated plots offered an opportunity to identify the extent of the plant root system and to examine the soil profile. The soil was of uniform composition in the 0 to 90 cm depth zone. The soil was typically about 50% sand, with silt and clay composing another 30%. Particles larger than sand were generally 0.5 to 2 cm in size, with occasional boulders up to 10 cm. These large particles were scattered at random through the upper soil profile. At a depth of approximately 100 cm a boulder horizon was encountered, and was not penetrated by the trench. The boulders ranged in size up to 40 cm in diameter and accounted for over 50% of the soil volume in that zone.

Several photographs were taken of the root distribution in the trenches and are presented in an appendix to this report. In general, no roots were observed in the upper 10 cm of the profile.

The heaviest root concentration was in the 20 to 60 cm depth zone. Numerous roots of 1/2 to 1 cm diameter were severed by the trenching and a few roots of 2 cm or larger were encountered. Root concentration decreased markedly at the 80 cm depth, and was minimal within the upper part of the boulder horizon.

Field data

The following data have been submitted in machine-readable format to the Desert Biome central data bank:

1. Measurements of soil moisture potential and soil temperature within Plots 1, 2 and 3 at selected depths from 15 to 105 cm, for the period October 6 through December 19, 1972 (DSCODE A3UQH03).
2. Measurements of soil moisture percent for Plots 1, 2 and 3, obtained with a neutron thermalization probe, at depths from 15 to 137 cm, for the period September 9 through December 19, 1972 (DSCODE A3UQH07).

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3. Measurements of soil density within Plots 1, 2 and 3, obtained with gamma attenuation probes, at depths from 7.5 to 114 cm, for the period October 6 through December 12, 1972 (DSCODE A3UQH06).
4. Precipitation and Class-A pan evaporation data, collected at the study site, for the period September 9 through December 19, 1972 (DSCODE A3UQH02).
5. Air temperature and relative humidity at the site, for the period October 6 through December 19, 1972 (DSCODE A3UQH02).
6. Measurements of plant leaf potential on Plots 1, 2, 4, and 5, made before sunrise and at midday, for the period October 30 through December 19, 1972 (DSCODE A3UQH05).

A summary of the soil potential and soil temperature data is presented in Table 1 of this report. The precipitation and pan evaporation data are presented in Table 2, and the leaf potential data are summarized in Table 3. Table 4 presents a summary of the moisture contents, as recorded with the neutron thermalization probe.

DISCUSSION

Water content-potential relationships were measured for several samples of Sonoita sandy loam during the 1971 phase of this project (Qashu et al., 1972). The relationship varied significantly from one sample to another. Particle size distributions were obtained for each of the samples. The clay content (less than 2 microns) was plotted against the water content at -15 bars, as shown in Figure 3 of this report. The linear relationship is apparent. It was evident that considerable error might result from the use of one or even several sets of soil samples to obtain a moisture release curve applicable to the entire root system of the study plant. Instead, *in situ* measurements of water content and water potential at several points within the root system were used to develop a moisture release curve. This technique eliminated the problems connected with obtaining representative samples. However, considerable scatter was expected in the data, as the potential values are point measurements and the moisture content is a volume integrated value. The data are plotted in Figure 4, with a line of best fit drawn through the points. In general, the scatter lies within the ± 0.5 percent and ± 0.5 bar measurement error in the data.

For subsequent analysis the line of best fit was used to characterize the moisture release curve for the soil within the root zone.

Table 1. Soil moisture potential and soil temperature at selected depths

Date (1972)	VEGETATED PLOT										NON-VEGETATED PLOT						Ave. Temp.	
	*15		30		60		75		100		*15		30		60			
	-bars																	
	T	ψ	T	ψ	T	ψ	T	ψ	T	ψ	T	ψ	T	ψ	T	ψ		
6 Oct	21.5	0.0	23.0	0.0	24.8	0.4	25.3	26.1	26.1	39.0	24.1	25.3	0.0	23.3	0.2	25.3	3.0	24.6
12 Oct	2.15	1.9	23.0	0.3	25.6	0.0	24.5	22.6	24.9	34.7	23.9	24.3	0.8	23.0	0.1	26.0	0.9	24.4
31 Oct	14.2	0.1	16.2	0.0	19.0	2.7	18.7	2.7	19.8	27.1	17.6	15.7	1.0	14.9	0.4	17.7	0.0	16.1
3 Nov	9.1	0.0	12.7	0.1	15.7	0.0	15.7	1.1	17.5	19.1	14.1	18.2	0.0	11.7	0.0	14.2	0.0	14.7
10 Nov	9.6	0.0	13.2	0.0	16.7	0.4	16.0	2.7	16.7	20.1	14.4	18.0	0.0	10.1	0.7	15.3	0.0	14.5
22 Nov	6.6	0.0	9.4	0.0	12.7	0.0	12.7	3.0	13.9	12.8	11.1	15.7	0.0	9.9	0.0	10.9	0.0	12.2
1 Dec	6.1	-0.0	9.4	0.0	11.5	0.0	11.7	0.2	12.7	8.1	10.3	13.7	0.0	8.6	0.0	11.4	0.0	11.2
19 Dec	6.1	1.2	8.6	0.7	9.0	0.0	9.6	0.4	10.6	12.8	8.8	8.0	1.3	6.1	0.0	10.1	0.0	8.1

* Depth in cm.

Table 2. Precipitation and Class-A pan evaporation, Santa Rita site (1972)

Period Ending	Precipitation for period, inches	Pan Evaporation for period, inches	Cumulative precip., inches	Cumulative evap., inches
9 Sep	--	--	--	--
5 Oct	2	--	2.05	--
9 Oct	--	--	2.05	0
30 Oct	2.25	3.06	4.25	3.06
3 Nov	--	.42	4.25	3.48
10 Nov	--	.91	4.25	4.39
12 Nov	.61	--	4.86	--
16 Nov	--	.66	4.86	5.05
17 Nov	.61	--	5.47	--
22 Nov	--	.35	5.47	5.40
1 Dec	--	.54	5.47	5.94
12 Dec	.27	1.47	5.74	7.41

Table 3. Leaf potential, measured with pressure bomb

Date	Average potential of samples, in atmospheres	
	Before sunrise	Mid-afternoon
30 Oct	--	-14.8
3 Nov	-11.1	-18.5
10 Nov	--	-26.7
1 Dec	-20.8	-34.5
19 Dec	-23.9	-40.6

Table 4. Soil moisture content variations -- vegetated and non-vegetated plot.

Date (1972)	Moisture content (% by vol.), total to 114 cm depth for each tube, numbered 1-12										
	1	2	3	4	5	6	7	8	9	10	12
9 Sept	1.53	1.57	2.03	2.03	1.67	1.49	1.62	1.67	1.72	1.78	1.62
13 Oct	2.53	2.83	4.05	2.92	3.76	3.15	3.23	2.83	3.08		
16 Oct	2.04	3.23	4.29	3.83	3.55	3.47	2.76	2.87	3.33	3.88	
3 Nov	2.78	3.37	4.00	3.89	3.60	3.43	3.19	3.14	3.50	4.29	3.38
22 Nov	2.64	3.58	4.20	4.29	4.04	4.02	3.30	3.36	4.03		3.92
1 Dec	2.85	3.42	4.11	4.00	3.82	3.94	3.15	3.19	3.94		3.76
19 Dec	2.69	3.31	4.07	3.99	3.73	3.66	2.84	3.02	3.87	4.24	3.72

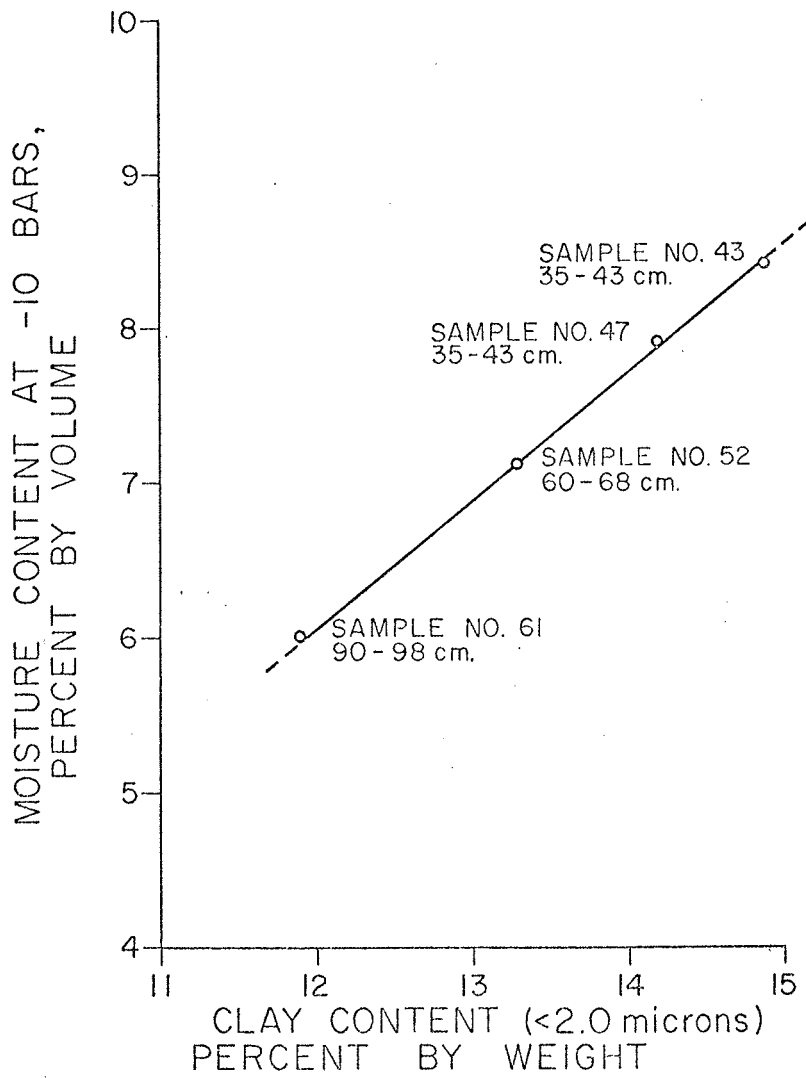


Figure 3. Effect of clay content on moisture isotherms

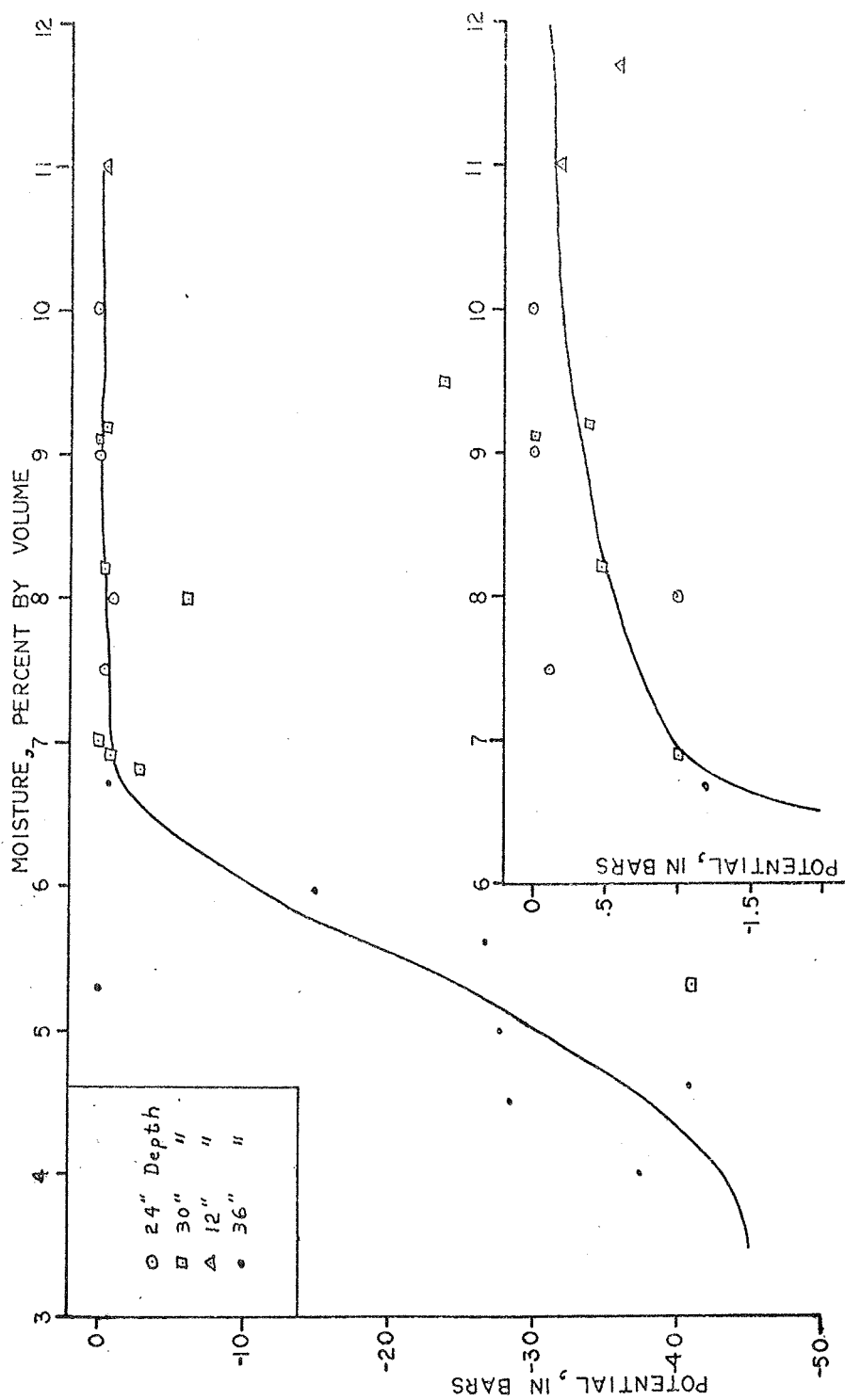


Figure 4. Moisture release curve for soil within vegetated Plot 3.

Hydraulic conductivity

Quantification of moisture flux in the soil requires knowledge of the moisture content-conductivity relation. The soil was observed to be highly variable in texture and composition during the installation of the plastic soil moisture barriers. Collection of samples sufficiently large to include this variability would destroy the plant. Consequently, an *in situ* method was utilized to determine the desired relationship. A three-day period was selected (October 13-16) during which significant moisture changes occurred throughout the profile. No precipitation was observed within the period. However, high humidity (over 85%) and low air temperatures (5 to 15 C) kept surface evaporation and transpiration low. Thus, moisture content changes within the profile can be attributed primarily to vertical redistribution. This movement is described by Equation (2).

$$\frac{\partial \theta}{\partial t} = - \frac{\partial}{\partial z} \left(k(\theta) \left(\frac{\partial \psi}{\partial z} + 1 \right) \right) \quad (2)$$

The potential gradients observed within the profile were uniformly larger than 5 cm/cm, and generally greater than 50. Thus, the vertical gradient due to elevation could be neglected, and Equation (2) becomes:

$$\frac{\partial \theta}{\partial t} = - \frac{\partial}{\partial z} \left(k(\theta) \frac{\partial \psi}{\partial z} \right) \quad (3)$$

For short periods and relatively small moisture content changes, it can be assumed that $k(\theta)$ remains constant. Equation (3) then becomes:

$$\frac{\partial \theta}{\partial t} = - k(\theta) \frac{\partial^2 \psi}{\partial z^2} \quad (4)$$

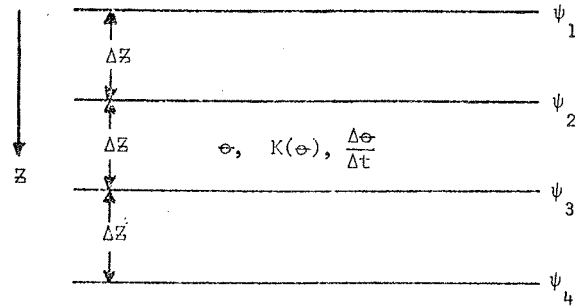


Figure 5. Finite elements used to obtain finite difference form of flow equation

Using the notation defined in Figure 5, Equation (4) can be written in finite difference form as:

$$\frac{\Delta\theta}{\Delta t} = -k(\theta) \left(\frac{\psi_4 - \psi_3}{\Delta z} - \frac{\psi_2 - \psi_1}{\Delta z} \right) \quad (5)$$

The vertical distribution of moisture potential and moisture content changes can thus be used to determine values for $k(\theta)$ at several different moisture contents.

Figure 4, the moisture release curve, was used to obtain potential gradients from the observed moisture content gradients. The results of computations for values of $k(\theta)$ are presented in Figure 6. The line of best fit was drawn by eye through the data points, using the assumption that $k(\theta)$ asymptotically approaches a constant value at high moisture contents.

The conductivity function defined by Figure 6 applies to the entire soil-root system complex. Conductivity measurements on individual soil samples may well yield values considerably different from these. However, this function should prove more meaningful for describing moisture movement due to potential gradients, whether created by plant water uptake or by infiltration-evaporation processes.

Thermally induced moisture movement

Data collected during the 1971 study indicated the presence of significant temperature gradients within the profile. These gradients appeared to be responsible for significant moisture movement. During the 1972 portion of the study, considerable effort was devoted to determining the magnitude of these thermally induced fluxes, and to estimate their relative importance. The consideration of thermally induced fluxes composed a portion of a dissertation arising from this study. The following discussion closely parallels material presented in that dissertation (Wheeler, 1972).

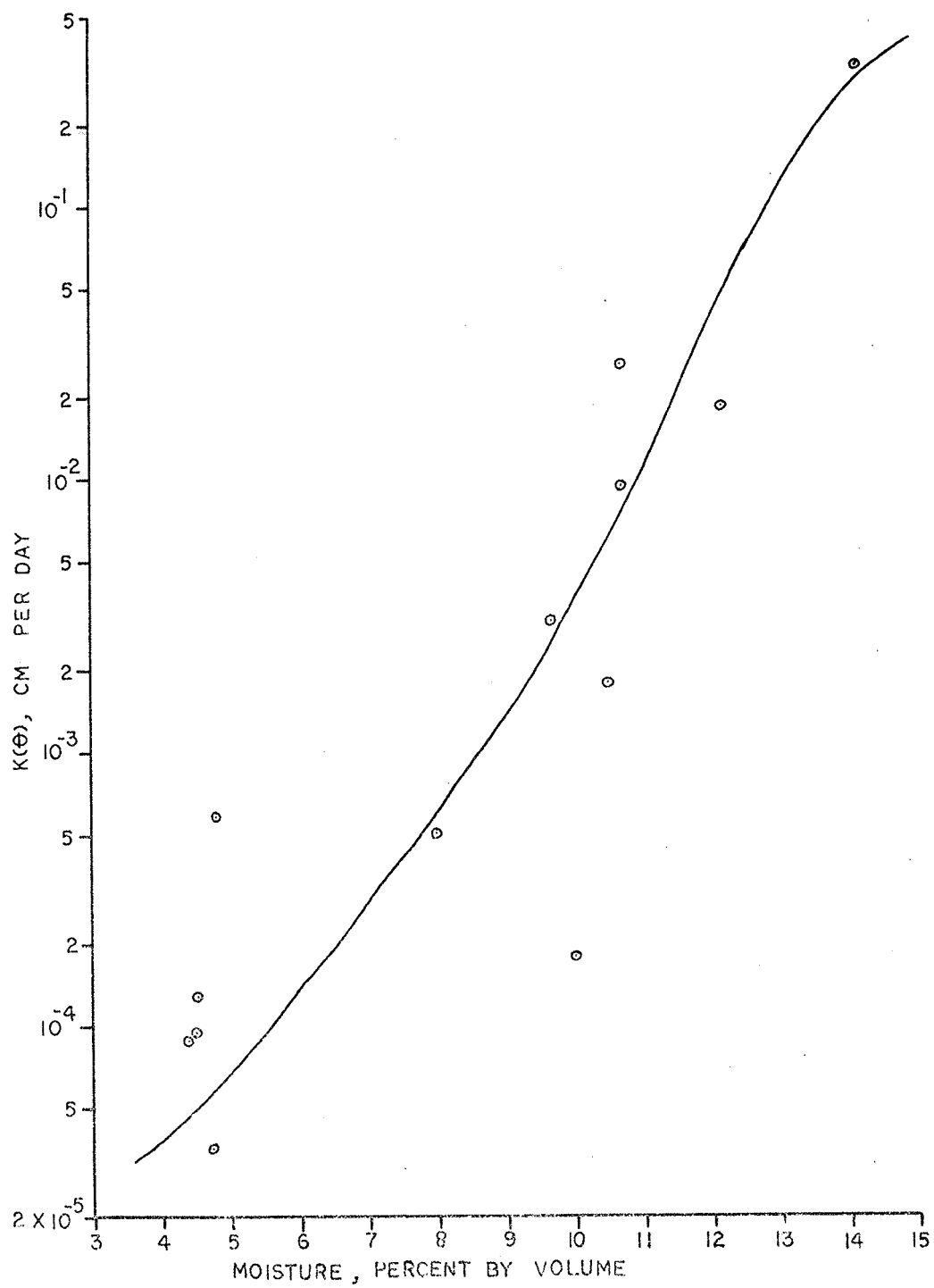


Figure 6. Relationship between conductivity and soil moisture content.

The movement of moisture in response to temperature gradients has been studied in some detail (Cary, 1965; Philip and de Vries, 1957). It has been observed that thermal gradients in soils cause water to move from a warm to a cooler area in both the liquid and vapor phases. However, data presented by Cary (1965) indicate that for potentials as high as -0.034 bars, thermally driven liquid flow accounts for only about 30% of the total thermally driven flux. Calculations made by Philip and de Vries (1957) confirm this observation, and demonstrate that thermally driven liquid flow essentially ceases at moisture contents corresponding to the -1 bar level for the soils of this study.

Vapor movement due to temperature gradients results from the increase in vapor pressure associated with a temperature increase. Psychrometers measure potential as a function of relative vapor pressure, and thus cannot reflect this change. Philip and de Vries (1957) present an extensive discussion of the theory of vapor flux due to temperature gradients. The following discussion is adapted from their paper.

The flux of water vapor due to temperature gradients is given by Equation (6):

$$q_{\text{vap}} = -D_{\text{atm}} \nu \alpha a h \frac{dp_0}{dT} \nabla T \quad (6)$$

where D_{atm} = diffusivity of water vapor in air,
 $= 0.274 \text{ cm}^2\text{sec}^{-1}$;

ν = mass flow factor, introduced to allow for boundary effects,
 $= 1.024$;

a = volumetric air content of soil;

α = tortuosity, allowing for increased path length of vapor flow through soil,
 $= 0.66$;

h = relative humidity

$\frac{dp_0}{dT}$ = change of saturation vapor density with temperature,
 $= 1.05 \times 10^{-6} \text{ gm cm}^{-3} \text{ } ^\circ\text{C}^{-1}$;

∇T = soil temperature gradient.

Equation (6) is referred to as the "simple theory" of thermally induced vapor flux. Values calculated from the equation do not agree with observed vapor flux values. Philip and de Vries (1957) suggest that this is due to the presence of micro-temperature gradients within the air-filled pores of the soil which are considerably larger than the average soil temperature gradient. These higher gradients, coupled with moisture flow through liquid islands between pores, result in the observed deviation from the simple theory. The authors present an analysis to include the higher temperature gradients, and derive an expression for the ratio of the flux predicted by their theory

to that predicted by the simple theory. The correction factor is given as:

$$\eta = \frac{A + \theta}{\alpha \cdot a} f \quad \text{with: } f = \frac{(\nabla T)_a}{\nabla T} \quad (7)$$

The coefficient "f" is the ratio of the temperature gradient within the air-filled pores to the overall temperature gradient. Values of "f" are calculated on the basis of heat flow considerations. Values of the coefficient for selected values of porosity and moisture content are given in Table 5. The corrected theoretical equation for vapor flux due to temperature gradients is obtained by combining Equations (6) and (7) to obtain:

$$a_{\text{vap}} = a \cdot h \cdot \frac{(a + \theta)}{\alpha \cdot a} \left(\frac{(\nabla T)_a}{\nabla T} \right) (1.94 \times 10^{-7}) \nabla T \quad (8)$$

Equation (8) is used by Philip and de Vries (1957) to calculate moisture fluxes induced by temperature gradients. They compare the fluxes predicted by their theory with experimental data obtained by other authors.

Table 5. Ratio of the temperature gradient in air-filled pores to overall temperature gradient

θ	Values of "f" for $a + \theta =$	
	0.5	0.3
0.0	1.9	3.0
0.1	1.7	2.0
0.3	1.7	2.1
0.5	1.8	

Good agreement exists between observed and calculated flux values for most of the data they present. In general, the flux increase down to a potential of about -0.1 bars. The magnitude then remains more or less constant until it begins to decrease rapidly at potentials of -80 bars or lower.

The application of Equation (8) to the prediction of thermally induced fluxes requires a knowledge of the relative humidity of the soil air, the moisture content, the temperature gradient, and the total porosity of the soil. The former three factors can be obtained directly or indirectly from psychrometric measurements, and the latter from laboratory analysis of soil samples. This permits an estimate of the thermally induced moisture flux utilizing field data obtained with the thermo-couple psychrometer.

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Combining Equations (7) and (8) of this paper, one obtains:

$$q_{\text{vap}} = h \cdot a \cdot n \cdot \nabla T (1.94 \times 10^{-7}) \text{ gm cm}^{-2} \text{ sec}^{-1} \quad (9)$$

The thermally driven vapor flux can be calculated from Equation (9), using values of a , h and n appropriate to various moisture contents. For the soil at the study site q_{vap} is essentially constant in the range from -1 to -40 bars, at a value of $2.2 \times 10^{-5} \text{ gm} \cdot \text{cm}^{-2} \cdot \text{day}^{-1} \cdot ^\circ\text{C meter}^{-1}$ (Wheeler, 1972).

An estimate of the flux produced by gradients in the matric component of the soil water potential can be made using Equation (10).

$$q = s_w K(\theta) \frac{d\psi}{dz} \quad (10)$$

The conductivity function, $K(\theta)$ is obtained from Figure 4 and Figure 6 of this report. Table 6 presents the results of calculations made to determine the moisture flux created by a one bar per meter potential gradient, as compared with that due to a temperature gradient of 1 C per meter.

Table 6. Comparison of moisture fluxes produced by potential and thermal gradients

ψ_p bars	$K(\theta)$ cm/day	moisture flux, q , for gradient of one bar per meter $\text{gm cm}^{-2} \text{day}^{-1}$	moisture flux, q_{vap} , for gradient of 1 C per meter $\text{gm cm}^{-2} \text{day}^{-1}$
-1	3×10^{-4}	3×10^{-2}	2×10^{-4}
-10	1×10^{-4}	1×10^{-2}	
-40	4×10^{-5}	4×10^{-3}	

From the data in Table 6 it is apparent that moisture flux due to temperature gradients is only significant under conditions of high temperature gradients or at very low potential values. Representative values for temperature and potential appear in Table 2. Temperature gradients average about 10 C per meter, while potential gradients are as large as 40 bars per meter. Thermally induced moisture flux is inferred to be one to several orders of magnitude smaller than moisture flow due to potential gradients.

As was observed in the 1971 phase of this study, near surface temperature variations are smaller within the vegetated plot than within the non-vegetated plot.

Plant water use

One of the long term objectives of research in the Desert Biome must certainly be that of determining the quantities of water utilized or transpired by the various plant species. The highly variable nature of water availability, both seasonally and annually, would lead one to expect a similar variation in plant water uptake. Many years, or perhaps decades, may be required to fully attain this objective.

One approach to calculating plant water use is to determine the potential evapotranspiration rate from standard meteorological data and one of the combination method formulas (Penman, 1948; Van Bavel, 1966), and then to reduce this potential evapotranspiration by a plant resistance factor. The plant resistance is diagrammatically represented in Figure 7.

Water extraction by the plant roots is expressed by the equation:

$$\frac{\partial \theta}{\partial t} = \frac{1}{r} \frac{\partial}{\partial r} r k \frac{\partial \psi}{\partial r} \quad (11)$$

where θ is the moisture content, t is the time, r is the radial distance from the root, k is the capillary conductivity and ψ is the suction in the soil. Solutions to this differential equation have been solved by Gardner (1960) and Visser (1964) with the following assumptions:

1. Steady state flow $\frac{\partial \theta}{\partial t} = 0$. The transpiration rate is considered constant during the balance period.
2. The capillary conductivity is constant and is related to the mean suction in the root zone.
3. Redistribution of moisture in the soil profile does not occur.
4. The exact geometry of the root system and root activity is known.

Because these assumptions do not hold for a field study, Rijetma (1965) lumped the parameters affected by the roots into a single factor, b , which depends on the root geometry, activity and depth, and developed the following equation:

$$E_t = \frac{\psi_r - \psi}{b/k} \quad (12)$$

where ψ_r is the mean suction at the root surface, ψ is the suction in the root zone, k is the capillary conductivity, E_t is the amount of evapotranspiration and b/k is the soil resistance (r_{s1}). Because it is difficult to measure the mean suction at the root surface, the equation is combined with the equation for liquid transport of water through the plant, defined as:

$$E_t = \frac{\psi_l - \psi_r}{R_{s1}} \quad (13)$$

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where R_{s1} is the plant resistance to water movement made up of the root cortex and xylem resistance. ψ_r is as before, ψ_l is the suction in the leaf tissue. The resulting combined equation is:

$$E_t = \frac{\psi_l - \psi}{R_{s1} + b/k} \quad (14)$$

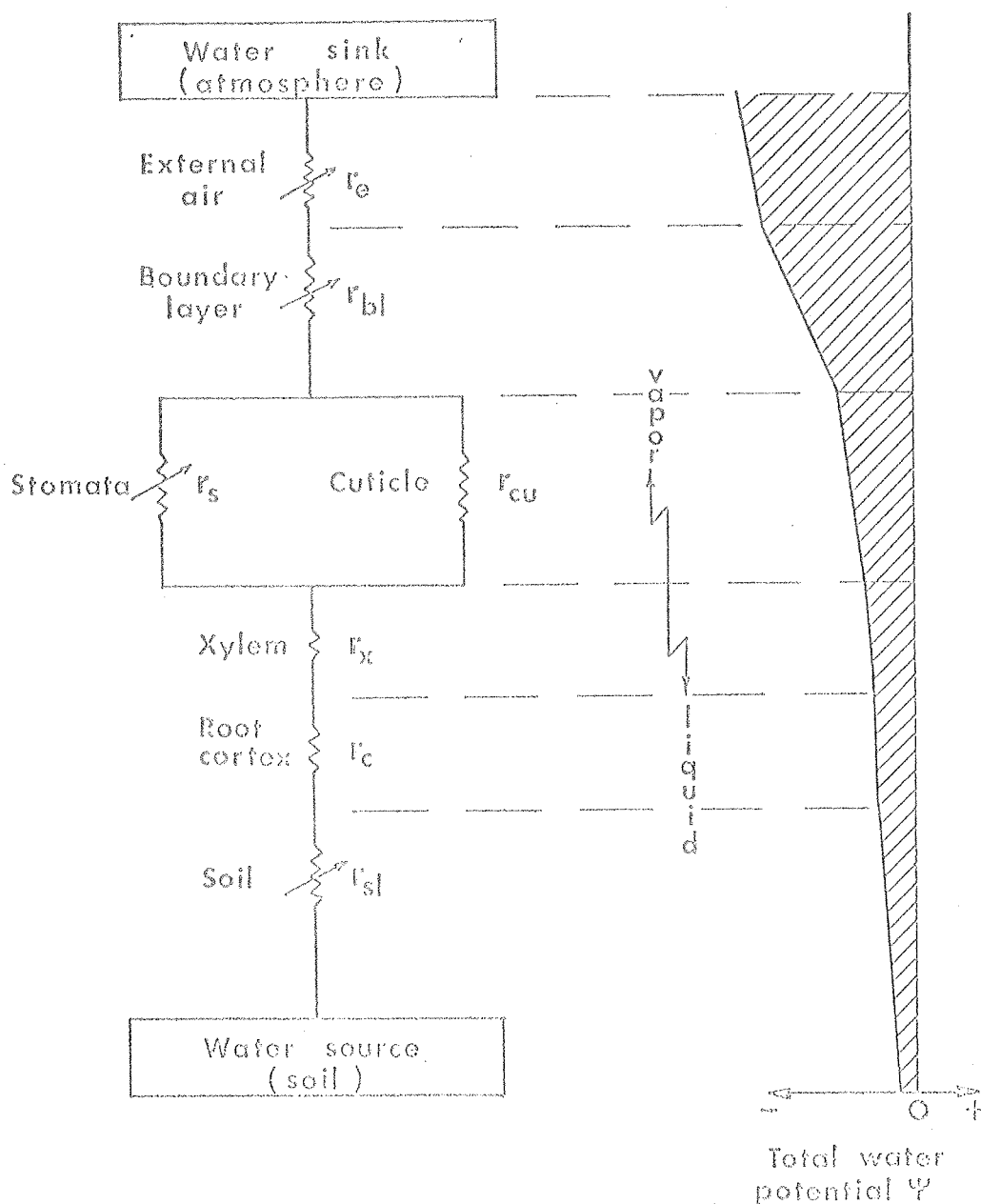


Figure 7. A diagrammatic representation of soil-plant-atmosphere resistances to water flow and the corresponding water potential gradient (Rose, 1966).

Solution of Equation (14) requires two time periods because the equation has two unknowns, R_{s1} and b . The leaf potential is measured using a pressure bomb system and the soil potential capillary conductivity k is determined from Figure 6, using psychrometers. Assuming b and R_{s1} are time independent, which is not a bad assumption, unless there is a large amount of root growth or moisture stress, the equation can be solved for the unknowns.

The time periods chosen should have substantial evapotranspiration and the moisture range should be from wilting point to field capacity. All the data were available, but solution of the simultaneous equations proved to be impossible because during the time when data were collected, the evapotranspiration rates were too low and the moisture range too narrow. Additional data are being collected which should give a solution to Equation (14).

During the night, when evapotranspiration rates approach zero, the plant potential should approach the soil water potential. However, if the root and soil resistance are large enough, sufficient time does not elapse for equilibrium to occur. Measurements of leaf potentials were made before sunrise and they are reported in Table 3. The nighttime leaf potential decreases from October to December although the soil potential increases as shown by an increased moisture content (Table 4). The implication is that the plant resistance is increasing with a resulting decrease in plant water conductance during the night, leaving sufficient time for the plant to recover to the soil water potential.

Mees and Weatherly (1957) have shown that 75% of the water flow through roots is through the root cells with the remainder through the root cell walls. This means that the plant resistance at this location is determined by the root cell metabolism. The average soil temperatures in the vegetative plot decreased from October to December (24.1 to 8.8 C), resulting in a decreased root temperature and a decrease in metabolic rate. The conclusion is that the root resistance increased during that time due to the temperature drop. Additional data are necessary to specify the functional relationship.

The observed daytime potentials decreased from October to December, although the energy input to the plant and the evapotranspiration that occurred decreased. Again, an increased root resistance due to a temperature drop would require that the driving potential (Equation 14) would have to increase to compensate for the increased resistance.

Another approach to the determination of plant water use is to compare net soil moisture changes within a vegetated plot to those within a non-vegetated plot in the same area. Some variation from plot to plot will exist even without the presence of vegetation.

The presence of vegetation on desert soils greatly alters the physical parameters affecting the net water loss; infiltration capacities, surface evaporation, soil temperature gradients, atmospheric energy inputs, etc. Thus no definitive answers are possible concerning the relative quantities of water lost by biological and physical processes. However, a comparison of the sort described can provide data on the relative quantities of water lost from vegetated and non-vegetated portions of the desert environment. Data on the cumulative quantities of precipitation and soil moisture changes within the vegetated and non-vegetated plots are presented in Figure 8. The similarity of the two plots is apparent, with the non-vegetated site showing a slightly greater increase. Moisture loss from the vegetated plot represents both transpiration and surface evaporation. No clear delineation of the relative magnitudes is possible for the entire time period represented. Certain portions of the period are characterized by relatively low evaporative loads, and during those periods moisture decreases in the deeper root zones can be interpreted as plant water uptake. However, changes of that sort are relatively few, and generally too small to be of computational value.

The plant canopy covers approximately 40% of the total plot area. Within the canopy a substantial portion of the soil moisture loss must result from transpiration.

The difference between precipitation and soil moisture changes is taken as the evapotranspiration loss from the vegetated plot. All rainfall was sufficiently gentle so as to prevent any significant surface runoff from the plot. A comparison of pan evaporation and evapotranspiration is presented in Figure 9. Evaporation rates varied from .06 to .43 cm per day, while evapotranspiration varied from .03 to .17 cm/day. The ratio of evapotranspiration rate to pan evaporation rate averaged 0.47 for the period.

Additional instrumentation is being installed and data collected to further answer some of the questions presented in the report.

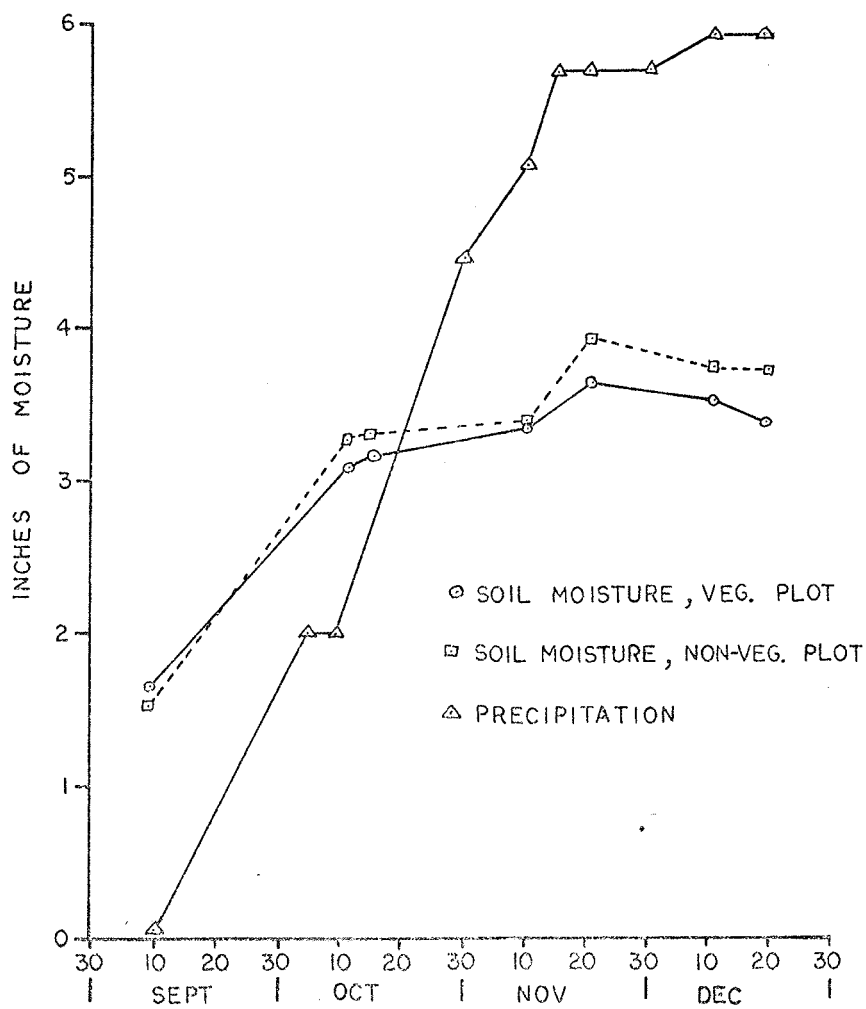


Figure 8. Comparison of cumulative precipitation and soil moisture at study site.

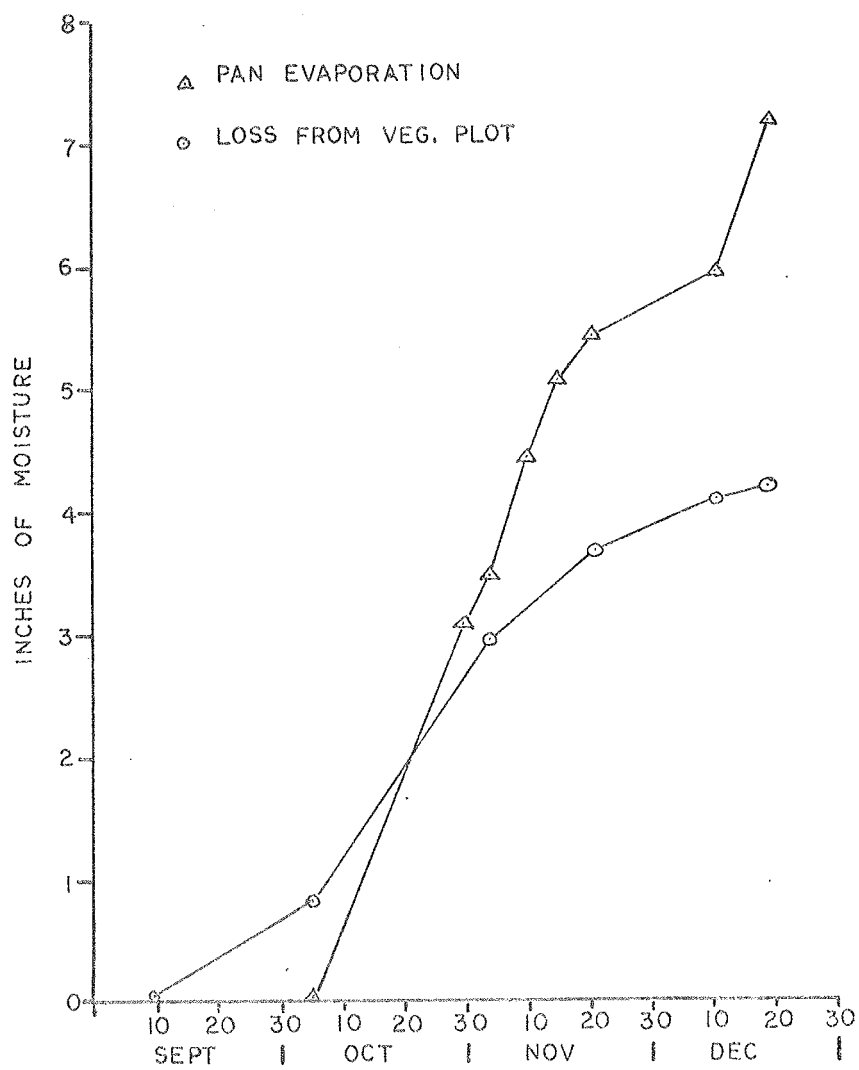


Figure 9. Comparison of cumulative moisture loss by vegetated Plot 3 with pan evaporation.

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1972 PROGRESS REPORT

EVALUATION OF CRITICAL SOIL PROPERTIES NEEDED
TO PREDICT SOIL WATER FLOW UNDER DESERT CONDITIONS

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Research Memorandum, RM 73-43

MAY 1973

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A B S T R A C T

Hydraulic conductivity and soil-water diffusivity have been measured for a desert soil over a suction range of 0 to -50 bars, using a transient outflow method. The work was carried out in the laboratory on soil cores, both artificially packed and taken from the field. Results show good agreement between experimental and calculated conductivity values, except at the higher soil suctions (>-6 bars). At these suctions, experimental values appear to be too high. Several reasons for this divergence are given. The most likely of these is increased fluxes due to a temperature gradient. The latter would be caused by the cooling effect of the water evaporating at the soil surface. Experimental evidence is needed to ascertain this hypothesis.

Future work will assess the contribution of temperature gradients to soil water movement and quantify the transmission coefficient associated with these gradients. These data will be combined into the proposed model to estimate water withdrawal patterns from desert soils.

INTRODUCTION

Biological activity and productivity in desert ecosystems are largely dependent upon water supply. To achieve the stated goals of the Desert Biome, a predictive model for estimating patterns of water withdrawal from soil as a function of depth and time was proposed. In order for such a model to be tested, soil water transfer properties as functions of depth and water content need to be determined.

In soil systems, water flows in response to hydraulic head, temperature and osmotic gradients. Each of these driving forces is associated with a transmission coefficient which must be evaluated before field measurements of gradients can be used to compute water movement in soil.

Under desert conditions, soil water potentials are well below -1 bar during most of the year. (See Qashu, 1972, and Wheeler, 1972). So far, little work has been done in characterizing water flow properties through soil at these low water contents. Existing methods relate to agricultural lands under irrigated conditions, so that they must be expanded to encompass the range of water contents or potentials found in a desert environment. A method to evaluate hydraulic conductivity and soil water diffusivity was tested in which soil psychrometers were used where previously tensiometers had been used. Unfortunately, psychrometers do not function with any degree of reliability below a water potential of -50 bars. Much lower potentials are encountered in the warm desert soils, especially in the surface layers. Therefore, other methods will have to be developed.

OBJECTIVES

The overall objective to this study was to develop and test under field conditions a theoretical model for predicting water withdrawal patterns from soil as a function of depth and time in the presence or absence of plant roots under desert conditions. The objectives given in the project proposal were revised as a result of discussions with R. J. Hanks to include basic soil water transfer properties as determined in the laboratory. It was concluded that these functions were not well known for the soils of the Desert Biome Validation Sites. The specific objectives of the research conducted during 1972 were:

1. To determine soil moisture characteristic curves or water content as a function of matric potential.
2. To evaluate hydraulic conductivity and soil water diffusivity as a function of matric potential or water content in the dry range.

3. To determine liquid and vapor phase fluxes of soil water.

METHODS

Sampling and physical properties

Soil samples were collected (to a depth of 1 m) from the Santa Rita Experiment Range in Tucson, Arizona, and from the Rock Valley, Nevada, site (to a depth of 50 cm). The samples included loose fragments, monoliths and undisturbed soil cores of various lengths and diameters. As of this writing, no work has been performed on the Rock Valley samples because of the difficulties encountered in receiving permission from A.E.C. to enter the site and bring samples back to the laboratory. All the work reported hereafter pertains to the Sonoran Desert soil (Sonoita series).

The less than 2 mm fraction of the soil was analyzed for particle size distribution and was found to be of sandy loam texture (63% sand, 20% silt and 17% clay). Bulk densities were determined in the field by the rubber balloon method and in the laboratory by the clod and core methods (Blake, 1965). Results are given in Table 1. The values are high due to approximately 20% of the particles being larger than 1 mm in diameter. Saturated hydraulic conductivity was measured at 1.5 cm hr^{-1} on the small soil cores. The electrical conductivity of the saturation extract was $0.55 \text{ mmhos cm}^{-1}$ while the saturated water content was found to be 26.2% on a dry weight basis.

Table 1. Bulk density of Sonoita sandy loam

Sample	Depth cm	Sample Weight g	Bulk Density g cm^{-3}
Field test	0 - 15	3090	1.79
5-cm cores	2 - 7	162	1.79
	10 - 15	157	1.73
3-cm core	2 - 32	3890	1.60
Soil clods	0 - 20	85	1.83
	20 - 50	134	1.81
	50 - 95	92	1.82
Average			1.77

Transfer properties

Soil water flux in one dimension is described by the Darcy equation

$$v_z = K_z + K_z \left(\frac{\partial h}{\partial z} \right) \quad (1)$$

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where K_z is the hydraulic conductivity of the soil in the vertical direction at depth z ($z = 0$ at the surface), and h is the soil water matric suction, defined here as positive in unsaturated soil. For the horizontal case

$$v_x = K_x \left(\frac{\partial h}{\partial x} \right) \quad (2)$$

Equations (1) and (2) consider water fluxes due only to matric suction gradients. Fluxes due to osmotic and temperature gradients may be combined with equation (2) to give

$$v_x = K \left(\nabla H + \frac{L_{wD}}{K} \nabla \pi - \frac{L_{wq}}{K} \nabla T \right)_x \quad (3)$$

where ∇H , $\nabla \pi$, and ∇T are the hydraulic head, osmotic pressure, and temperature gradients respectively; L_{wD} is the conductivity associated with water transfer due to salt concentration gradients, and L_{wq} represents the effect of the temperature gradient on water transfer in the vapor and liquid phases.

Hydraulic conductivity (K) was measured under isothermal conditions (24 ± 1 C) on 30-cm length of 10-cm diameter cores by a transient flow method modified from that of Weeks and Richards (1967)*. At first, water was withdrawn from one end of the column through a hollow ceramic cell under controlled suction. But as the column dried out, the ceramic cell was removed and the water allowed to evaporate freely into the ambient atmosphere, while the tensiometers, which were inserted at four different distances from the end at which water was withdrawn, were replaced by soil psychrometers as they went off scale. The soil psychrometers had been previously calibrated in potassium chloride solutions at 25 C according to the procedures outlined by Wiebe et al. (1971). The volume of outflow was measured by a burette attached to the ceramic cell and by weighings of the entire apparatus when the column was evaporating. The volume of outflow and the four suctions were recorded periodically. It was estimated that, for this soil at least, the osmotic pressure component, as measured by the psychrometers, was negligible since the electrical conductivity of the saturated extract was so low. Letey (1968) has concluded that the value of the coefficient L_{wD} was relatively low in all soil systems, although it may approach the value of K as the soil suction increases.

Two soil cores were used. One column (Column 1) was packed in the laboratory with loose soil from the 0 to 20 cm depth at an average bulk density of 1.4 g cm^{-3} . It was later found that this value was too low, as shown in Table 1. Only the tensiometer range was covered in this trial. The second column (Column 2) was taken in the field from the 2 to 32 cm depth. Its average bulk density was calculated at 1.6 g cm^{-3} . The suction at 2.5 cm from the drying end of the column reached -50 bars at the end of the experiment. After the run was completed, the field core was sectioned into 1 cm lengths and water contents were determined gravimetrically.

* Their equation (6) should read: $\dots (1 + n_t b_j)$ instead of $(1 \times n_t b_j)$.

Calculation of hydraulic conductivity and soil water diffusivity were carried out on an IBM 360/50 Data Processing System using a program written in Fortran IV. This program yields as intermediary results values of volumetric water content as a function of matric suction. These variables are assumed to be related by an equation of the form

$$\theta(h) = ah^{-b} \quad (4)$$

In this equation, the constants a and b are calculated by the least squares method taking logarithms of both sides of equation (4) (h is expressed in cm of water or millibars). The relation between K and h is represented by

$$K(h) = ch^{-d} \quad (5)$$

where $K(h)$ is expressed in cm hr^{-1} in cm of water, and c and d are empirical constants calculated by the least squares method from the logarithmic form of the equation. Diffusivity is related to hydraulic conductivity by the following equation

$$D_{x,t} = K_{x,t} \left| \left(\frac{\partial h}{\partial \theta} \right)_{x,t} \right| \quad (6)$$

The reciprocal of $\left| \left(\frac{\partial h}{\partial \theta} \right)_{x,t} \right|$ is the differential water capacity ($C_{x,t}$), which can be calculated from the derivative of equation (4) using a numerical differentiating subroutine in the program mentioned above.

RESULTS

The moisture characteristic curves for the two columns for desorption are given in Figure 1. Data points correspond to experimentally determined values. The lines correspond to values calculated from the transient flow method according to equation (4). Gravimetric water contents were obtained by dividing θ by the bulk density. These curves are compared with data from Wheeler (1972) using the desorption isotherm he obtained for a soil sample from the same study site at a depth of 35 to 43 cm. An equation was fitted to these data taking logarithms of both variables and applying the linear least squares technique. It must be noted that the moisture characteristic curve for Column 1 is extrapolated from data covering only the -0.03 to -1 bar range. No attempt was made to investigate hysteresis of the water content-suction curves. Wheeler (1972) has shown that hysteresis for this soil is quite small.

Unsaturated hydraulic conductivity values calculated from Column 1 over the suction range -0.03 to -1 bar are shown in Figure 2. The same range is covered in Figure 3 for Column 2, whereas values covering the range -0.03 to -50 bars suction for Column 2 are given in Figure 4. The experimental points for K as a function of h for three positions along the column are shown. Again, the straight line represents the least squares logarithmic equation which can be written in the form of equation (5). The comparison

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of individual values of K in Figures 2 through 4 and values computed from equation (5) show that 39% of the 180 relative error values are less than 30%; 71% of these values are less than 50%. The agreement is much better if only Figures 2 and 3, covering the tensiometer range of soil suction, are compared.

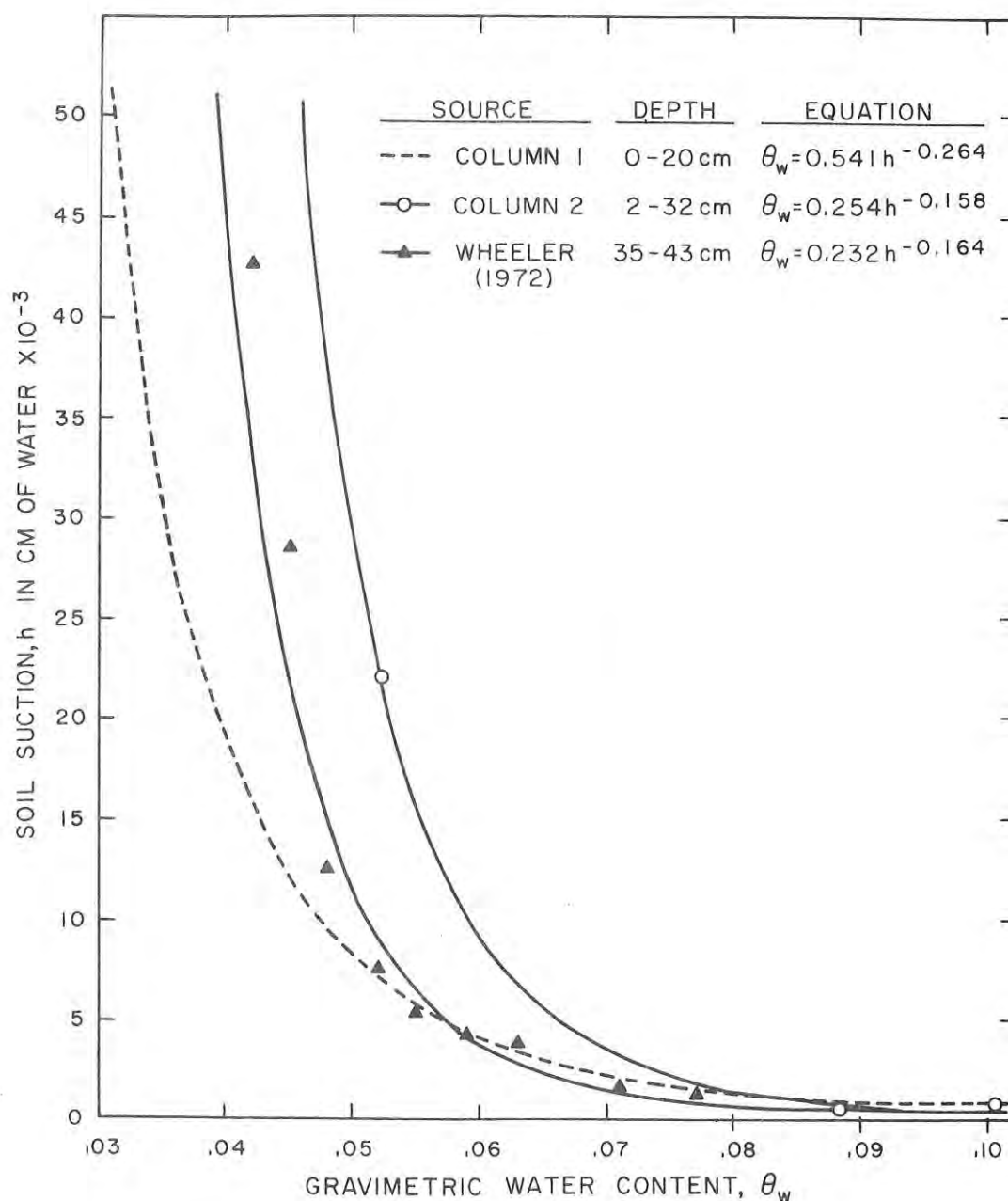


Figure 1. Gravimetric water content (θ_w) as a function of soil matric suction (h) during desorption of Sonoita sandy loam.

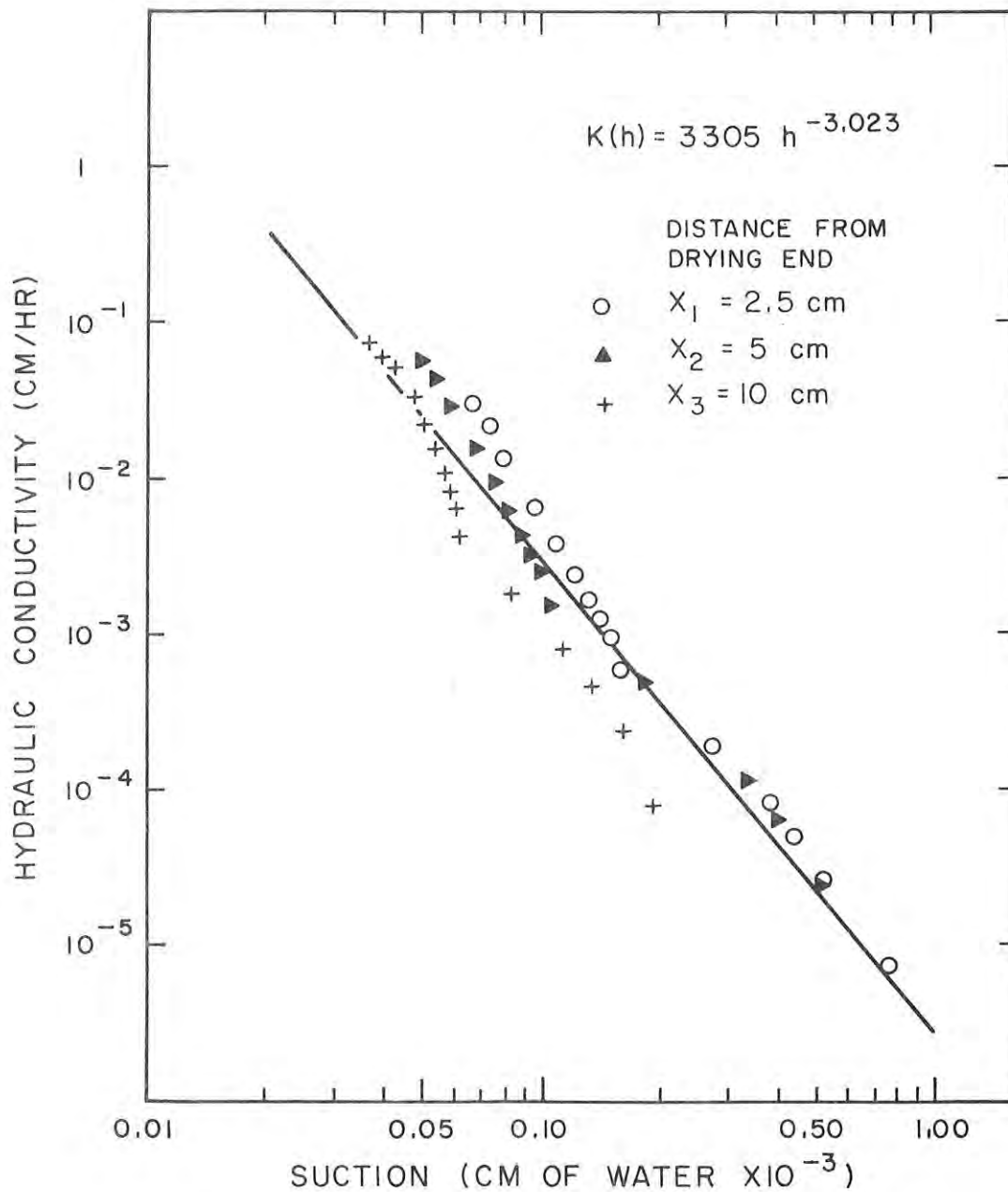


Figure 3. Experimental points given for hydraulic conductivity at three locations and plotted as a function of matric suction for Column 2. Data cover only the tensiometer range.

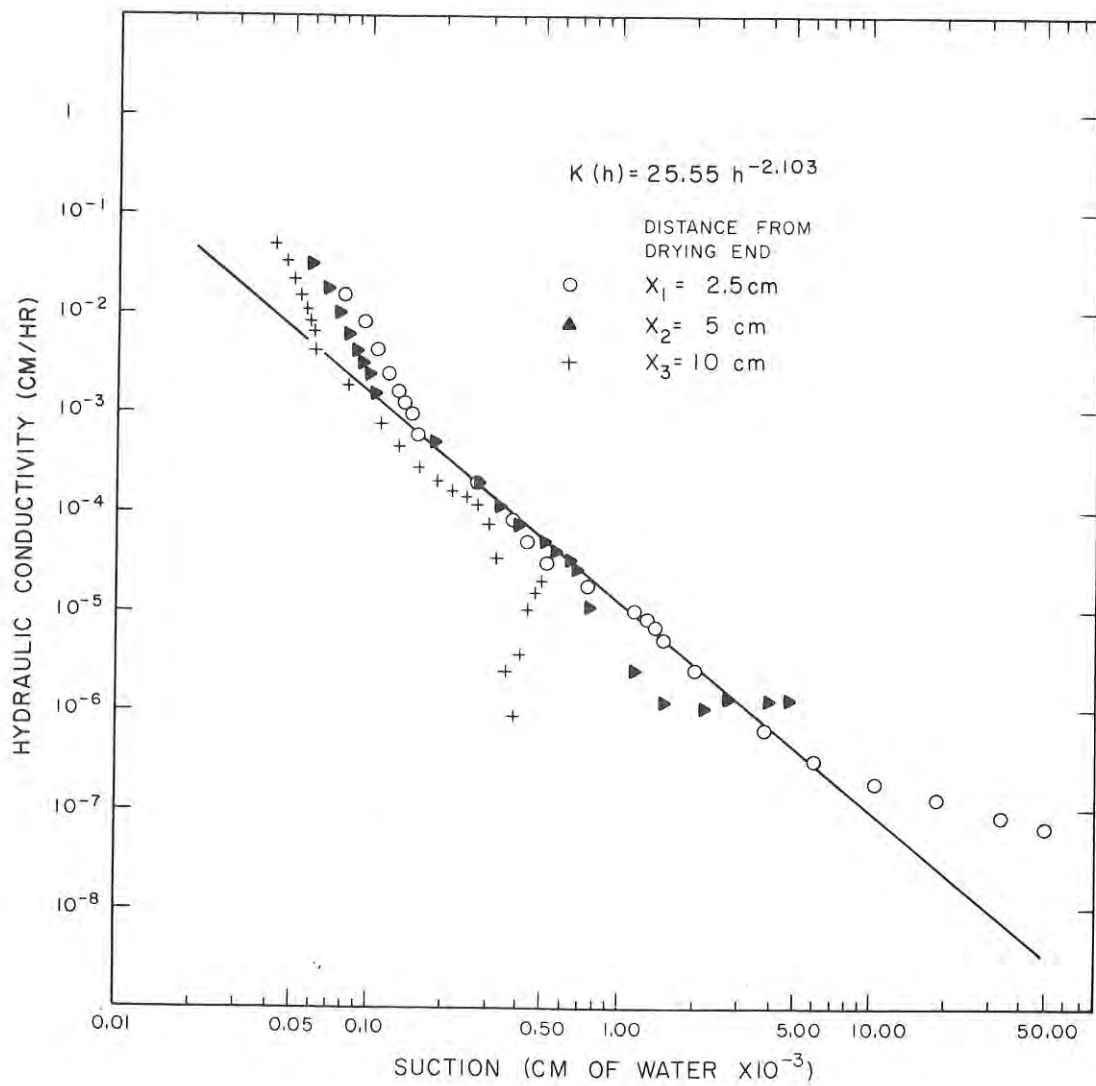


Figure 4. Hydraulic conductivity plotted for matric suctions up to -50 bars for Column 2.

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Weeks and Richards' method assumes the relationship between suction (h) and distance (x) from the drying end of the column to obey an exponential function represented by

$$h(x)_t = m_t x^{-nt}, \quad x > 0 \quad (7)$$

at any time (t) greater than zero. The greater disparity noted in Figure 4 can be attributed to the fact that in the drier range ($h > -5$ bars) this relationship does not hold. Reasons for this will be given in the discussion section.

DISCUSSION

The water characteristic curve for desorption (Figure 1) obtained experimentally by Wheeler (1972) is in close agreement with the curve calculated from Column 2. Better agreement still might have been obtained had the soil samples been for the same depth. Wheeler's data show that a shift of these curves towards lower water contents occurs with increasing depth in the profile, due to decreasing clay content as the depth increases. The equation obtained from Column 1 diverges most. This may be the result of extrapolation to -50 bars suction from data covering only the tensiometer range.

The general agreement between experimental and calculated conductivity values is good. Examination of Figure 4 suggests, however, that perhaps two equations, for the wet and dry portions respectively, would fit the data points better. Above -6 bars suction, the experimental points tend to lie consistently above the calculated curve. Several reasons for this may be pointed out.

First, as mentioned earlier, equation (7) is not obeyed at these higher suctions. Suctions calculated from this set of equations at the first position along the column ($x_1 = 2.5$ cm) would be somewhat lower than the measured values. The experimental K values would then fall closer to the calculated line.

Second, it was thought that vapor phase fluxes might contribute increasingly to the total flux of water at higher suctions. However, calculations of the water flux due to vapor diffusion alone, at a point in the column 2.5 cm from the drying end where suction was -50 bars, accounted for only 4% of the total flow. However, the same calculations carried out at the plane $x = 1$ cm, for which gravimetric water content was 0.03 (determined at the end of the experiment), showed that all the flux was in the vapor phase. The diffusion coefficient for vapor was found to be $2.51 \times 10^{-5} \text{ cm}^2 \text{ sec}^{-1}$, a value that correlates well with the work of Jackson (1964 and 1968) on Pachappa loam. Rose (1963) and Philip and De Vries (1957) have estimated that liquid flow ceases at a water content corresponding to about 0.6% relative humidity.

This value in turn would correspond to a suction of -700 bars at 24 C and to a gravimetric water content of 0.03% for the Sonoita soil.

A third possibility, and probably the most likely, is that a temperature gradient across the first few centimeters of the column may have occurred due to the cooling effect of the water evaporating at the surface of the soil. During studies unrelated to the present project, soil water flowed upward in a vertical column evaporating at its surface, while the hydraulic head gradient was zero. Therefore, in this study also, the flux could have increased while the hydraulic head gradient remained constant. And, since K was calculated as the ratio of the flux over the hydraulic head gradient, this would provide an explanation of why experimental K values were higher than calculated values. However, temperatures were not monitored during this experiment, leaving this hypothesis to be verified.

EXPECTATIONS

The research conducted in 1972 yielded data on the water transfer properties of the Santa Rita Experiment Range soils. Similar data will be collected for the Rock Valley soils.

Experiments will be conducted to characterize the fluxes due to temperature gradients for both the Sonoran and the Mohave desert soils. Because commercially available soil psychrometers unfortunately go off scale at about -50 bars pressure, and because it is too time-consuming to construct one's own, diffusion type experiments will be conducted to investigate moisture movement at soil water contents corresponding to pressures greater than -50 bars.

These results combined with those reported here will be used to test the model described in this study's proposal.

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1972 PROGRESS REPORT

DISTILLATION-CONDENSATION OF WATER AND NUTRIENT
MOVEMENT IN A DESERT ECOSYSTEM

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Research Memorandum, RM 73-44

MAY 1973

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ABSTRACT

Shrub vegetation on hill and wash sites in the Mohave Desert is similar in size and density. Soils immediately beneath shrubs on the hill slopes displayed a higher permeability (5 to 10 x faster infiltration) than soils of shrub interspaces, even though a raised mound of soil is formed at the base of each shrub. It is hypothesized that in addition to throughfall and stemflow, water supply to shrubs is enhanced by the micro-watershed attributes of the surrounding soil surface.

Seedling counts following a November rain (38 mm) showed that seedling density under shrubs was 10 times that in open spaces, with a higher mean weight per seedling in canopy habitats.

Evidence of variation in soil chemistry beneath shrub canopies is derived from pH values (open area 8.7, under *Larrea* 6.9, under *Fraseria* 8.1, under *Atriplex* 10.2), water-holding capacity, cation exchange capacity and elemental content. The pH of the immediate environment of the plant roots proved to be acidic (5.5), and extractant solution modified to pH 5.5 released higher levels of some soil elements than NH_4OAc extraction, particularly with regard to phosphorus, although Ca was extracted at about one tenth the concentration by the acid solution. Mg and Na were also less available under acid extracting conditions. The data suggest that roots modify their immediate chemical environment to accentuate major nutrient concentrations and mollify potential toxicities. Soils beneath shrubs varied in chemical content from soils sampled in interspace areas.

Cultures of seedlings of *Larrea divaricata*, *Atriplex canescens* and *Hymenoclea salsola* exhibited best growth on water which was chemically equivalent (inorganically) to leachate from soil occurring in shrub interspaces. Good growth occurred on nutrient solution equal to the pH 5.5 extract, but all seedlings died when watered with a solution chemically equivalent to leachate from soil taken beneath *Larrea* plants.

Little difference was found in chemical content of *Larrea* leaves between the Rock Valley site (A.E.C. Nevada Test Site) and Dump Canyon (Death Valley). *Atriplex* leaves were high in Na, Ca, K and Mg. Dead wood tended to concentrate Ca, and other cations, while P is removed from dead wood.

Methodology was inadequate to measure the quantity or quality of condensation water.

INTRODUCTION

Nutrient cycling in deserts is little understood, and is complicated by low soil water content for much of the year, and persistently high salt content. Studies of the distillation and condensation of water in desert soils (Evenari, 1962; Stark and Love, 1969) have raised questions concerning the importance of water distributed in this manner to plants, and particularly to nutrient cycling. Soil water which goes into the vapor phase during daytime under the influence of the strong heating of the soil surface should be chemically pure and essentially "distilled water". When the soil cools at night, this water condenses on soil particles and is particularly noticeable on the undersides of larger rocks. Since the distillation-condensation process has been going on for centuries on these same rock surfaces, it is hard to believe that there could be significant amounts of soluble salts left on these rock surfaces. Also, the periods during which free or mobile soil water exist in gravelly and sandy soils such as are found on the bajadas in Death Valley, are very short, usually only a few days after storms, and since most desert plants do take up water during the 3- or 4-month growth period, water concentrated by distillation-condensation should be important to the plants. The undersides of rocks which have mats of roots during the growth phase are observed to be dry in the evening, and moist the next morning from condensation. It has been suggested that plants on gravelly or sandy soils depend heavily on distillation-condensation water during the growing season.

This pattern of water uptake leaves some unanswered questions concerning nutrient uptake. The desert soils of Death Valley have a pH of about 7.6 to 10.2 and very high salt concentrations (Ca 2900 $\mu\text{g/g}$; Mg 3,680 $\mu\text{g/g}$; Na, 1400 $\mu\text{g/g}$). Some plants, such as *Allenrolfea occidentalis* (Wats) Kuntze. and *Atriplex confertifolia* (Torr. & Frem.) Wats. are well adapted to salty soils, and actually store large amounts of some of the abundant cations. Some of the plants which grow on the gravelly and sandy soils in Death Valley, however, are adapted to concentrate only moderate amounts of salts and are found mainly on the drier soils. *Larrea divaricata* Cav. and some annuals are much lower in salt content than is *A. confertifolia* which grows in the same soils. If the ephemeral soil solution, which is quite alkaline (pH 8.8-10.0) and high in salts is the main nutrient supplier, then the low-salt-tolerant plants must be highly selective in elemental uptake.

Observations show that existing individuals of the three dominant plants mentioned above nearly always have some dead organic matter associated with the root system. Often this is a dead root system from a plant which inhabited the spot much earlier, or it may be parts of the existing plant which have died. The roots of most of the

Living plants have been observed to be mycorrhizal during some parts of the year, particularly during the growth period. It has been postulated that dead, buried organic matter would have an ideal balance of micronutrients which could be available to mycorrhizal fungi for possible transport directly into the living roots. The dead organic matter is another potential direct source of nutrients for plant roots.

Rain water or bulk precipitation is a potential source of elemental input, but rain in the desert is infrequent and the annual input from rain is expected to be low. The amount of elements returned to the soil annually by throughfall (rain washing over the leaves) and stemflow (water washing down the stems) is not known, but is likely to be small because of the infrequency of the rains.

Lateral transport of elements in dust is an important factor near unpaved roads or eroded areas, but desert pavement tends to keep lateral movement to a very low level where there has been no disturbance of the pavement.

These observations raise some questions about the mode of nutrient cycling in deserts, and particularly about the requirements of desert plants for nutrients.

OBJECTIVES

The objectives of this work were to explore the various potential sources of nutrients for desert plants, and to study the importance of distillation-condensation in the soil as a water and nutrient source. The study concentrated on rocky and gravelly soils in Death Valley in *Larrea divaricata*, *Franseria dumosa* and *Atriplex confertifolia* vegetation. The goal was to determine what sources of nutrients and water are most important to these plants.

METHODS

Dump Canyon in Death Valley, one mile east of the Grapevine Ranger Station, was selected as the main study site because of the abundance of large rocks and the wide distribution of soils of gravel/sand type. The Nevada Test Site was selected as a secondary study site.

The area is hilly with *Larrea divaricata*, *Franseria dumosa* Gray. and *Atriplex confertifolia* as dominants. The plants are spaced naturally at 1-3 m, with seasonal annuals growing abundantly at the base of the shrubs, and sometimes in the open.

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The area receives about 50-60 mm of precipitation annually, although the actual rainfall is quite variable. Annual air temperatures range from about -1 to +46 C. Wind is a persistent and strong environmental factor which helps to keep the relative humidity below 5-10% during the day and 30-40% at night throughout much of the year.

Four soil pits were dug (two on hills and two in small washes), to 1 m depth and the soil profiles described. The four sites represent two examples each of the local variability between hill and wash locations. Soil samples were taken at 5 cm intervals to 35 cm depth and also from 60-65 cm depth for analysis. Zero tension lysimeters with plastic reservoirs were installed at 0.9 to 1.0 m in all four pits.

Four rain collectors made of 20 cm (i.d.) plastic funnels and attached to plastic reservoirs by Tygon tubing were set in holders in the field to catch water for water quality studies. The funnels were covered with cheesecloth to keep out insects.

The soil samples were analyzed for soil separates using nested sieves and the American Classification. Bulk density was determined for 0-10 cm and 20-25 cm from 8 locations (Buckman and Brady, 1969). Soil pH was determined for all depths collected. Samples which had passed a 1 mm sieve were extracted with 1N NH_4OAc for determination of the extractable cations, and the cation exchange capacity was determined on these same samples according to the procedures described by Jackson (1958). Since 1N NH_4OAc is used mainly for extracting cations from agricultural soils, it was felt that this extractant would have little relationship to the extractant in the immediate vicinity of the roots of desert plants. Tests of the pH of crushed and intact moist roots using pH papers showed that the roots produced a pH of about 5.5 in their immediate environment. For this reason, a second set of extractions was run on a series of soil samples from 5 cm intervals beneath the three different living shrub species, beneath dead shrubs and in the open. All extractions were run on an atomic absorption spectrophotometer (Techtron AA-120) for Ca, Cu, Fe, K, Mg, Mn, Na, and Zn. Total organic nitrogen plus soluble nitrates was determined on all samples using the modified micro-Kjeldahl procedure (Jackson, 1958) and phosphates were determined colorimetrically using the molybdenum blue procedure (Black et al., 1965).

Since it did not rain until the end of the study, no natural soil leachate could be collected. To find out approximately how much of each of the biologically important elements are available in the soil solution, funnels were set up in the field, and soil samples from various depths and from the open and under shrubs of the three species were leached with 500 ml of deionized water (pH 6.8). The water-holding capacity of the soil samples was determined by subtracting the ml of leachate from the original ml added to the soil after 1 hr drainage. The elemental content and pH were determined by the same procedures used for soils.

The numbers of seedlings germinating after 38 mm of rain was determined by counts/ m^2 under the three shrub species and of m^2 plots in the uphill adjacent watershed on 100 sites in the wash and on clay soils.

The undersides of rocks are potential sites for the condensation of water and for the solution of salts by condensed water. Some surface rocks had white mineral crusts while others did not. The dominant rock types present were determined, and 100 rocks were turned over and the nature and type of crust was recorded for each, along with rock type. To determine if there are soluble materials which are biologically important on the undersides of rocks, 12 rocks were washed with 100 ml of deionized water, and another 16 rocks were washed with 100 ml of deionized water adjusted to pH 5.5 using HCl. The water was applied to an area of 10 x 10 cm on the undersides of rocks of various compositions, and the pH and elemental content of the water after washing were determined as with soils.

Another method of studying the elements available to roots growing in mats under rocks which received daily natural condensation water, was to place ashless filter paper under marked rocks for periods of 1 hr, 24 hr, and 30 days. Ten of the rocks used for this study had root mats, and ten did not. Another ten rocks were in a wash, while those mentioned previously were on the slopes. Some filter papers were supported by rings so that they did not touch the soil or rocks. pH papers were placed under the rock not touching the filter papers, but rarely was there enough moisture moving to produce a reaction in the pH papers. The 260 filter papers from field tests were treated in two ways. One group was placed one at a time in a funnel and rinsed with 10 ml of deionized water so that a group of 10 papers from a single run was leached to make 100 ml which was analyzed for elemental content and pH as with the soils. The second group of 10 papers was put into an Erlenmeyer flask, predigested with concentrated nitric acid and the digestion completed with tri-acid ($\text{HNO}_3 - \text{H}_2\text{SO}_4 - \text{HClO}_4$). Controls of 10 unexposed papers were run in the same manner to determine if there were any interfering elements in the filter paper. The digestate was run for elemental content (Ca, Cu, Fe, K, Mg, Mn, Na, and Zn) on the atomic absorption spectrophotometer. Total nitrogen was determined by the modified microKjeldal procedure, and phosphates were determined colorimetrically by the molybdenum blue method (Black et al., 1965).

The permeability of the soil in the open and under the shrubs was determined by seating a 20 cm diameter cylinder in the soil to a depth of 4-5 cm and timing the infiltration of 1 liter of deionized water into the soil.

Three times during the year, before growth began (February) during growth (May) and after growth was completed (July), leaves and small branches of *Atriplex confertifolia*, *Larrea divaricata*, and *Franseria dumosa* were collected, cleaned, dried at 70 C, ground to pass a 1 mm sieve, and 0.5 g subsamples digested as described for filter paper

2.3.5.4.-6

(with uptake in 15 ml 6N HCl). The digestate was analyzed in the same manner as was the filter paper except that the molybdophosphoric acid yellow reaction was used for phosphorus. Samples of old wood above and below ground, live wood with bark, roots, and litter were analyzed in the same manner as the leaves.

The movement of water in the soil by distillation-condensation was measured gravimetrically using a field balance. The percent moisture present under large rocks was determined after 6 p.m. and again at 6 a.m. each day in the field to determine if distillation-condensation was occurring. Gravimetric moisture determinations of soils and leaves were made periodically.

The radionuclide studies originally projected as a part of this work could not be carried out in the field because of unforeseen licensing problems.

FINDINGS AND DISCUSSION

The results presented below are for the specific study sites in Death Valley and Rock Valley. The extent to which these data may safely be extrapolated is not known at this time, but comparisons with data collected and analyzed in a similar manner suggest that these results may have generally broad applicability.

Soils

The permeability of the soil proved to be low, 3.5 cm/hr for deionized water standing over 314 cm² of soil in the open (Table 1). The actual infiltration rate was probably much lower since no guard ring was used, which allowed horizontal flow. Also, the influence of raindrop impact is not included in this study. As water strikes the surface of the soil, very fine clay particles float to the surface and seal it so that air cannot move out freely, and water cannot move in readily. Therefore, only the slowest rains of long duration would penetrate the soil in the open to a depth where the moisture would be beneficial to the roots. A defloculating substance (Pentrex) was applied which improved the permeability slightly (32 min). The properties of impermeable desert soils are known and this knowledge was used in "runoff" farming in early times in Israel (Tadmor et al., 1971). The soils on the slopes have 14.0% silt and clay at 5 cm, 40% fine sand and 46% coarse sand and gravel.

The penetration of water in the wash areas was much faster than in the open (18.3 - 42.8 cm/hr, theoretical, Table 1). With this information and a knowledge of the topography, one would expect that the impermeable hills would shed great quantities of water into the washes and that plants in the wash would be much taller and more vigorous than those on the slopes because of the extra water. Subjective observation

of the vegetational distribution pattern shows that this is not the case. The shrubs on the slopes are about the same in height and vigor as those in the wash. In dry years, the shrubs in the wash may be "greener", but where the same species are involved, they are usually about the same size as the plants on the slope. This prompted an investigation of the permeability of the soil under shrubs. Water must enter at some point on the slopes or the vegetation would not be so uniformly distributed or so uniform in size. The base of each shrub has a mound of lighter soil combined with much organic matter. At first glance, these mounds would appear to be poor places for water entry because of their elevation, but repeated tests (Table 1) showed that these areas directly under shrubs are much more permeable (infiltration rate of 41.5 - 125 cm/hr) than are the open soils (5 to 10 x faster infiltration under shrubs than in the open). The presence of partly decomposed organic matter under the shrubs appears to prevent the formation, upon wetting, of solid clay skins and hence maintains a freer flow of air and water at the air-soil interface.

Table 1. Infiltration rate on Death Valley soils (avg cm/hr)

Site	Location	cm/hr
1	open hill	3.5
2	open wash	18.3
3	open hill	7.8
4	open wash	42.8
1	under <i>Larrea</i>	83.3
1	under <i>Franseria</i>	41.5
1	under <i>Atriplex</i>	125.0

Thus, in theory, in a rain of average intensity, the water penetrates slightly in the open but is quickly sealed off by clay and begins to run over the surface until it reaches a shrub base where it quickly moves into the soil. Where desert pavement and the natural vegetation have been undisturbed there is little erosion, but gully erosion on a small scale is common where bulldozers have cleared the surface of the clay soils, or along car tracks. Because of the low soil permeability in the open, each shrub has its own microwatershed which supplies it with water. Unfortunately, this was not observed during an actual storm, but the theory held up under simulated storm conditions. Adams et al. (1970) found that soil which had been subjected to fire was very water repellent in *Larrea* deserts. Lyford and Qashu (1969) found 2 to 3 times greater infiltration under shrubs in Texas deserts. Sammis et al. (1972) described the theory of infiltration in some detail.

2.3.5.4.-8

This pattern of water movement might have considerable significance to nutrient cycling, seed germination and plant growth. The growth form of many desert shrubs conforms to Y or V patterns which would funnel water to the base of the plant through stem flow. Also, most of the leaves which fall from the shrub land at its base. Later, sand partly covers these and decay begins. The runoff and funneling patterns would supply more water beneath a shrub than elsewhere, making more water available for leaf decay and hence a recycling of elements in the leaves back into the soil.

The zone directly under a shrub is also a main point for the germination of annual seeds, especially in a dry year. In a wet year with over 40 mm of rain at a time, seeds germinate in a variety of microhabitats. In a dry year, such as 1972, very few seeds germinate in the open, ($0.01/m^2$) but many germinate under shrubs ($10-250/m^2$). This difference in germination is probably partly due to insufficient leaching of inhibitors in seeds in the open in a dry year, but greater leaching under the shrub which receives more water. Counts of the numbers of seedlings present in November 1972, two weeks after 38 mm of rain, showed that 10 times as many seedlings per meter square (av 4.0) were found under shrubs as in the open (av. 0.4).

Atriplex had the largest numbers of seedlings (55% of the count) with a concentration of seedlings at the margin of the shrub canopy and in the shallowest litter. *Atriplex* tends to form deeper litter (to 2 cm) than do the other species and the soil mounds have rapid infiltration which could influence leaching and germination. *Larrea* had 15% of the total seedlings counted with weak mound formation, except in very old specimens. *Franseria*, with the lowest infiltration rates and good mound formation, had 30% of the seedlings counted on clay soils and provided a good germination site. These data represent only one sampling during the cool, moist period of the year (November), and mainly fall or low-temperature germinators were found.

Larrea has been found to have large numbers of young seedlings in the spring. Invariably, the seedlings under shrubs were larger than those in the open. The average dry weights of groups of ten seedlings under the shrubs were 0.089 g compared to 0.0536 g for groups of ten seedlings in the open. Where small rocks impede water movement in a low spot, or where a rock has been moved, germination may be slightly better than on flat or convex desert pavement surfaces. Soil moisture to 5 cm under the shrubs, three weeks after the rain, was 2.36% compared to 1.73% in the open (November, 1972). Whether growth differences are the result of moisture differences or N and P differences is not known.

Shrubs can alter soil pH as seen in the soil immediately under *Larrea divaricata* which has a pH of about 6.9 - 8.2, while that under *Franseria dumosa* has a pH of 7.7 - 8.3, and that under *Atriplex confertifolia* has a pH of 8.8 - 10.2 (Table 2). This alteration of soil pH, with the addition of acids, cations and anions, as well as the alteration of infiltration rate, creates a soil chemistry very different from that in the open.

Table 2. pH of Death Valley Soils

Site	Depth(cm)	pH
1 (open)	0-5	8.3
	5-10	8.7
	10-15	8.7
	15-20	8.9
	20-25	8.6
	25-30	8.8
2	0-5	8.4
	5-10	8.5
	10-15	9.0
	15-20	9.0
	20-25	8.9
	25-30	8.0
3	0-5	8.6
	5-10	8.6
	10-15	8.6
	15-20	8.7
	20-25	8.8
	25-30	8.8
4	0-5	8.6
	5-10	9.0
	10-15	8.5
	15-20	8.7
	20-25	8.7
	25-30	8.7
Soil		
Under <i>Larrea</i>	0-5	Range 6.9 - 8.2
Under <i>Franseria</i>	0-5	Range 7.7 - 8.3
Under <i>Atriplex</i>	0-5	Range 8.8 - 10.2
Under rocks with roots	0-5	Range 7.3 - 9.0
Under rocks no roots	0-5	Range 8.6 - 8.7
Soil leachate (D.W.)		
Under <i>Larrea</i>		Range 6.9 - 6.9
Under <i>Franseria</i>		Range 8.0 - 8.2
Under <i>Atriplex</i>		Range 10.1 - 10.2
In open		Range 8.6 - 8.8

When soil was collected from the open and beneath the three shrub species in 20 cm depth increments, the pH of distilled water leachate of soil in the open ranged from 8.6 - 8.8 while that under *Larrea* was 6.9, under *Franseria* 8.0 - 8.2, and under *Atriplex* 10.1 - 10.2 (Table 5). Again, the shrubs appear to have modified the chemistry of their immediate environment so that *Larrea* soils are less alkaline, and *Atriplex* soils are considerably more alkaline than soil of the same depths without shrubs.

The water-holding capacities of these soils, when saturated, also differ. Soil under *Atriplex* holds less water (52.1%) than soil under *Larrea* (59.8%) or under *Fraseria* (66.9%). Schumm and Lusby (1963) described seasonal variations in infiltration capacity of northern desert hillslopes indicating a difference in water-holding capacity of the soil.

The elemental content of soil indicates quite different levels of extractable elements when 1N NH_4OAc was used and when pH 5.5 HCl (to approximate the conditions adjacent to roots) was used (Tables 3 and 4). The NH_4OAc extraction which is typically used for agricultural soils shows 2350 $\mu\text{g/g}$ for Ca, while the pH 5.5 HCl extraction shows about one-tenth as much, or 240 $\mu\text{g/g}$ at 0-5 cm depth for the open site 3. Copper is slightly lower (0.23 $\mu\text{g/g}$) in the pH 5.5 extraction than in the NH_4OAc extraction (0.40 $\mu\text{g/g}$). Iron, on the other hand, is higher in the pH 5.5 extraction, 35 $\mu\text{g/g}$, compared to 0.5 $\mu\text{g/g}$ in the NH_4OAc extraction (0-5 cm, site 3). Potassium is only slightly lower in the pH 5.5 extraction (81 $\mu\text{g/g}$) than in the NH_4OAc extraction (95 $\mu\text{g/g}$). Magnesium, an element needed in relatively small amounts, is moderately high (1950 $\mu\text{g/g}$) in the NH_4OAc extraction compared to 11 $\mu\text{g/g}$ in the pH 5.5 extraction. Manganese, a trace element, was slightly higher in the pH 5.5 extraction (0.55 $\mu\text{g/g}$) than in the NH_4OAc extraction (0.1 $\mu\text{g/g}$).

Total nitrogen was determined by the modified microKjeldahl method, and was about the same in February as in June. Sodium, which can be toxic to some plants, was highest in the NH_4OAc extraction, but not more than 1.5 x higher than in the pH 5.5 extraction (59 $\mu\text{g/g}$, Tables 3 and 4). Phosphorus was about 10 x higher (10.3 $\mu\text{g/g}$) in the pH 5.5 extraction than in the NH_4OAc extraction (1.1 $\mu\text{g/g}$). Since phosphorus is extremely important to plant growth and is generally high in desert plant leaves, it would appear that the pH 5.5 HCl extraction would more nearly provide levels of P needed by the plants than did the other extraction. Zinc availability was slightly different between the two extractions (0.40 $\mu\text{g/g}$ and 0.55 $\mu\text{g/g}$ at 0-5 cm, site 3). These differences in extractable elements appear to be related to the pH of the extracting solution. The solution most like the pH of the root microenvironment should be best.

Although only one level (0-5 cm) and one site (3) were compared, the same general relationships hold for soils lacking shrubs for most depths and sites. The pH 5.5 HCl extraction does not show high levels of elements which might be toxic at any levels to 35 cm, while the 1N NH_4OAc extraction has high levels of Ca at all levels, high levels of Mg at all levels, and high Na at 25-30, and 30-35 cm and at 55-60 cm (595-1300 $\mu\text{g/g}$), which could be toxic or cause nutrient imbalances or microorganism deficiencies which would be detrimental to roots. Judging by nutrient levels needed in liquid culture of plants (Hewitt, 1966), the levels of elements in the pH 5.5 extraction should support plant growth.

Table 3. Content of ammonium acetate extractable elements in Death Valley and Rock Valley soils sampled at interspaces (avg µg/g soil)

<u>Death Valley</u>											
Site	Depth(cm)	Ca	CU	Fe	K	Mg	Mn	N	Na	P	Zn
1	0-5	2800	0.35	1.0	92	2400	0.20	282	65	1.1	0.35
	5-10	2825	0.33	1.1	93	2360	0.20	259	81	1.0	0.35
	10-15	2925	0.45	1.2	93	2510	0.18	238	74	1.0	0.45
	15-20	2725	0.40	1.4	92	2600	0.08	476	71	1.0	0.35
	20-25	2725	0.33	1.2	93	2580	0.15	322	71	1.0	0.38
	25-30	3450	0.48	1.1	93	2960	0.14	280	595	1.0	0.35
	55-60	2375	0.45	1.0	93	1290	0.11	266	875	3.0	0.30
2	0-5	2075	0.39	1.4	90	1120	0.30	182	22	1.4	0.20
	5-10	1900	0.35	1.7	90	1115	0.20	182	22	0.6	0.38
	10-15	1900	0.35	1.4	93	1260	0.20	182	28	1.1	0.32
	15-20	1900	0.30	1.3	94	1480	0.20	196	38	1.0	0.30
	20-25	1090	0.45	1.0	95	1017	0.20	210	59	1.0	0.45
	25-30	2000	0.40	0.8	95	1555	0.17	367	66	1.5	0.40
	55-60	1875	0.35	0.7	96	1360	0.13	189	860	0.9	0.38
3	0-5	2350	0.40	0.5	95	1950	0.10	329	71	1.1	0.40
	5-10	2600	0.37	0.7	94	2800	0.30	336	94	1.5	0.39
	10-15	2675	0.35	1.0	94	2800	0.05	280	94	1.6	0.43
	15-20	2625	0.45	1.0	94	2720	0.10	-	99	1.6	0.40
	20-25	2650	0.44	0.5	95	2360	0.15	-	595	1.6	0.55
	25-30	2600	0.48	0.5	95	3680	0.12	210	98	1.3	1.00
	55-60	2250	0.40	0.5	93	790	0.13	238	1400	1.4	0.40
4	0-5	2175	0.33	1.0	89	1050	0.15	-	18	1.5	0.48
	5-10	2225	0.33	1.0	89	1190	0.23	210	22	1.8	0.43
	10-15	2425	0.40	1.0	90	1570	0.27	252	27	1.0	0.43
	15-20	2450	0.40	1.0	92	1660	0.20	266	30	1.4	0.38
	20-25	2650	0.39	1.0	92	1760	0.20	224	40	1.2	0.35
	25-30	2250	0.35	1.0	92	1960	0.15	231	65	3.0	1.00
	55-60	2150	0.40	1.0	89	3375	0.12	224	1200	1.6	0.55
<u>Rock Valley</u>											
Wash	0-5	2050	0.30	0.7	94	80	0.45	168	47	1.7	0.50
	5-10	2100	0.45	0.5	96	81	0.35	504	565	1.2	0.75
	10-15	2025	0.38	0.7	92	77	0.33	413	77	1.6	0.53
	15-20	2125	0.35	0.7	94	80	0.30	119	89	1.7	0.53
Hill	0-5	2825	0.40	0.9	95	3520	0.20	136	59	2.7	0.24
	5-10	2700	0.45	1.0	92	2720	0.18	420	80	3.0	0.35
	10-15	2500	0.45	1.0	92	3420	0.40	259	60	4.1	0.20
	15-20	2950	0.38	1.0	93	1340	0.20	182	62	1.8	0.30

Table 4. Content of pH 5.5 extractable elements in Death Valley soils (avg $\mu\text{g/g}$ soil) from interspaces and under shrubs

Site	Depth(cm)	Ca	CU	Fe	K	Mg	Mn	N	Na	P	Z
3 open	0-5	240	0.23	35.0	81	11	0.55	287	59	10.3	0.55
	5-10	220	0.18	21.0	81	13	0.35	231	37	6.7	0.30
	10-15	230	0.15	15.0	84	13	0.20	259	55	5.9	0.30
	15-20	210	0.30	27.0	83	9	0.25	273	54	11.5	0.60
	20-25	209	0.30	26.0	81	9	0.30	245	53	10.3	0.55
4 open	0-5	170	0.20	16.0	74	9	0.35	175	47	3.7	0.20
	5-10	175	0.15	17.0	78	9	0.40	210	32	4.7	0.20
	10-15	165	0.15	9.0	78	9	0.25	248	36	4.0	0.20
	15-20	185	0.20	16.0	76	9	0.25	255	43	4.9	0.10
	20-25	184	0.20	11.0	79	9	0.15	168	51	4.8	0.10
3 under dead <i>Larrea</i>	0-5	280	0.23	13.0	65	17	0.55	903	50	4.0	0.10
	5-10	213	0.30	25.0	81	10	0.50	364	48	8.0	0.30
	10-15	233	0.20	30.0	87	10	0.50	399	43	10.3	0.38
	15-20	203	0.43	27.0	89	6	0.23	308	58	8.3	0.30
	20-25	240	0.28	27.0	90	5	0.20	259	96	8.5	0.28
3 under live <i>Larrea</i>	25-30	280	0.37	24.0	90	4	0.20	301	177	8.3	0.25
	30-35	303	0.38	23.0	89	4	0.20	746	230	8.8	0.20
	0-5	235	0.30	13.0	87	15	0.45	826	66	0.4	0.38
	5-10	222	0.33	27.0	85	11	0.27	350	46	0.5	0.50
	10-15	203	0.33	29.0	86	10	0.25	385	41	0.4	0.45
1 under dead <i>Franseria</i>	15-20	206	0.25	28.0	87	11	0.25	280	47	0.5	0.55
	20-25	206	0.28	22.0	87	13	0.25	287	94	0.6	0.50
	0-5	78	0.28	7.0	80	12	0.30	1904	49	2.2	-
	5-10	172	0.15	18.0	89	11	0.28	826	49	20.0	0.50
	10-15	115	0.23	21.0	88	6	0.25	581	35	17.0	0.10
1 under live <i>Franseria</i>	15-20	108	0.25	25.0	88	6	0.23	574	40	14.1	0.10
	20-25	140	0.15	31.0	89	6	0.25	420	45	16.5	0.15
	25-30	150	0.20	28.0	88	6	0.25	441	40	14.0	-
	30-35	155	0.15	12.0	88	4	0.23	-	260	7.0	-
	0-5	128	0.45	9.0	89	24	0.45	1386	92	52.0	-
1 under dead <i>Atriplex</i>	5-10	95	0.40	15.0	90	9	0.30	1400	36	16.0	-
	10-15	75	0.38	15.0	89	7	0.28	553	31	10.0	-
	15-20	73	0.20	17.0	89	6	0.25	532	24	8.0	-
	20-25	90	0.18	14.0	89	5	0.28	350	34	8.0	-
	25-30	107	0.30	14.0	90	5	0.23	364	90	7.0	-
1 under live <i>Atriplex</i>	0-5	198	0.33	12.0	86	17	0.38	644	74	5.3	0.20
	5-10	148	0.38	22.0	87	10	0.35	329	59	7.8	0.25
	10-15	202	0.50	28.0	90	6	0.30	287	67	11.3	0.40
	15-20	200	0.50	26.0	91	4	0.30	380	178	11.8	0.40
	20-25	90	0.23	12.0	67	70	0.63	252	112	3.3	0.10
1 under dead <i>Atriplex</i>	25-30	82	0.20	11.0	62	48	0.63	310	156	5.8	0.10
	30-35	39	0.20	9.0	62	48	0.92	-	378	7.0	0.10
	0-5	105	0.20	20.0	168	28	0.63	756	237	9.5	0.23
	5-10	106	0.20	18.0	169	25	0.63	322	240	8.0	0.25
	10-15	75	0.25	19.0	590	55	1.10	336	600	7.5	0.23
1 under live <i>Atriplex</i>	15-20	94	0.20	19.0	72	33	0.90	350	180	7.3	0.20
	20-25	81	0.33	15.0	70	50	0.78	336	99	6.0	0.10
	25-30	80	0.50	15.0	73	50	0.63	287	92	5.3	0.10
	30-35	90	0.50	15.0	72	50	0.63	252	87	4.5	0.10

Site 3 does not have any *Franseria dumosa*. The texture of the soils, their moisture and the C.E.C. (Table 5) are not vastly different among sites 1, 2 and 3, although site 3 has the highest C.E.C. The lack of *Franseria* on site 3 would not appear to be related to the physical characteristics of the soil, but may be linked to their chemical properties. Site 3 does have less surface moisture than profiles 1 and 2, but the storage at depth is not greatly different (Table 6). The high levels of Mg which are known to be present at 25 cm and below from the NH_4OAc extraction suggest that this element could be limiting to the survival of *Franseria*, which also has low foliar Mg compared to that of *Atriplex* foliage (Table 9). Site 3 also had more water extractable Ca, Fe, K, Mg, Mn, Na, P, and Zn (Table 7) than did the other sites. The absence of *Franseria* on site 3 could be coincidence, or it could be related to the abundance of Na, or Zn or Cu below 25 cm, or to some unmeasured element.

These data suggest that the uptake of element by the roots of desert plants may be governed by the chemistry of the immediate environment of the root rather than the broad soil chemistry. We know from the NH_4OAc extractions that high levels of Ca and Mg occur along with Na in these soils, but it is unlikely that the roots actually live in this type of immediate chemical environment. The fact that the roots of all three shrub species studied appear to maintain a pH of about 5.5 - 6 in soils with an overall pH of 7.8 - 10.2 to 30 cm (Table 2) suggests that the root is able to modify its immediate environment to solubilize and extract levels of biologically important elements needed by the plant, without saturating the soil solution with possibly toxic levels of abundant Ca, Na, and Mg cations. This could be, conceivably, the mechanism which allows the low concentrator plants such as *Larrea* to survive in alkaline soils. Certainly the balance of cations and anions in the pH 5.5 HCl extractions is better for most biological terrestrial uptake than that in the 1N NH_4OAc extraction. The pH 5.5 HCl extractant is probably not the same extractant used in the dynamic environment by the plant, but the pH is correct.

In general, the soil under dead *Larrea* (estimated 5+ years dead) had more P (at 20-25 cm) and less Mg and Zn for the same sites than did the soil under live *Larrea*. The difference in P under the living shrub (0.6 $\mu\text{g/g}$) and that under the dead shrub (8.5 $\mu\text{g/g}$) is fourteen-fold at 0-5 cm, indicating that this element is in strong demand by living plants, whereas it tends to build up under dead shrubs lacking annuals or other growth (Table 4), and under low rainfall. The differences in phosphate at all depths vary widely from those under live and dead *Larrea* suggesting some basic differences in use and release between dead and live shrubs.

Soil under dead *Franseria* shrubs had higher levels of Ca, Fe, P at 25-30 cm, and lower Na than did the soil under living shrubs.

Table 5. Cation exchange capacity of Death Valley soils (meg/100g)

Site	Depth(cm)	E.C.
1	0-5	8.8
	5-10	10.2
	10-15	9.0
	15-20	8.5
	20-25	8.5
	25-30	3.3
	55-60	7.8
2	0-5	5.4
	5-10	6.8
	10-15	7.0
	15-20	7.5
	20-25	8.7
	25-30	7.9
	55-60	7.1
3	0-5	10.0
	5-10	10.5
	10-15	10.5
	15-20	10.9
	20-25	10.3
	25-30	10.0
	30-35	7.0
	55-60	6.5

Phosphorus was highest under dead *Franseria* at all but the 0-5 cm depth. Differences in extractable P under *Franseria* and *Larrea* suggest basic differences in use or production of phosphorus in the soil. Soil under dead *Atriplex* shrubs had more Ca, different Cu distribution, less K, Mg, Mn, Na (suggesting downward leaching), and variable P than occurred in the same depths of soils under live *Atriplex*. Since the female of this shrub sheds large quantities of fruits and leaves, many of which remain at the base of the shrub, the amount of nutrients available for release annually should be much higher than for *Franseria* which is small and has sparse, small leaves and fruits which are only partly shed, and *Larrea* which sheds only a portion of its small leaves annually and disperses large quantities of wind-blown fruits. The annual organic accumulation under *Atriplex* appears to be much larger than for the other two species so the higher levels of pH 5.5 extractable K, Mg, Mn, and Na probably result from leaf and fruit decay over long periods of time with low leaching levels. The difference between living and dead *Atriplex* soil phosphate is not great in this instance. The soils from the open generally

have more Ca, less N, P, and Na than the soil under shrubs as a result of reduced leaching in the open and increased release of elements from decay under shrubs. These differ by species as well as by site.

Table 6. Percent moisture in Death Valley soils in February, 1972

Site	Depth(cm)	% Moisture
1	0-5	3.06
	5-10	5.22
	10-15	6.72
	15-20	6.69
	20-25	7.44
	25-30	6.66
	55-60	5.64
2	0-5	10.70
	5-10	4.49
	10-15	5.11
	15-20	4.35
	20-25	4.28
	25-30	4.90
	55-60	3.30
3	0-5	2.87
	5-10	7.18
	10-15	8.00
	15-20	8.97
	20-25	7.70
	25-30	6.61
	55-60	4.63
4	0-5	1.67
	5-10	3.12
	10-15	6.02
	15-20	7.20
	20-25	7.17
	25-30	8.04
	55-60	10.56

When the elemental content of distilled water leachate (pH 6.8) of soil in the open and under shrubs was compared, there were considerable differences in the amounts of Ca, K, P, and Zn (Table 7). Site 1 had such a slow infiltration rate with time that it was difficult to leach the soil without extensive evaporation losses. For this reason, most leaching tests were run on soils from sites 2 - 4. The wash sites, 2 and 4, were generally lower in Ca, K, Na, P, and Zn than were the hill sites, except for cemented layers (1 and 3, Table 7). These differences would be expected in light of the greater water movement in the washes, and the solubility of some compounds of these elements. Similar differences occurred with the pH 5.5 extractions (Table 4). Often elemental deposition patterns in the soil are dependent on how intensive and heavy the last rains were.

A study conducted by a student, Ruth Squires, used 1) water equivalent chemically (inorganically) to the leachate from open ground, 2) nutrient solution equivalent (inorganically) to water leachate of soil from under *Larrea*, and 3) nutrient solution equivalent chemically (inorganically) to the pH 5.5 extract of soil under *Larrea*, to water vermiculite cultures of seedlings of *Larrea divaricata*, *Atriplex canescens* and *Hymenoclea salsola*. The results showed that these plants survived and grew best over a seven-week period on water which was chemically equivalent (inorganically) to leachate from open soil. Good growth occurred for most species on nutrient solution equal to the pH 5.5 extract, and all seedlings died when watered with nutrient solution equal inorganically to the water leachate of soil under *Larrea*. However, less *Larrea* seedlings (57%) died when they received water chemically equivalent to that from the open ground than when they received pH 5.5 extractions (80-88% mortality). *Atriplex* grew and survived well on nutrient equal to the water extract of open soil, indicating that this species is better suited to the saline habitat than is *Larrea*. Why all plants died in nutrient solution equivalent to that of water extract under *Larrea* is not known, but this solution contained much more Ca (8 x), less Fe (10 x), more K (2 x), the same Mg, Mn, N, less Na, P (13 x less), and less Zn than did the solution from open soil. Any combination of deficiencies and imbalances could occur in the *Larrea* solutions. The purpose of this study was to determine what general types of soil solutions favored growth and survival. The results indicate that water leachate of open soil, acted on by the roots with their pH adjustment, is the best of the three tested. Apparently a solution equal to the pH 5.5 extract of soil is not well balanced for growth and survival when the pH action of the roots is added, although some plants did survive. These data suggest that uptake is dependent on the action of the roots on the soil solution and not so much on the solution itself.

Table 7. Elemental content of soil leachate from Death Valley soils in the open and under shrubs using distilled water as a leaching agent (mg/l)

Soil in open	Depth(cm)	Ca	Cu	Fe	K	Mg	Mn	Na	P	Zn
1	0-20	0.4	0.01	0.05	2.1	2.8	0.0	16	0.00	0.00
2	0-20	0.3	0.00	0.05	4.6	2.2	0.0	25	0.02	0.00
	20-40	0.3	0.02	0.15	4.1	2.5	0.0	31	0.07	0.00
	40-60	0.3	0.05	0.20	4.6	2.8	0.0	26	0.13	0.00
3	0-20	1.1	0.05	8.80	8.0	8.6	0.8	95	2.86	0.13
	20-40	1.2	0.04	1.70	6.1	5.9	0.2	64	0.61	0.03
	40-60	3.3	0.00	0.40	7.7	8.6	0.6	52	2.10	0.05
4	0-20	0.3	0.05	3.70	4.6	2.1	0.2	22	0.44	0.02
	20-40	2.5	0.03	5.20	6.7	9.6	0.5	19	1.10	0.07
	40-60	0.6	0.04	4.30	4.5	2.7	0.1	22	0.37	0.03
Soil under <i>Larrea</i>										
Site 1	0-20	96.0	0.03	0.20	9.1	8.8	0.2	25	0.03	0.01
Site 2	0-20	100.0	0.05	0.30	9.0	10.0	0.2	30	0.09	0.02
Site 3	0-20	100.0	0.04	0.28	9.2	9.6	0.1	30	0.48	0.01
Soil under <i>Franseria</i>										
Site 1	0-20	80.0	0.03	0.15	9.3	9.3	0.1	30	0.34	0.01
Site 2	0-20	100.0	0.04	0.25	9.2	10.0	0.1	38	0.20	0.02
Site 3	0-20	67.0	0.03	0.25	9.2	8.9	0.1	40	0.16	0.01
Soil under <i>Atriplex</i>										
Site 1(male)	0-20	59.0	0.04	0.50	9.1	3.9	0.1	65	0.10	0.01
Site 2(female)	0-20	61.0	0.03	0.20	9.1	4.3	0.1	65	0.08	0.01
Site 3(female)	0-20	41.0	0.03	0.30	9.2	3.7	0.1	70	0.01	0.01

Soil from under *Larrea*, *Franseria* and *Atriplex* was much higher in water extractable Ca, K and Mg (in some cases) than was soil at the same depths in the open. The difference between water soluble Ca in the open and under shrubs suggests that the Ca in the open is in some form which is not readily water soluble, whereas the Ca under shrubs is in a water soluble form. This could be another modification of the soil by the shrub.

Surprisingly, less water soluble Ca and Mg occurred beneath *Atriplex* than beneath the other two species. This could be related to solubility and pH since both *Larrea* and *Franseria* have lower pH readings in soil immediately beneath them, but this is only speculation. More Na occurred under *Atriplex*, which is reasonable since the foliage of this plant is very high in Na (Table 9).

Distillation-condensation did occur during the study year, but attempts to measure the quality of condensation water showed that it was impossible to collect this water without contacting either the root or soil, or rock. All of these surfaces have soluble

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elements on them, so that the true quality of the condensed water was not ascertained. The elemental content of filter papers placed under rocks did not vary greatly with time of exposure, suggesting that what was found on the filter papers was local contamination and not materials transported or dissolved by the water over time.

Distillation-condensation performs a vital function daily by bringing water which is presumably relatively pure to the root surfaces. With this water, the roots are able to live and to adjust the pH of their immediate surroundings to levels favorable for nutrient uptake. This study, in a dry year, suggests that most elemental uptake occurs from soil in the immediate vicinity of roots using condensation water, and not the soil solution which lasts for only a few days or weeks after storms.

Perhaps the low permeability also prevents the loss of water from the soil surface. After a rain, the surface 1-2 cm dries, losing water to the atmosphere. Once this surface zone is dry, however, little water is lost from the soil surface. The dry, surface clay has many tiny air spaces which do not connect directly to one another. These probably act to restrict the movement of air in and out of the soil, thus reducing vapor losses as well. After an October rain, the plants took up enough soil moisture to flower or begin growth independent of distillation-condensation.

Another side effect of low permeability is the crusts formed on the undersides of surface rocks. The crusts are high in Ca and K. They appear to form by the crystallization of salts from the small puddles under rocks as they dry after a rainstorm.

The undersides of rocks are sites of root concentration, fungal activity, arthropod activity, nutrient uptake, condensation of water, and sometimes litter accumulation from wind or small animal collections. For this reason, the undersides of rocks are key centers of biological activity and are extremely important in desert soils.

When the undersides of surface rocks were washed with deionized water or acidified deionized water, the elemental content was quite variable (Table 8). Much of the variation may be the result of varying degrees of biological activity under the rocks, and possibly their composition. When deionized-distilled water with a pH of 5.5 (HCl) was used for washing, the amount of most elements readily available was considerably higher than when plain deionized water was used. This tends to confirm the acid action of roots on rocks and soil, and it indicates that readily soluble elements are available on rock surfaces despite centuries of distillation-condensation.

Table 8. Elemental content of water from washing the undersides of rocks, Death Valley

Rock type	Extractant	Ca	Cu	Fe	K	Mg	Mn	Na	P	Zn
Rhyolite	pH 5.5	730	0.4	28	24	25	0.8	10	0.01	0.2
	pH 5.5	285	0.5	90	53	181	4.0	12	0.50	0.9
	D.W.*	220	0.3	5	26	18	0.5	5	1.25	0
	D.W.	90	0.9	5	15	5	0	4	1.40	0
Basalt	pH 5.5	875	1.2	175	77	240	10.0	30	0.03	2.2
	pH 5.5	535	0.8	95	73	240	5.0	48	0.04	0.9
	D.W.	285	0	5	53	23	0	13	0.37	0
	D.W.	140	0	0	57	16	0	51	1.60	0

*D.W. = deionized, distilled water

Plants

A comparison of the elemental content of *Larrea* leaves from Death Valley and Rock Valley show that the latter had the highest content of Cu, Fe, N, Na, and Zn (Table 9). These differences show up in the two soils when hill sites are compared for Mg, Mn, Na, and Zn (Table 4). The slightly high Mn in Rock Valley soils does not appear to be responsible for the high Mn in Rock Valley *Larrea* leaves, and differences in other elements in the two soils are not necessarily reflected in the elemental content of these leaves. Phosphorus was slightly higher in the Rock Valley hill soils than in the Death Valley hill sites, but little difference in leaf phosphorus was found. Soil textural differences could explain some of the differences, particularly if textural variations are such that they influence water movement. The Rock Valley and Death Valley *Larrea* appears to differ in elemental content as much as other vegetation from over a hundred miles away would differ.

No analysis of the differences in elemental content of plants growing on the hills versus those growing in the wash was made. The soils differ between hill and wash locations, probably from differing amounts of leaching (Table 4). For all general comparisons, Rock Valley may be compared to Death Valley in terms of soil and plant chemistry but not species composition. The nutrient cycling phenomena described for Death Valley impermeable soils would probably apply to other desert areas with similar impermeable soils.

Table 9. Range of the elemental content of plants from Death Valley and Rock Valley ($\mu\text{g/g}$)

Death Valley	Plant Part	Ca	Cu	Fe	K	Mg	Mn	N	Na	P	Zn
<i>Larrea d.</i>	Wd.	325	7.0	68	2500	4000	2	-	300	2900	7.5
		1000	10.5	82	4200	5000	8	-	675	3200	10.5
<i>Atriplex c.</i>	Wd.	7800	7.0	130	4200	2500	12	-	415	4300	8.8
		14000	9.0	3100	8500	3250	42	-	5500	-	10.3
<i>Franseria d.</i>	Wd.	4000	8.0	140	13250	2000	8	-	800	-	13.2
		4750	12.5	215	18750	3500	15	-	2850	-	13.2
<i>Larrea d.</i>	lvs.	9500	7.0	185	16500	1750	21	17976	130	600	12.0
		16250	9.5	255	19500	2400	40	19096	294	1600	16.0
<i>Atriplex c.</i>	lvs.	16250	8.5	185	34750	9000	40	11060	100000	600	11.0
		31500	9.5	280	39500	11000	63	17584	137500	1900	13.0
<i>Franseria d.</i>	lvs.	12600	8.0	172	5000	1900	22	21112	1375	3200	16.0
		24750	15.0	400	17750	3750	60	31892	4500	-	31.0
<i>Larrea d.</i>	Old Wd.	8500	11.0	475	500	4800	15	4480	315	600	19.0
		21250	15.0	6750	9500	19500	65	8092	1900	650	73.5
<i>Atriplex c.</i>	Old Wd.	13250	9.5	130	1000	4500	22	5404	950	2900	12.5
		28500	13.0	5500	30000	18750	82	13076	47500	-	17.5
<i>Larrea d.*</i>	Roots	6000	9.5	110	5400	750	5	-	600	5800	8.0
		7500	10.5	475	5500	2250	15	-	800	-	11.0
<i>Atriplex c.*</i>	Roots	13250	9.5	580	25750	4500	22	-	22250	2900	14.5
		-	11.5	865	30000	7500	22	-	47500	-	16.5
<i>Larrea d. *</i>	Litter	10500	10.0	3400	2250	2500	40	-	47600	5800	14.5
		12250	12.0	3700	2500	3000	40	-	48000	-	15.0
<i>Atriplex c. *</i>	Litter	28500	10.5	130	10750	18750	22	5404	950	-	12.5
		28500	10.5	130	10750	18750	22	-	2250	-	13.0
<i>Franseria d.*</i>	Litter	21500	13.0	7250	3500	6000	88	-	1800	-	19.0
		21500	13.0	7250	3750	6250	89	-	1800	-	22.0
Rock Valley											
<i>Larrea d.*</i>	lvs.	9750	9.8	220	8250	1550	12	19152	250	750	14.0
		16500	15.5	450	15500	3000	25	21728	1450	1400	18.2

* Limited data (under four measurements)

In terms of elemental content, living wood of *Atriplex* was consistently highest of the three species in Ca, Fe, Mn, and Na. This plant appears to be a true concentrator plant adapted to dry soils high in salts. *Larrea* wood was consistently low in Ca, Fe, K, Mn, and Na. It grows at the other extreme and does not concentrate cations to a high level. It does not appear to build the high moisture tension related to water and salt uptake which *Atriplex* has, but *Larrea* is slightly high in Mg (Table 9). *Franseria* wood tends to fall between *Larrea* and *Atriplex* wood in its elemental content.

The same general relationship holds for the leaves of these three desert species. *Atriplex* has leaves which are high in Ca, K, Mg, Mn, and Na. The sodium levels in *Atriplex* leaves are extremely high, exceeding 100,000 $\mu\text{g/g}$, compared to 294 $\mu\text{g/g}$ for *Larrea* and 450 $\mu\text{g/g}$ for *Franseria* (Table 9). These data suggested that *Atriplex* is less selective in elemental uptake than are the other two species, and that it has evolved to survive with the salt by selective uptake. However, water leachate of soil from beneath *Atriplex* was quite low in Na (Table 7) as was the pH 5.5 extract (Table 4). Calcium, K, Na, and Mg were high (relative to temperate zone humid forests) in all desert leaves. Pine needles from Jeffrey pine forest show about 1000 $\mu\text{g/g}$ Ca (Stark, 1972) compared to 9500 to 31500 $\mu\text{g/g}$ for desert plants. Copper, Fe, K, Mg, N, P, and Na were generally higher in the desert vegetation than in pine needles. The high levels of nitrogen and phosphorus in the desert vegetation suggest that these plants are prepared chemically for rapid growth once water becomes available.

It was originally hypothesized that old, dead wood could be an excellent source of well-balanced, biologically important elements which could be available to mycorrhizal fungi which are known to associate with the roots of some desert plants and decaying wood. It is now known that some fungi concentrate very high levels of elements, although desert fungi have not been studied (Stark, 1972). If the mycorrhizal fungi concentrate high levels of elements from wood which is already high in elemental content, then the balance and concentration of cations and anions would not necessarily be favorable to the living roots. Also, old, dry dead wood near the surface of the soil acts as a wick when it rains, soaking up salts and water. As the water evaporates, the salts are left behind and become more concentrated. Thus, *Larrea* live wood had 325-100 $\mu\text{g Ca/g}$, while dead wood of various ages had 8500-21250 $\mu\text{g Ca/g}$, or over 21 times more Ca.

The copper content of live and dead wood did not increase very much over time (Table 9). Iron was about 82 x more concentrated g/g in dead *Larrea* wood than in live, K was about 2 x more concentrated, Mg was about 4 x more concentrated, Mn was 7 to 8 x greater, Na was the same to 3 x greater, P was about 1/5 of the level found in living wood, and Zn was about 7 x greater (Table 9), indicating that as dead wood ages in the soil it increases in cations to levels which would appear to be poorly balanced for the living plant. Phosphorus, on the other hand, is withdrawn from the wood, possibly by fungi, and may be moved to points in the ecosystem where growth is occurring.

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Atriplex dead wood varied in elemental content, but concentrated most elements in the same manner as did *Larrea* wood, but to a lesser degree. Old *Atriplex* wood had from 2 x to 10 x more of each element except P (Table 9). The old wood of *Franseria* was not studied.

Although radionuclides were not available to determine if P and other elements are moving from dead wood into living roots via mycorrhizal fungi, this source of elements for desert plants would seem to be much less important than originally hypothesized. Wood which is deeper in the soil and is not so strongly subjected to the "wick" phenomenon might still be useful to mycorrhizal fungi. Certainly fungi and roots associate readily with subterranean dead wood, but the reason for this relationship is not clear.

The roots of *Larrea* and *Atriplex* are quite high in Ca, Cu, Fe, K, Mg, Na, and Zn (Table 9), relative to roots of forest vegetation. *Atriplex* has roots which are extremely high in K and Na compared to roots from non-desert areas.

The litter of the three species tends to be high in those elements which are abundant in the living leaves (Table 9).

The moisture content of the leaves of these three desert species increases during the growth period (late March-May) and decreases to low levels during the cold and drier season. Moisture uptake and growth coincide closely with the periods of strong distillation-condensation (Stark and Love, 1969). *Larrea* tends to have under 100% moisture on a dry weight basis (71.7 - 91.3), while *Atriplex* usually remains over 200% (220.8 - 419.5%), and *Franseria* has a bit over 100% (108.6 - 133.4%). It is reasonable to assume that *Atriplex* maintains high levels of internal moisture by virtue of its high salt concentration.

Skujins (1972) found low nitrogen levels in soils from Curlew Valley, northern Utah. The sampling procedure suggests that samples were taken from areas between shrubs and where dead organic matter is scarce. These results agree with those from similar sites in Death Valley, but the situation under shrubs where there is more organic matter would appear to be very different. This may be particularly true since cryptogamic crusts are less abundant in the warm desert than in the cold desert. The higher nitrogen levels in the surface soil of Curlew Valley agree with the conditions in Death Valley under shrubs. Dutt and Hanks (1972) discuss the dynamics of nitrogen transformations on warm desert soils. McKell and Kline (1972) also found more nitrogen under the shrubs than in the open in northern desert soils. The levels of nitrogen in the cold desert soils were generally higher than those from the warm desert.

Studies of the total P content of desert soils by Jurinak and Griffin (1972) showed the most inorganic P at the surface with higher organic P at depths to 70 cm in Curlew Valley soils. These results agree generally with studies of extractable P in Death Valley soils.

Studies of the elemental distribution in cold desert plants (West, 1972) show generally lower levels of K, Na, P, and Mg, and higher Cu and Mn than was found in warm desert plants.

EXPECTATIONS

This work will not be continued because the author has moved to an area which is remote from the desert. If work is to be continued on this general topic, the role of dead wood and fungi in supplying phosphorus and water should be studied. More work should be done on the uptake of elements, and on the nutritional requirements of desert plants. All aspects of this study should be continued to obtain valid, long-term data which reflect climatic variation.

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1972 PROGRESS REPORT

PREDICTING NITROGEN TRANSFORMATIONS AND AMMONIA
VOLITALIZATION IN WARM DESERT SOILS

G. R. Dutt, Project Leader

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Research Memorandum, RM 73-45

MAY 1973

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Report Volume 3

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A B S T R A C T

A digital computer model predicting the nitrogen and salt content of soil water draining from irrigated agricultural soils has been completed and verified (Dutt et al., 1972). To further test this model and extend its usefulness, continued laboratory, field and computer research has been conducted.

An attempt was made to apply the model to simulated nitrogen transformations, nitrogen movement and plant uptake of N in a warm desert soil under range grass. For the site selected, a soil moisture model predicting water movement in layered soils was required to describe the soil textural parameters important in the infiltration and storage of plant-available moisture. With the moisture flow data as input, the Biological-Chemical Program predicted $\text{NO}_3\text{-N}$ concentrations in the surface 10 cm of soil within experimental error of field-obtained values in the top 15 cm for a simulation period of 45-130 days. Difficulty in the 0-45 day period and the predicted concentration in the 0-15 cm depth was due to that portion of the model which predicts the net mineralization-immobilization rate and the breakdown of organic residues. Once the indicated modifications are made to this subroutine, the model is expected to be applicable to warm desert range grass systems, and may be further verified on data which is now available.

A laboratory study was performed to acquire data necessary to develop a digital computer subroutine compatible with the overall model which would predict losses of ammonia by volatilization from desert soils. Preliminary work verified that the experimental procedure selected for the data collection is sufficiently accurate to provide basic information necessary to develop this subroutine.

INTRODUCTION

Over the past ten years, the chief investigator has been working on computer models of soil-water systems. The U.S. Bureau of Reclamation, under contract agreement, financed the development of a systems analysis model for predicting nitrogen in irrigation drainage water. This model has been verified for some agricultural soils and predicted values compare favorably with verification data tested to date. The model, in fact, is a systems analysis model considering the dynamic soil-water system and may be directly applicable to a Desert Biome model in its present form under certain conditions. It would seem that the current model needs to be evaluated and possibly modified if it is to be used as a subroutine in a Desert Biome model.

OBJECTIVE

The objective of this study is to evaluate the applicability of the current version of a digital computer model predicting the transformation and movement of nitrogenous compounds in soil-water-plant systems, to a warm desert ecosystem. If the model fails to duplicate the field observations, those observations, and others which could be readily made at the site, could then be used to indicate what portions of the computer model should be modified to enable its use under these input conditions.

METHODS

The Site*

The site selected to test the computer simulation model previously described in the literature by the principal investigator and colleagues (Dutt, et al., 1972) was on the Page-Trowbridge Experimental Ranch located 28 miles due north of Tucson, Arizona. The range belongs to the University of Arizona and is fenced so that the vegetation has not been disturbed by livestock for several years.

This location, hereafter called the Page Ranch site, is located in the NE $\frac{1}{4}$ of SW $\frac{1}{4}$, Section 27, Township 9S, Range 14E at an elevation of approximately 3580 feet. This site was the location of a range fertilization study conducted by Bahe Billy in 1967 and 1968 under the direction of Dr. J. L. Stroehlein (Billy, 1970).

* Material in this section was extracted from Billy, 1970.

The Soil*

The soil at the Page Ranch site is an Ustollic Haplargid, fine, mixed, thermic, Whitehouse sandy loam. It has an unusually deep, permeable A1 horizon overlying a very deep, slowly permeable, heavy textured, prismatic B horizon. The grass root zone extends well down to approximately 24 inches and from there down the roots are few and fine in size. The soil is slightly acidic (pH 6.5) at the surface and increases with depth to approximately 8.2 at 3 feet. Calcium carbonate nodules are observed at 24 inches and below. The site is on a 1% slope with a westerly aspect.

Vegetation*

The plots selected for the 1967-1968 experiment were located among invading mesquite with Lehmann's lovegrass as the dominant grass. Mixed within were scattered plants of Boer lovegrass. The three dominant spring annuals were six weeks fescue, filesee, and Indianwheat. Undesirable vegetation included barrel cactus, burroweed and other minor weeds.

Experimental Procedure*

In the spring of 1967, 35 plots, each 20' x 30', were selected and staked. Thirty of these plots were then selected randomly and preclipped two inches above the ground between May 31 and June 5, and loose plant materials removed. The five remaining plots were used to estimate the effect of clipping on grass growth.

Seven treatments were assigned to the 35 plots as follows:

<u>Treatment</u>	<u>Date of fertilizer application</u>
1	June 5, 1967
2	July 3, 1967
3	July 13, 1967
4	July 22, 1967
5	August 7, 1967
6	Check (unfertilized)
7	July 12, 1967 (not pre-clipped)

The fertilizer material applied in all cases was granulated ammonium nitrate-phosphate (30-10-0) applied at 50 lb/acre. This rate of N had been previously shown to give maximum yield return of forage production on soil and vegetation similar to those at the Page Ranch site.

The plots were harvested on August 19, 1967, September 13, 1967, and October 12, 1967, and moisture determination, dry weight of tops and seeds, and chemical analyses performed on the harvested vegetation on each date. Additionally, in 1968, the spring annuals were harvested. A final harvest occurred on October 16, 1968, and the vegetation was analyzed in the same manner.

* Material in these sections was extracted from Billy, 1970.

2.3.5.5.-4

Sampling of individual plants (10 plants/plot) in each of the 35 plots occurred prior to each fertilizer application, and soil samples (5 cores/plot) were taken five times throughout the growing season in 1967. Plant N and P and soil $\text{NO}_3\text{-N}$ and available $\text{PO}_4\text{-P}$ were determined on these soil and plant samples.

Computer Simulation

The Page Ranch range fertilization study summarized above offered a unique opportunity to test the applicability of the soil-water-plant systems analysis model. This model has previously been verified in certain agricultural applications and it was hypothesized that it could produce reasonably accurate simulation of this native grass environment. If the model failed to duplicate the determinations made during the range fertilization study, those determinations, and others which could be readily made on this site, could then be used to indicate what portions of the computer model should be modified to enable its use in the prediction of the soil-water-plant system in desert environments.

From the outset, it was recognized that because of the sandy loam A horizon overlying a slowly permeable B horizon in the Whitehouse soil (both of which are important in the storage of plant-available moisture) the moisture flow part of the model would not be applicable. This computer program was developed to predict the moisture regime independently of the chemical and biological changes in the system by modelling the unsteady, one-dimensional infiltration, redistribution, plant root extraction, and drainage of soil water in homogeneous, isotopic, nonhysteretic soils. Dr. R. J. Hanks made available a soil moisture model he had previously developed which is capable of predicting similar parameters in layered soils and also adapted laboratory data and data from the range grass study to meet the input requirements of his model. The model supplied by Dr. Hanks was then executed and its output (on magnetic tape) utilized as input data to the Biological-Chemical Model.

RESULTS AND DISCUSSION

Inputs

Input requirements of the computer model have been described by the principal investigator and colleagues (Dutt et al., 1972), and those which are required by the soil moisture model of Dr. Hanks are similar to those normally needed. In order to obtain input data which was not available from the dissertation of Billy or other literature, soil samples were taken at several depths at the Page Ranch site. At the location where these samples were taken, the A horizon, although quite close to sandy loam as reported by Billy, was actually loam in texture (see Table 1).

Table 1. Initial soil chemical analysis of Whitehouse loam from Page Ranch site

Depth cm	NH_4^+	NO_3^-	Ca^{++}	Mg^{++}	Na^{++}	HCO_3^-	CO_3^{--}	Cl^-	SO_4^{--}	C.E.C. meq/ 100 gm	Organic Matter $\mu\text{g/gm}$	C/N Ratio
0-7.62	0.00	0.113	2.40	1.00	0.390	3.60	0.00	5.64	5.83	6.45	$1.53 \cdot 10^4$	13.6
7.62-21.6	0.00	0.129	3.80	1.40	1.52	4.80	0.00	8.46	4.17	7.74	$1.07 \cdot 10^4$	13.0
21.6-38.1	0.833	0.0968	2.20	3.60	4.61	5.60	0.00	8.46	5.83	31.5	$1.52 \cdot 10^4$	9.68
38.1-48.3	0.00	0.121	2.20	1.00	5.70	6.80	0.00	8.46	5.83	21.1	$7.77 \cdot 10^3$	8.86
48.3-78.7	0.00	0.121	2.80	1.40	8.91	3.40	0.00	14.0	8.33	18.1	$4.49 \cdot 10^3$	8.57
78.7-107	0.00	0.113	4.20	2.80	16.7	3.80	0.00	16.9	10.8	16.5	$3.50 \cdot 10^3$	10.0
107-112	0.00	0.121	3.40	1.80	16.4	4.80	0.00	14.1	12.5	13.2	$3.75 \cdot 10^3$	15.0
112-122	0.00	0.113	2.40	0.40	12.6	4.80	0.00	11.3	9.16	9.36	$2.51 \cdot 10^3$	15.9

2.3.5.5.-6

Mathematical functions or tables relating the pressure head (h) and unsaturated hydraulic conductivity (K) to volumetric moisture content (θ) are necessary in that portion of the overall model which describes the infiltration, redistribution, evaporation, and root plant withdrawal of soil moisture under growing vegetation. To obtain these relationships retentivity measurements were performed in triplicate on disturbed or core samples (when possible) from three depths according to methods described in the literature (Black, 1965). The relationships shown in Figures 1, 2 and 3 between pressure head and moisture content were obtained by interpolation of the experimental results of Table 2.

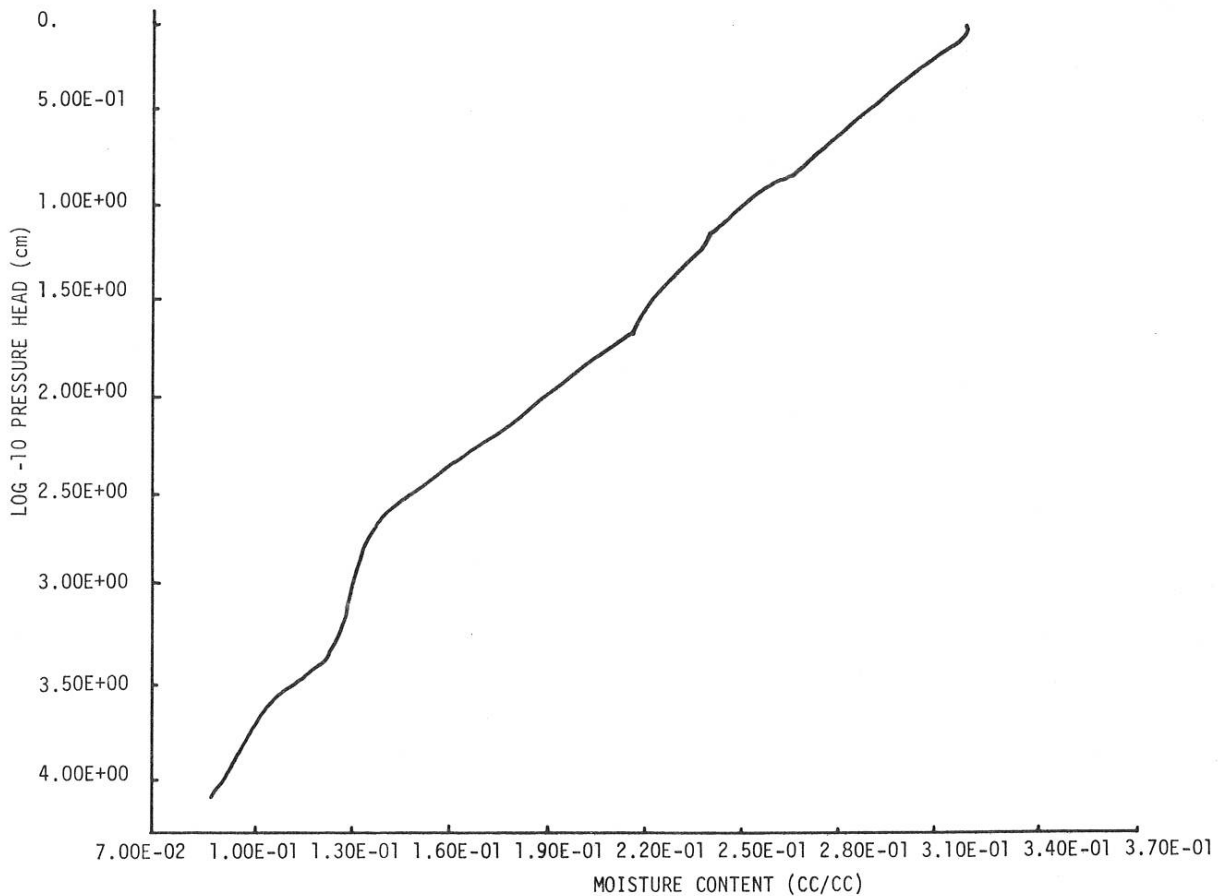


Figure 1. Whitehouse loam, 3.0-85 cm.

2.3.5.5.-8

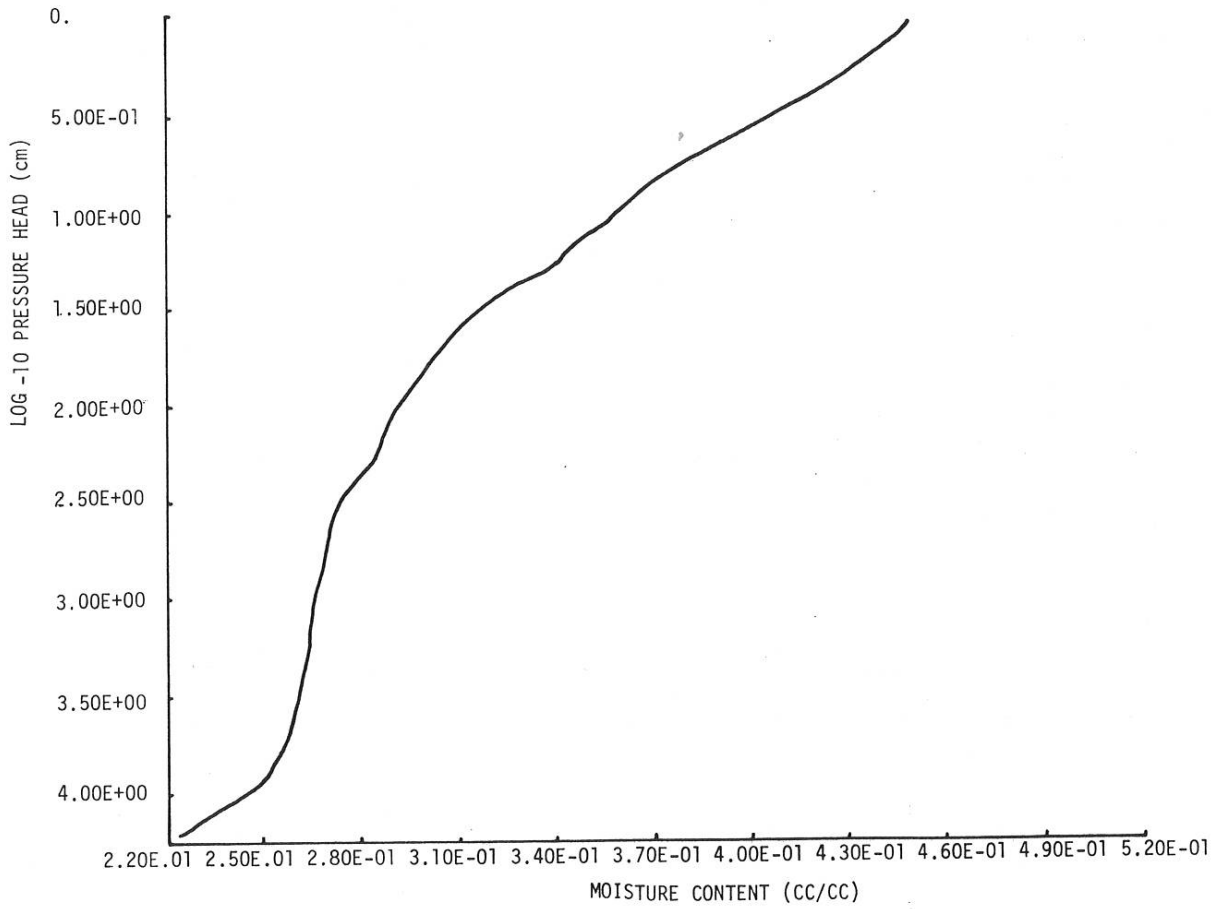


Figure 3. Whitehouse loam, 15.0-19.0 cm.

2.3.5.5.-7

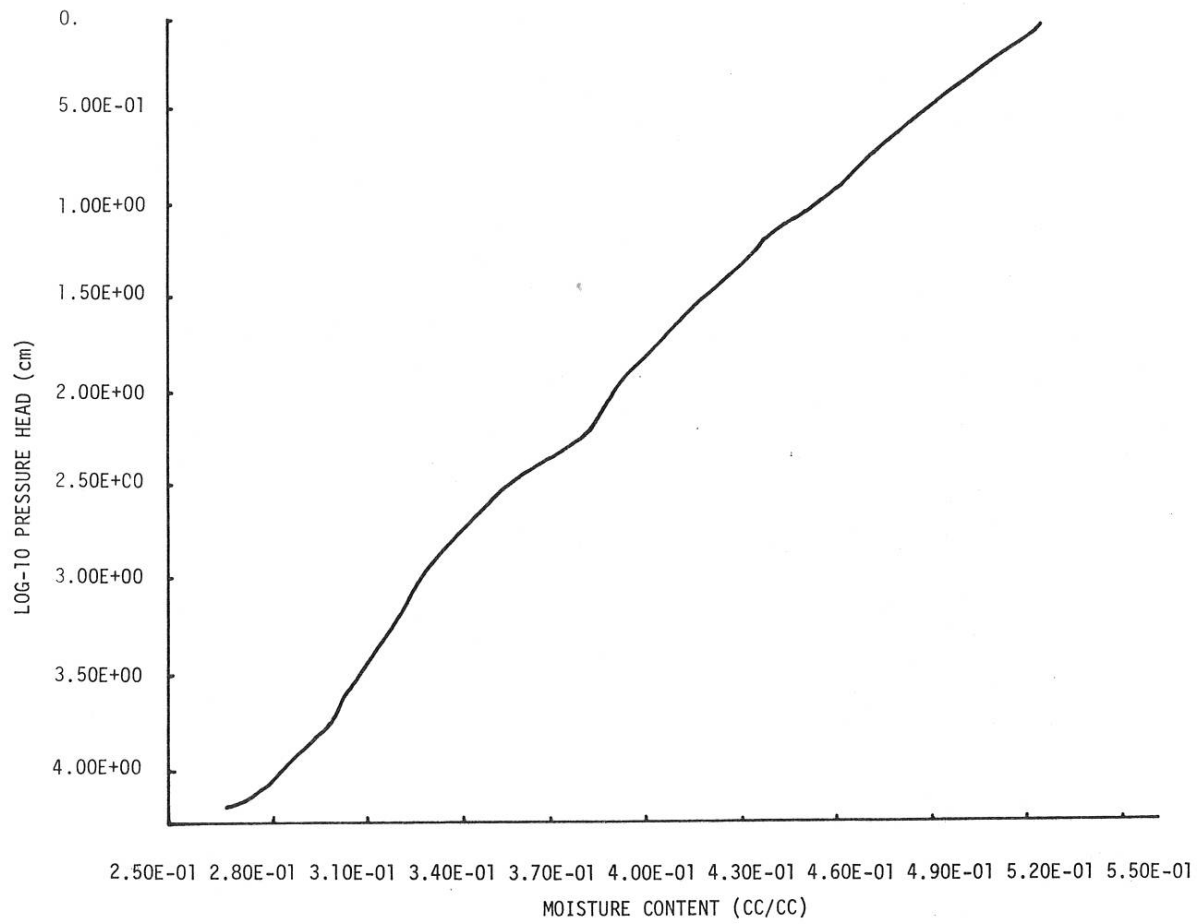


Figure 2. Whitehouse loam, 8.5-15.0 cm.

Table 2. Physical properties of Whitehouse loam from Page Ranch site

Depth (cm)	Bulk Density (gm/cm ³)	K _{Sat'd} (cm/min)	Sat'd	Volumetric Moisture Contents (cm ³ /cm ³)							
				5.09 ₁ x 10 ¹	1.02 ₂ x 10 ²	2.04 ₂ x 10 ²	Pressure (cm H ₂ O)	2.10 ₃ x 10 ³	5.26 ₃ x 10 ³	1.03 ₄ x 10 ⁴	1.54 ₄ x 10 ⁴
3.0-8.5	1.81	1.52x10 ⁻⁴	.3194	.2099	.1724	.1527	.1409	.1218	.097	.0971	.0801
8.5-15	1.26	2.32x10 ⁻⁶	.5242	.4057	.3880	.3711	.3509	--	.3005	.2822	.2580
15-19	1.45	2.37x10 ⁻⁵	.4515	.3060	.2930	.2860	.2712	--	.2599	.2456	.2267

2.3.5.5.-10

Laboratory measurements of the saturated hydraulic conductivities determined by the constant head method (Black, 1965) are also shown in Table 2 for each of the three depths. From this data and the modified Millington-Quirk equation (Stockton and Warrick, 1971), unsaturated hydraulic conductivity values were estimated for each of the three depths over the pressure range from 0-15 bars. These relationships are shown in Figures 4, 5 and 6.

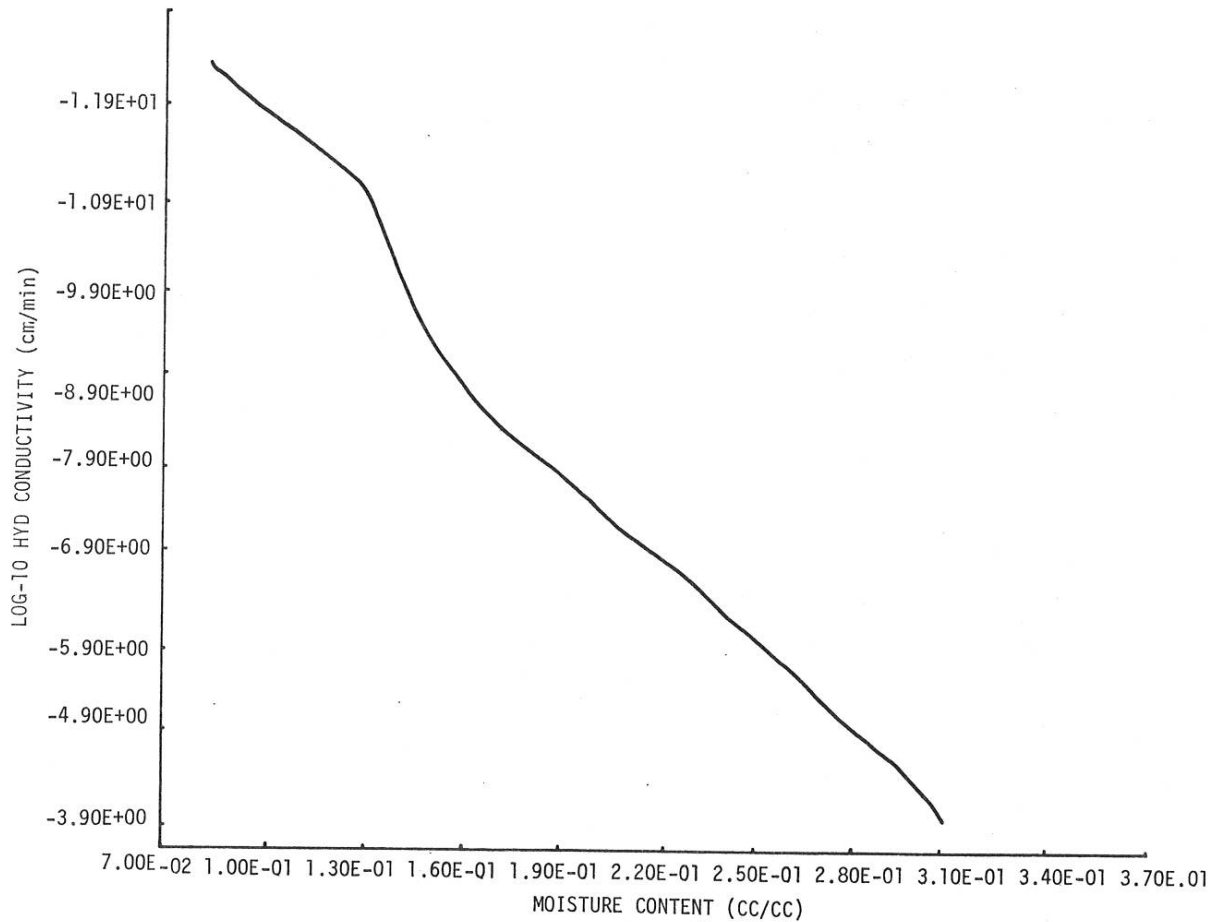


Figure 4. Whitehouse loam, 3.0-5 cm.

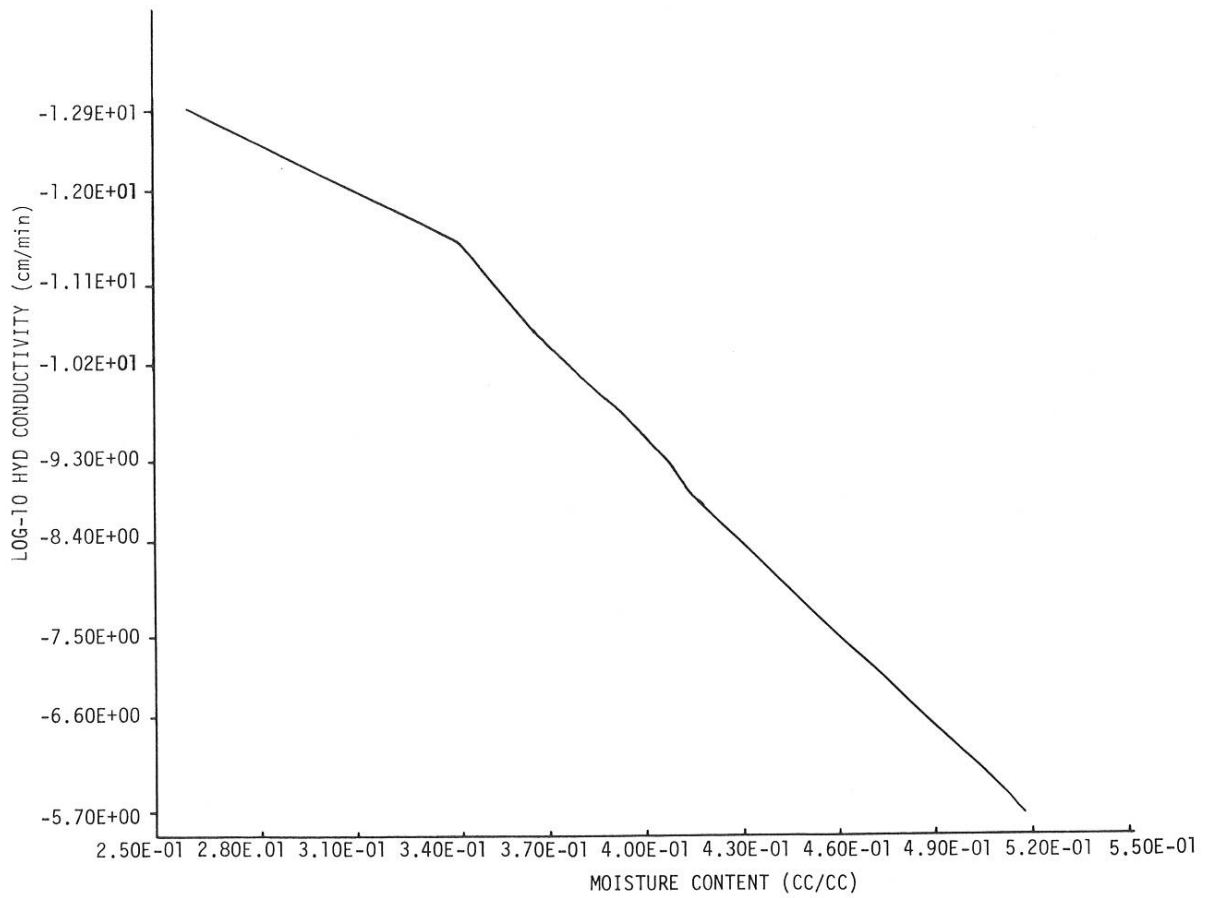


Figure 5. Whitehouse loam, 8.5-15.0 cm.

2.3.5.5.-12

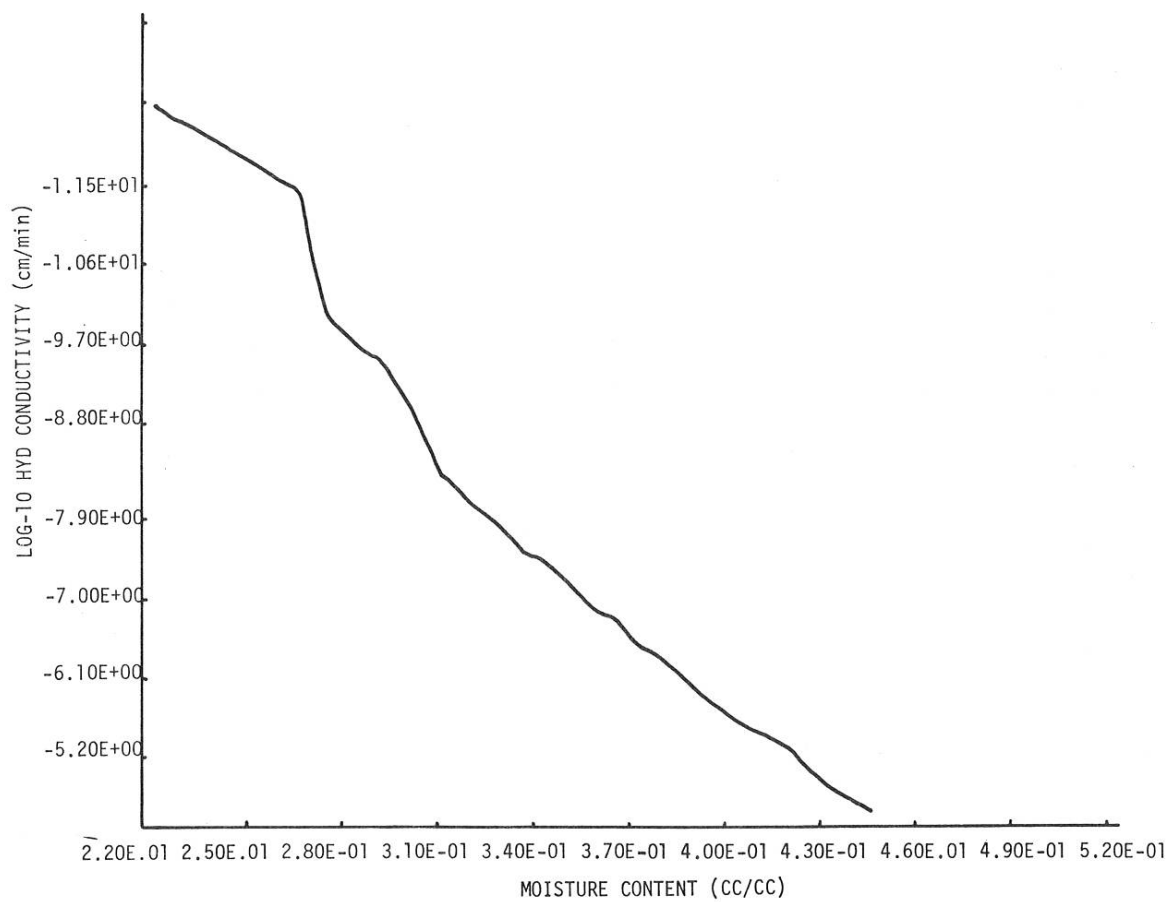


Figure 6. Whitehouse loam, 15.0-19.0 cm.

The maximum or "potential" rates of soil moisture removal over the growing season by the roots of growing vegetation and evaporation from the soil surface, are other inputs that are required to predict the moisture regime under field conditions. Field determinations of the evapotranspiration rate from blue panicum grass at the University of Arizona Mesa Experimental Farm (Erie et al., 1968) were selected to approximate the "potential" rate of plant root extraction expected at the Page Ranch site (see Figure 7). Average effective root distribution for the composite native vegetation was approximated so that 0.75 of the extraction would occur in the top 30.5 cm of soil and 0.25 from 30.5-61 cm depth, as shown in Figure 7. Rainfall records for the period of June - October, 1967, were available and utilized, but no temperature data from the Page Ranch site were recorded. Instead, average monthly maximum and minimum temperatures from the Willow Springs Ranch, located approximately eight miles north of the Page Ranch site, were utilized.

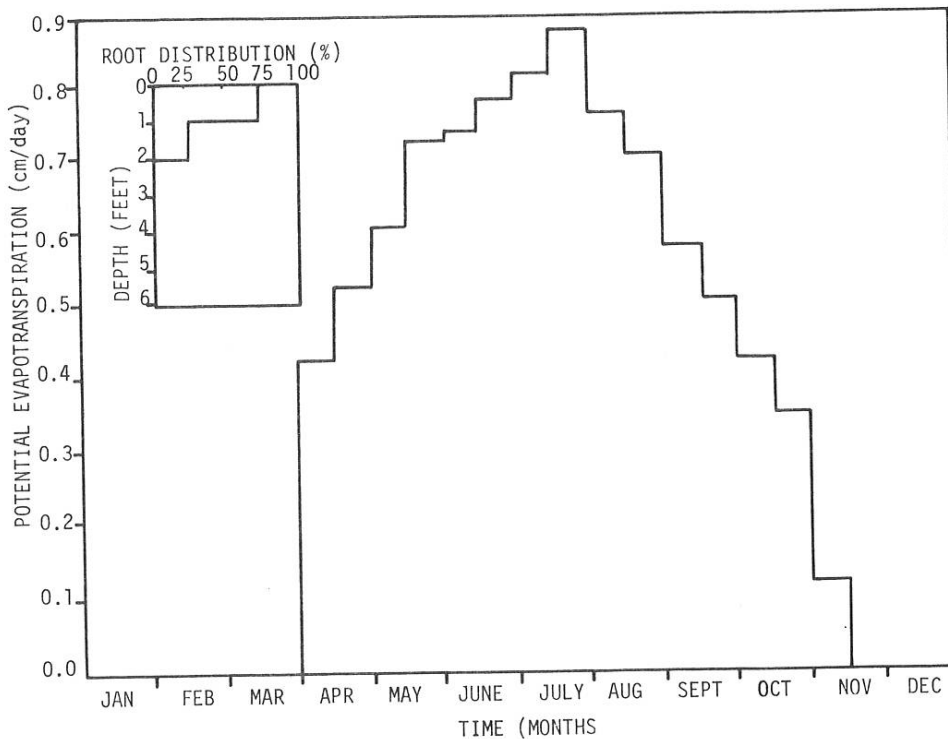


Figure 7. Field determinations of the evapotranspiration rate from blue panicum grass at The University of Arizona Mesa Experimental Farm (Erie et al., 1968) selected to approximate the maximum rates allowable at the Page Ranch site.

2.3.5.5.-14

Assumptions

For the purpose of reducing computer execution time, the spatial unit for modelling purposes was considered to be a one cm^2 area of soil along a vertical flow line from the surface to a depth of 50 cm. Further, only one textural change, occurring at 16 cm, was considered. Four distinct horizons (each composed of several Δx segments) were visualized to represent the initial chemical composition of the profile. A zero flux boundary condition was assumed at 50 cm and a variable flux (for evaporation) or head (for infiltration) boundary assumed at the soil surface.

Due to the low hydraulic conductivity values of the soil, it was assumed that rainfall rate would exceed the infiltration rate of the soil, resulting in ponding of water at each rainfall. This assumption causes the precipitation from each rainfall to be highly dependent on the length of time the water is ponded on the soil surface, so that this length of time can be utilized to characterize each rainfall. The date, day number, length of time free water was available at the soil surface to infiltrate, and predicted infiltration values, are shown in Table 3.

Table 3. Day number, date, duration, and predicted infiltration of each rainfall from June 20, 1967 (DAY = 0) through October 27, 1967 (DAY = 130)

Rainfall		Duration* (day)	Infiltration (cm)
Date	Day No.		
6/20/67	0	1.00	3.67
7/3/67	13	0.12	0.46
7/10/67	20	0.02	0.09
7/12/67	22	0.22	1.18
7/22/67	32	0.07	0.37
8/5/67	46	0.62	3.16
8/7/67	48	0.10	0.51
8/14/67	55	0.43	2.26
8/17/67	58	0.30	1.52
8/18/67	59	0.01	0.05
8/19/67	60	0.23	1.17
8/29/67	70	0.55	2.79
9/6/67	78	0.10	0.50
9/13/67	85	0.10	0.49
9/25/67	97	0.30	1.49
10/12/67	114	0.80	3.62
		TOTAL =	23.33

* Length of time free water is assumed present at soil surface.

The extremely low saturated hydraulic conductivity values measured in the laboratory were judged not to represent those of the soil *in situ*, probably because of shrink-swell and cracking characteristics which can be readily observed. These measured conductivities are used as scaling factors in the Millington-Quirk procedure to predict the hydraulic conductivity at any moisture content, $K = f(\theta)$. Lack of faith in the accuracy of the laboratory procedure made it necessary to increase the value of K_{sat} by a factor of 60 in the upper modelling horizon, and 600 in the less permeable lower horizon to more accurately represent field observations of the moisture intake rate. Addition of $\log_{10} 60$ to the vertical scale of Figure 4 and $\log_{10} 600$ in Figure 5 yields the conductivity values used in the upper and lower modelling horizons, respectively. The pressure head-moisture content relationships shown in Figures 1 and 2 are unchanged.

Further, it may be noted that in the range fertilization study by Billy, the fertilizer was applied on June 5, but in the computer simulation day 0 corresponds to June 20. This difference is due to the fact that no precipitation occurred at the site during the period from June 5-20 and that the model is incapable of predicting fertilizer input at the soil surface without accompanying infiltration. Since fertilizer applied by the model at June 5 would not enter the soil profile until day 15 due to the absence of precipitation, the starting day number was made to correspond to the date of the first rainfall after the application.

Computer Simulation

The Moisture Flow Program was executed for a period of 130 days and its output written on magnetic tape. Following a tape-tape data "interfacing" program, which is necessary to modify data formats (Dutt et al., 1972), the predicted soil-water characteristics were utilized as input data to the Biological-Chemical Program and the latter executed for the same time period. Output from both submodels may then be used to characterize the conditions predicted for the Page Ranch site from June 20, 1967, to October 27, 1967.

Table 3 may be re-examined to observe the infiltration predicted to occur from each of the 16 rainfalls during the simulation period. Total infiltration predicted was 23.3 cm (9.12 in.) which compares favorably with the 26.3 cm (10.4 in.) of precipitation observed from June through October due to the permeable sandy loam or loam surface horizon.

The relationship between infiltration and evapotranspiration (moisture storage) is shown in Figure 8. Each of the peaks corresponds with a rainfall (increase in moisture storage in the profile). Portions of the graph with negative slopes are due to evapotranspiration loss of soil moisture (decrease in storage). The progressive decrease in negative slope between moisture applications is due mainly to drying of the A horizon, resulting in decreased evapotranspiration rates as moisture becomes

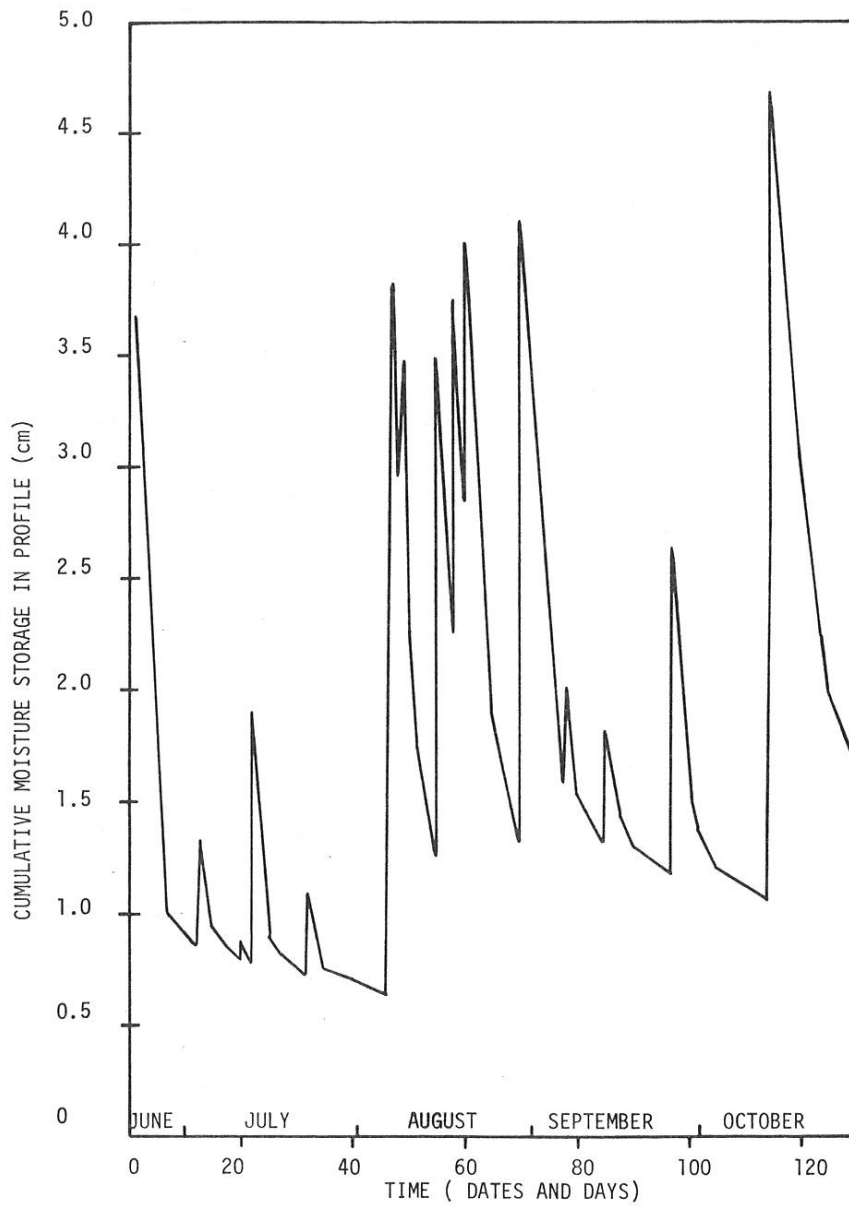


Figure 8. Cumulative moisture storage versus time in dates and days for the simulation period. Cumulative moisture storage = 0 at day 0 (June 20).

less available to plants in that zone. At all times following the first rainfall, total water in the Whitehouse profile exceeded that which it contained initially, although the surface frequently reached its air dry moisture content. This anticipated observation, caused by increased storage in the heavy B horizon, as shown in Figure 9, was responsible for the availability of some soil moisture to the vegetation throughout the 130-day period. Total evaporation from the soil surface was about 4.7 cm and total plant uptake was 16.9 cm of soil moisture.

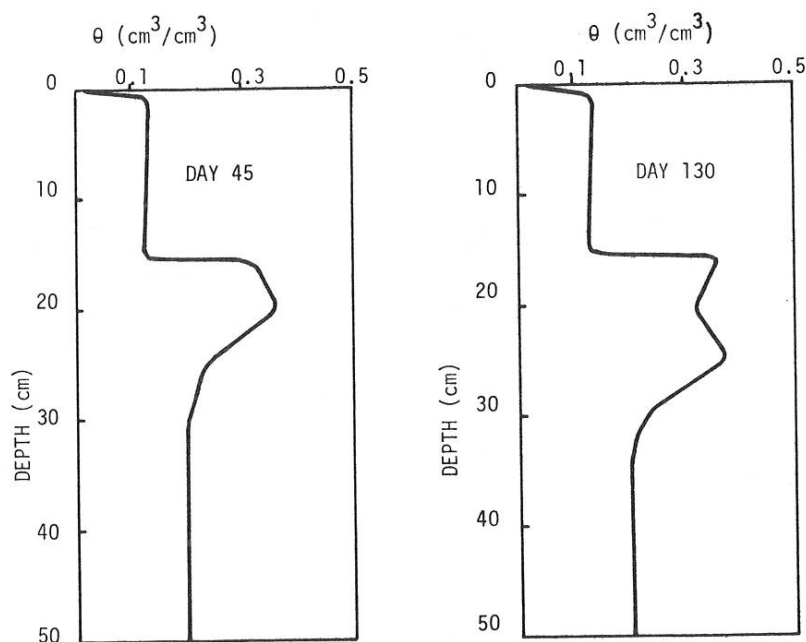


Figure 9. Moisture profiles in Whitehouse loam at day 45 and day 130 showing increased moisture in the heavy textured B horizon (16-50cm).

The effect of available soil water on the transpiration rate may be observed from Figure 10, in which cumulative moisture uptake is plotted for the 130-day period. The greatest transpiration rates (i.e., greatest slopes) occurred from August through October, in spite of the highest "potential" transpiration occurring in July (Figure 7), because of the increase in available soil water stored in the B horizon. It may be

2.3.5.5.-18

noted that although potential transpiration and rainfall were higher in July than in September (Figure 7, Table 3), the transpiration predicted in July was only 1/3 that for September (Figure 10). The total "potential" transpiration for the 130-day period was about 80 cm, while only about 20% was actually predicted to be available to the vegetation.

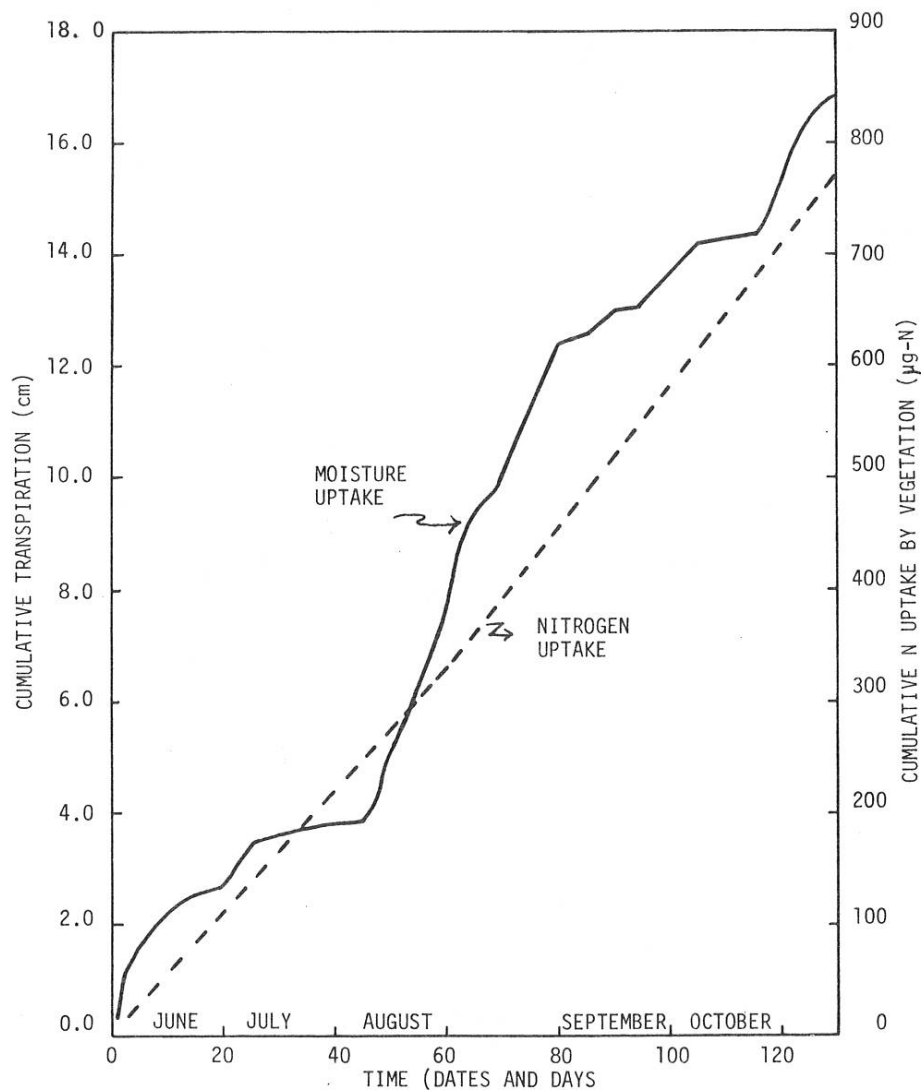


Figure 10. Cumulative transpiration (cm of H₂O) and cumulative nitrogen uptake (µg NO₃-N) by the vegetation for the 130-day period of simulation. $r^2 = 0.966$.

Estimates of the nitrogen uptake rate by the growing vegetation were obtained from the plant-N analyses performed on August 19 and October 12 by Billy. These estimated rates were $6.07 \mu\text{g NO}_3\text{-N/day}$ from June 20 to August 19 (DAYS 0-60), and $7.03 \mu\text{g NO}_3\text{-N/day}$ from August 19 through October 27 (DAYS 60-130), and are linearly related to the predicted moisture uptake by the vegetation ($r^2 = 0.966$). The model predicted that with the input assumptions and data used in this simulation, the soil root zone contained sufficient $\text{NO}_3\text{-N}$ to supply the plants throughout the 130-day period; i.e., all estimated $\text{NO}_3\text{-N}$ uptake (Figure 10) was actually withdrawn by the vegetation. Nitrogen concentration in the vegetation could not be compared with measurements made by Billy because the current model does not predict the mass of the vegetation.

Ultimate evaluation of the accuracy of the model is obtained by examining the soil $\text{NO}_3\text{-N}$ values predicted during the simulation with the field determinations by Bahe Billy from June through October. None of these determinations, including the initial $\text{NO}_3\text{-N}$ concentration, had been used in determining the modelling inputs or assumptions. The predicted values are compared to laboratory determinations made by Bahe Billy on core samples from the 0-15 cm depth in Figure 11. When interpreting these results, it should be recalled that the site used by Billy had a much deeper A horizon than the site on which the supplemental input data was determined five years later. For this reason the 0-10 and 0-15 cm depths were compared to the field observations made on 0-15 cm cores.

To explain the results of Figure 11, it was necessary to examine the detailed printed output from the computer simulation. In addition to the fertilizer application, on day 0 large amounts of organic matter were assumed to occur in the soil profile (particularly in the surface 1 cm of soil) to simulate the presence of fresh organic matter from decaying vegetation. The Biological-Chemical Program, developed primarily for agricultural applications, handled this organic matter in the same way it would a crop residue; i.e. rapid decomposition of residues with low C:N ratios which resulted in the mineralization of very large amounts of NH_4^+ and subsequently NO_3^- . The excessive amount of NO_3^- occurring in the profile from days 0-45 is from this source.

About day 45 the period of the highest rainfall began (see Figure 8), leaching the NO_3^- to below about 10 cm. The extent of this leaching accounts for the difference between the 0-15 cm predictions and the 0-10 cm predictions. This explanation is supported by the much greater decrease in $\text{NO}_3\text{-N}$ in the 0-10 cm zone than in the 0-15 cm zone following the rainfall on day 46 (see Figure 11).

It appears that after the extraneous $\text{NO}_3\text{-N}$ from organic matter decomposition was removed from the surface by leaching (as is the case with the 0-10 cm line), the model produced reliable predictions of the $\text{NO}_3\text{-N}$ concentration. From day 45 through 130, the modelling predictions were within the experimental error of the field determinations made by Billy.

2.3.5.5.-20

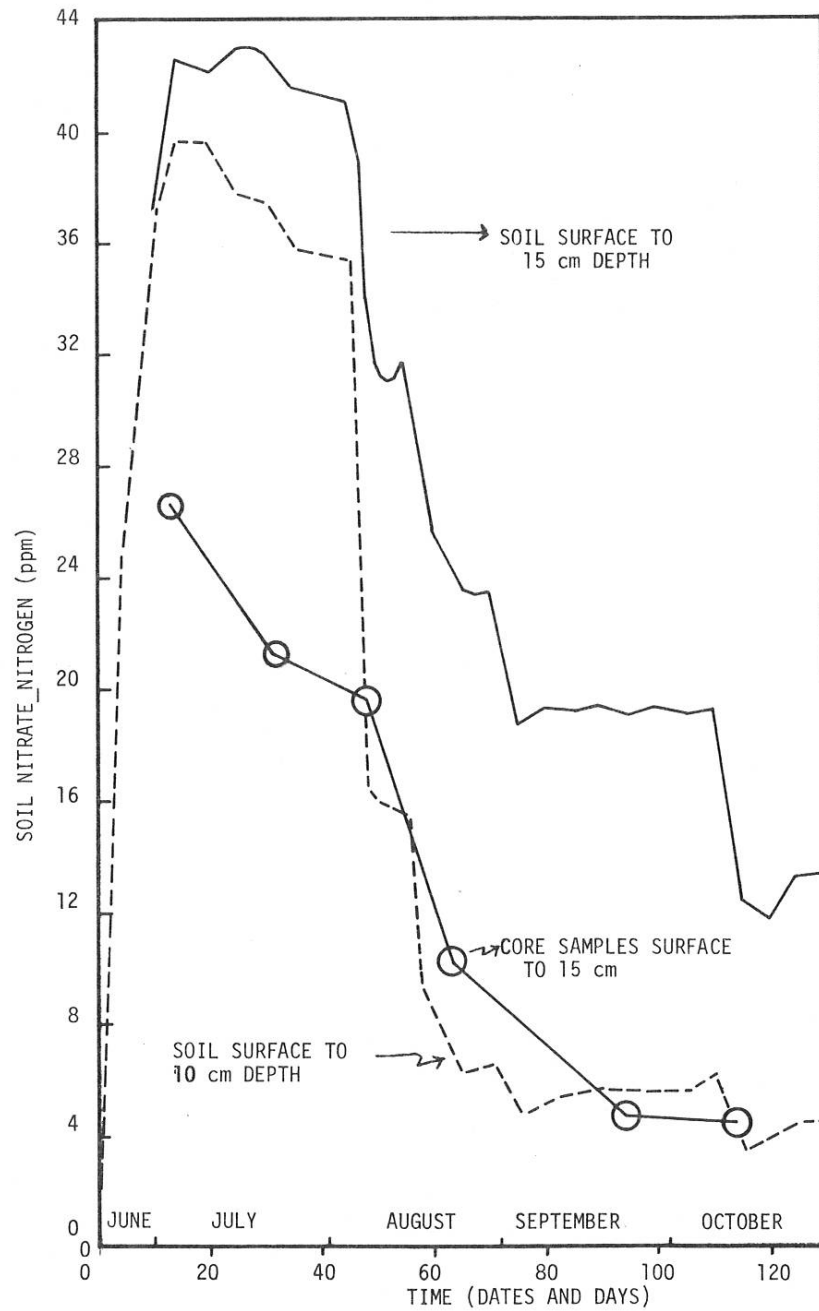


Figure 11. Measured and predicted soil nitrate concentrations (ppm) for the 130-day simulation period.

It is anticipated that with more time (and more precipitation), continued leaching of the 0-15 cm depth would decrease the NO_3^- -N concentration there to a level only slightly greater than that in the 0-10 cm zone, since both zones are totally within the A horizon. Further, it should be recalled that the observed NO_3^- -N concentrations are shown as linear between the arbitrary sampling dates for convenience of presentation only. Although this factor should be noted when graphically comparing actual (discrete) and predicted (continuous) data, it is unlikely that the actual concentration in the field ever reached those which were predicted on days 10-45 because of the explanation proposed above.

Probably the major modification needed to utilize this systems model to simulate warm desert soils is in the subroutine that predicts the mineralization-immobilization of soil nitrogen. The routine (as previously developed and used in this study) is principally concerned with predicting the influence of crop residues at varying C:N ratios on the system, and has been verified in certain agricultural applications (Dutt, et al., 1972). However, under native desert vegetation, where C:N ratios in the soil are commonly 8:1-10:1 (Fuller, pers. communication), the amount of plant residues returning to the soil is much lower than the return from crop residues on agricultural soils. It appears that in the systems analysis model of desert soils, proper maintenance of the "residual" soil organic fraction, although quite low in actual mass, would be best achieved if it was modelled separately from the more readily decomposed fresh organic residues. The observations from this simulation study suggest that the organic fraction should be considered in two pools: the first always present in some degree as the "residual" soil organic matter (C:N=8:1-10:1), and the second the more readily decomposed organic fraction resulting from fresh plant material (C:N ratio of the residue). With modifications of this type, it is anticipated that the current systems analysis model, using the moisture flow model of Dr. Hanks in cases where homogeneity should not be assumed for the physical parameters affecting soil water, can yield accurate simulation of desert grass land.

An important, and frequently limiting, factor regarding the usefulness of any systems analysis model is the computer time required in the simulation. Since the time required for a model to execute a given problem depends on the type of computer system, compiler options, efficient use of peripheral devices and other factors, and algorithms for determining computer charges are so variable, the most useful standard is often the actual cost of executing a problem on one computer system. For the Page Ranch simulation study, the computer costs and a few important parameters of each submodel are listed in Table 4.

Table 4. Computer times and charges required for 130-day Page Ranch simulation study on Control Data Corporation 6400 computer system at University of Arizona Computer Center

Submodel	CPU Time (Sec)		Submodel cost	Comments
	Compilation*	Execution		
Moisture Flow	12.6	72.5	\$12.98	14 nodes, at $\Delta t_{\max} = 0.1$ day.
Interface	3.7	18.4	4.92	Tape-tape data conversion and print.
Bio-Chemical	40.4	87.1	21.59	11 segments, $\Delta t_{\max} = 0.1$ day.

* FTN compiler option.

EXPECTATIONS

The utilization of the soil moisture program written by Dr. Hanks increases the applicability of the model to systems in which the physical parameters affecting moisture redistribution cannot be considered homogeneous with depth. With the modifications which were made during this study, the program is completely compatible with the rest of the systems analysis model.

From this study, it appears that the model can be modified from a form designed for agricultural applications to a form which will yield accurate simulation of desert grassland systems. Major changes will be required in the subroutine which predicts the net mineralization-immobilization rates and the decomposition of organic residues. The organic nitrogen will be divided into two pools: one of which represents the residual soil organic nitrogen, and the other decomposing plant residues.

SUPPLEMENT

INTRODUCTION

Evaluation of nitrogen losses from desert soils via ammonia volatilization and the incorporation of a volatilization subroutine into the existing computer model is necessary to improve predictions of nitrogen behavior in warm desert soils. Desert soils which commonly exhibit properties of high temperature, high pH and low moisture content can display as a result of these properties a significant loss of nitrogen as ammonia.

OBJECTIVES

The specific objectives of this study are:

1. Experimentally determine the ammonia partial pressures above NH_4Cl solutions at various pH levels and compare experimental values to theoretically calculated values.
2. Determine the partial pressures of ammonia for complex systems containing other anions abundant in desert soils such as carbonates and sulfates. Subsequently, to illustrating that the ammonia partial pressures from chloride solutions agree with the theoretical values.
3. Evaluate experimentally the effect of clay minerals and desert soils of different physical and chemical properties on the partial pressure of ammonia.
4. Use the experimental results to incorporate the volatilization of ammonia nitrogen into a computer model compatible with the model previously developed (Dutt, et al., 1972).

METHODS

Ammonia partial pressures above solutions of NH_4Cl

As a test for the reliability of the experimental design and technique for the analysis of the ammonia volatilization from solutions and soil systems, the experimental partial pressures of ammonia over NH_4Cl were compared with the theoretical values.

Gas collection system

Gas samples above NH_4Cl solutions were collected by means of a mechanical press precalibrated to squeeze out 400 ml of gas above 500 ml solutions of 0-1M NH_4Cl in one liter polyethylene bottles. A similar press technique was utilized by Blanchor (1967)

2.3.5.5.-24

to study the ammonia partial pressures in soil inhibiting seed production. Tests run on the precalibrated press indicated that the volumes collected were within the accuracy of 400 ± 5 ml or within 0.125% error.

The ammonia gas was trapped by passing it through 8.0 ml of 0.1 N HCL as it was pressed from the polyethylene bottles. A dual trap system containing two solutions of 8.0 ml of 0-1N HCL indicated that all of the ammonia was collected in the first trap even at high pH values where the ammonia partial pressures were high.

Ammonia analysis

The trapped ammonia was determined colorimetrically via nesslerization in 0-1N HCL described by Yuen and Pollard (1952). The color was developed in a total volume of 10.0 ml with the addition of 1.0 ml of Nessler's reagent to the trapping solution.

Sample preparation

The ammonium chloride solutions were 0.1 M in 500 ml of deionized water. Various pH levels were obtained by the addition of standard NaOH. The standard NaOH was added to deionized H_2O to make a total volume of 500 ml. Subsequent to the addition of the NaOH, the NH_4Cl salt was added and the bottle immediately stoppered as a final step to prevent any loss of ammonia.

Equilibration of the samples was attained by shaking the samples mechanically for 2 hours at a room temperature of 25 ± 1 C. The samples were finally placed on a combined shaker and water bath set at 25 ± 0.5 C prior to analysis.

Calculations

The partial pressures were calculated using the ideal gas law

$$P_{NH_3} = n RT/V$$

where P_{NH_3} is the partial pressure of ammonia in mm Hg., n is the number of moles of ammonia gas collected, R is the gas constant with a value of 62.4 liters mm Hg/mole degree, T is the temperature in degrees Kelvin and V is the volume in liters of the gas collected.

The number of moles (n) of ammonia was determined by nesslerization, the temperature (T) was maintained at 298 ± 0.5 K with a constant temperature water bath and room temperature of 25 ± 0.5 C, and the volume (V) of gas was determined by precalibration to be 0.390 liters or 400 ml of gas squeezed from the sample bottle minus 10 ml retained in the delivery tube leading from the sample bottle to the 0.1N HCL trap.

Ammonia partial pressures above other salt solutions and soil systems

According to the procedure outlined for NH_4Cl solutions, the partial pressures above ammonium sulfate solutions were determined at various pH levels.

Ammonium solutions containing other anions abundant in desert soils such as $\text{CO}_3^{=}$ will also be tested to determine any anion effect on the ammonia partial pressure prior to determining the effects of clay minerals and complete soil systems.

RESULTS AND DISCUSSION

The experimental and theoretical partial pressures above $0.1\text{M NH}_4\text{Cl}$ are illustrated in Table 5. The experimental and theoretical values agree well ($r^2 = 0.999$), verifying the reliability of the experimental technique in measuring partial pressures of more complex systems. A minimum of three experimental values were determined for each partial pressure. The average deviation of these values listed in the same table indicate the good precision obtained with our experimental design.

With solutions containing sulfate, the ammonia partial pressures were only slightly higher than the solutions containing chloride. Table 6 gives the experimental ammonia partial pressures above $0.1\text{M (NH}_4)_2\text{SO}_4$ solutions. The average deviations are as low as previously obtained with the chloride solutions.

Table 5. Experimental and theoretical P_{NH_3} above $0.1\text{M NH}_4\text{Cl}$ at 25 C and at various pH and Na^+ levels

pH	Na^+ (moles/l)	P_{NH_3} (mm Hg)		Average Deviation
		Theoretical	Experimental*	
8.00	4.55×10^{-3}	.0613	.0555	$\pm .0021$
9.03	3.12×10^{-2}	.421	.385	$\pm .0093$
10.10	8.52×10^{-2}	1.15	.997	$\pm .049$

* Mean of 3 or 4 experimental values.

Table 6. Experimental P_{NH_3} above $0.1\text{M (NH}_4)_2\text{SO}_4$ at 25 C and at various pH and Na^+ levels

pH	Na^+ (moles/l)	P_{NH_3} (mm Hg)*	Average Deviation
7.55	2.26×10^{-3}	.0307	$\pm .0017$
7.88	4.55×10^{-3}	.0564	$\pm .0039$
8.40	1.45×10^{-2}	.179	$\pm .013$
8.79	3.09×10^{-2}	.362	$\pm .0076$
9.13	5.90×10^{-2}	.712	$\pm .011$
9.65	1.13×10^{-1}	1.333	$\pm .045$

* Mean of 3 experimental values

EXPECTATIONS

The preliminary findings reported here verify the experimental methodology to be utilized throughout this investigation, with precision demonstrated by low experimental deviations and accuracy demonstrated by agreement with the theoretical values. The remaining objectives can now be approached with the confidence that the data so obtained will be sufficiently accurate to be the basis of the computer subroutine.

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1972 PROGRESS REPORT

SOIL AS A FACTOR IN MODELLING THE PHOSPHORUS
CYCLE IN THE DESERT ECOSYSTEM

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Research Memorandum, RM 73-46

MAY 1973

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Report Volume 3

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A B S T R A C T

The research conducted in 1972 emphasized a nutrient assay of soil from the Curlew Valley site, phosphorus inventory of the vegetation and rabbit droppings, and further chemical characterization of soil phosphorus, which also included determination of the kinetics and energetics of the calcium carbonate-phosphate system.

Nutrient assay of the Curlew Valley soil included measurement of the growth responses of corn and crested wheatgrass to additions of N, P and micro-nutrients. The effect of the soil crust on growth was also assessed. The results indicated that the maximum N and P levels of 200 and 80 kg/ha of N and P, respectively, increased biomass production 500% over the check treatment. As little as 50 and 20 kg/ha of N and P, respectively, increased biomass production 367% over the check.

Polynomial relationships were generated from the yield data to predict biomass production of crested wheatgrass from the phosphorus soil test values for the condition when adequate N is added to the soil and also for when no N is added to the soil. The data also showed that crested wheatgrass gave a 67% greater growth response to phosphorus than corn when no nitrogen was added to the soil. It was concluded that, by addition of phosphorus at the time of seedling, seedling vigor of crested wheatgrass could be improved, thereby increasing the probability of success when establishing new stands.

The long-term nutrient supplying capacity of the soil was determined by harvesting the crested wheatgrass at six-week intervals. The results of the third harvest showed that the N, P, and micro-nutrient treatments yielded 2,043% more biomass per pot than the check. The rate of P uptake by crested wheatgrass during the 24-week growth period was found to vary between 10.6 $\mu\text{g P/day/pot}$ found in the check treatment and 44.2 $\mu\text{g P/day/pot}$ found at the maximum N and P levels.

A phosphorus inventory of five plant species and the droppings of rabbits and cows was tabulated. The phosphorus content of crested wheatgrass was found to vary between 175 ppm for the dead grass in February to 1550 ppm for the viable grass in May. It was estimated that less than 3% of the above ground phosphorus is cycled in rabbit droppings.

For ease in thermodynamic modelling, a study was conducted that modified a previously derived relationship between ionic strength, which is used in the calculation of activity coefficients of ionic species, and the electrical conductivities of natural aqueous systems. The new relationship incorporated a correction for possible ion-pair formation. The relation found was:

2.3.5.6.-2

$$I \approx .013 \text{ EC} \quad r = .996$$

where I is the ionic strength, and EC is in millimhos/cm at 25 C. This relationship allows the ionic strength of a solution to be determined without chemically analyzing the system.

The kinetics and energetics of the calcium carbonate-phosphate system were studied. The rate constants and thermodynamic parameters for both the adsorption and desorption are tabulated and discussed.

INTRODUCTION

The goal of this project is to gain insight into the role of phosphorus in the production of vegetative biomass in a cold desert ecosystem. Soil phosphorus is important because of its relationship to the nutrition of native vegetation. Plant nutrient availability is a major ecological factor in determining plant biomass production and distribution. To provide the information needed to evaluate the cycling of phosphorus in the ecosystem, the intensity, capacity, and kinetic factors which regulate the movement and distribution of soil phosphorus in the profile are being studied. An inventory of the phosphorus content of the major plant species and rabbit droppings found at the Curlew Valley site was also undertaken. An inventory of the amount of phosphorus cycled by the above-ground system is vital to prediction of phosphorus flow in the phosphorus cycle submodel.

Research conducted in 1971 was primarily directed toward the chemical characterization of the soils of the Curlew Valley site. The distribution, form and movement of phosphorus in the soil received particular attention. The 1972 research stressed plant nutrient availability in soils as an ecological factor in determining plant biomass production; the chemical characterization of phosphorus also received attention. The intensity, capacity, distribution, and form of soil phosphorus was determined in 1971. However, the rate of indigenous phosphorus release in the soil and the effect of added phosphorus on the rate and amount of plant growth were still needed to complete the model. The 1971 results showed that the form of soil phosphorus was predominately calcium phosphates. It was found that the previous year's results could be refined and improved by correction for the formation of ion-pairs. Since the vast majority of soil phosphorus was the calcium phosphate mineral complex, the logical extension of the chemical characterization was the determination of the mechanism and rate of the adsorption-desorption process for the calcium carbonate-calcium phosphate mineral system. The results of the rate expressions obtained from the laboratory prediction of phosphorus release were compared with the rate of phosphorus uptake by crested wheatgrasses determined in the fertility response experiments. The results are interpreted in terms of the postulated mechanism for phosphorus interaction with calcium carbonate. These data will be vital in the modelling of the phosphorus cycle and in the ultimate modelling of biomass production and distribution among the vegetative constituents, and the flow of energy and matter within the ecosystem.

OBJECTIVES

The objectives of the research conducted in 1972 were:

1. To investigate the general fertility status of the soil at the Curlew Valley site with emphasis on the relation between the phosphorus content and the biomass production.
2. To determine the potential capacity of the Curlew Valley soil to sustain plant biomass production when natural nutrient cycling was interrupted by the action of man.
3. To inventory the phosphorus content of natural vegetation, litter and animal residues at the Curlew Valley site.
4. To continue the chemical characterization of phosphorus in the soils of the Curlew Valley site. Specifically, to determine the mechanism and kinetic rate constants for the phosphorus flux between the solution and the calcium phosphate mineral system which is dominant in the Curlew Valley soils.

The objectives accomplished in 1972 differ from those given in the original proposal in that field plots to assess the growth responses and species distribution changes of the native vegetation under field conditions were not conducted. The elimination of the field trials was the result of a reduction in the project funding.

METHODS

Fertility experiments

Soil for the fertility experiments was sampled from the surface 46 cm in March of 1972 at a site just north of hectare 6 of the crested wheatgrass site at Curlew Valley. The natural vegetation around the site was representative of the sagebrush-dominated complex common to the area. Chemical characterization of the soil was essentially identical to that described in the 1971 progress report (RM 72-38) and in the results section of this report (DSCODE A3UJD01 and A3UJD02).

The soil was sieved through a 6 mm screen and two kg aliquots were weighed into white plastic pots. Nitrogen was added in the form of ammonium nitrate solution at the rate of 50, 100 and 200 kg/ha. Phosphorus was added in the form of phosphoric acid at the rate of 20, 40 and 80 kg/ha. Potassium was added in the form of potassium sulfate solution at the rate of 100 kg/ha. Micronutrients were added together in solution as: Cupric sulfate, 20 kg/ha; zinc sulfate, 50 kg/ha; ammonium molybdate, 1kg/ha; sequestrine 330 iron chelate, 10 kg/ha; and sequestrine manganese chelate, 10 kg/ha.

The seed used was *Agropyron desertorum*, var. Nordan, foundation seed from the 1970 harvest of the Crops Research Division, No. Great Plains Research Center, Box 459, Mandan, North Dakota, 58554; and *Zea mays*, var. Iochief.

The experimental design was 3 replications of an incomplete factorial in N and P with comparisons with potassium, micronutrients, and soil crust additions. Further detail is given in DSCODE A3UJD05. In addition, 3 replications of each phosphorus treatment, including crust additions, were incubated moist in the lab to determine phosphorus soil test values at each fertilizer level when no extraction by a crop occurred.

Phosphorus soil test values are determined as ppm of 0.5 M sodium bicarbonate soluble phosphorus. Plant tissue phosphorus content was determined by perchloric acid digestion. Phosphorus content of solutions was determined by the ascorbic acid method of Murphy and Riley (1962).

Long-term phosphorus and micronutrient supplying ability of the soil was determined by repeated harvesting of the crested wheatgrass. The grass was clipped 2 cm above the soil surface and dried in paper bags at room temperature. The dry weight of the tops was measured. Phosphorus content of the tops was determined and an 8 mm plug of soil was taken and analyzed for phosphorus content after each harvest. Nitrogen was added as needed while all other nutrients were supplied in the initial treatments.

The fertility experiments were conducted in a growth chamber where light conditions were maintained at a 16 hr day and 8 hr night. Temperature was maintained at 25 C during the light period and 12 C during the dark period. Relative humidity was not controlled but was observed to be approximately 40% a majority of the time.

Phosphorus inventory

The phosphorus content inventory of vegetation of five plants and droppings of two animal species was accomplished by random sampling at four different times of the year. The rabbit droppings, however, were collected from a randomly selected square meter in both the crested wheatgrass and sagebrush communities; dried, weighed and analyzed for phosphorus content. Further detail is available in DSCODE A3UJD03.

Chemical studies

Saturation paste extracts were prepared from soil samples collected from hectares 6 and 42 of the crested wheatgrass plot and hectare 39 of the sagebrush plot of the Curlew Valley site. Nine samples were taken at each site to depths up to 165 cm. The chemical analytical data for approximately 124 river waters used in this study were picked at random from two sources (Geological Survey Water Supply Paper, 1969; Thorne and Thorne, 1951).

Electrical conductivity was determined with a Beckman Model RC-19 conductivity bridge using a 2-ml pipette cell (G1) with a cell constant of 1.00. The concentrations of the

2.3.5.6.-6

following ions were determined by standard methods (Black, 1965; Perkin-Elmer, 1971): Ca^{++} , Mg^{++} , Na^+ , K^+ , HCO_3^- , $\text{CO}_3^{=}$, $\text{SO}_4^{=}$, Cl^- , phosphorus, and boron.

The measured ionic concentrations were corrected for ion-pair-formation to "actual" ionic concentrations using the method described by Adams (1971). The dissociation constants used for the ion-pair calculations were obtained from Garrels and Christ (1965). The activity coefficients for the ion pairs were assumed to be unity. The analytical data were corrected in the various experiments for the following ion pairs: CaSO_4^0 , CaCO_3^0 , CaHCO_3^+ , MgHCO_3^+ , NaSO_4^- , KSO_4^- , MgCO_3^0 , CaHPO_4^0 , $\text{CaH}_2\text{PO}_4^+$, and CaOH^+ .

Calcium ion activity was measured with an Orion liquid ion exchange specific ion electrode coupled to an expanded scale pH meter and a calomel reference electrode. "Electrode" activity coefficients were determined from the ratio of calcium activity measured by the electrode and the "actual" or ion-pair corrected calcium ion concentration (Adams, 1971).

The sorption of phosphate was studied by shaking aqueous suspensions of calcium carbonate in solutions containing variable amounts of K_2HPO_4 . X-ray diffraction studies showed the crystalline form of the calcium carbonate to be calcite. The surface area of the calcite and soil was measured by the ethylene glycol retention method of Bower and Gschwend (1952).

In order to examine the crystal surface, samples of the phosphated and pure calcite were sent to the Department of Anatomy, University of California, Davis, where electron micrographs of platinized replicas were taken.

The suspensions of calcium carbonate were shaken in a thermostated water bath which maintained the temperature at ± 0.5 C. After the suspensions were shaken, the calcium carbonate was separated by means of a Millipore microfiber glass filter. Aliquots taken for phosphate sorbed were calculated from the difference between initial and final phosphate concentration.

Solubility criteria for the existence of calcium phosphate minerals were determined by the method of Clark and Peech (1955) which was modified to include the octocalcium phosphate solubility expression reported by Lindsey and Moreno (1960) and corrected for ion pairs. It should be pointed out that, in the construction of the solubility diagram, a range of K_{sp} values for hydroxylapatite can be chosen. Values given by Wier, Chien and Black (1971) vary between 109.2 and 120.2. The value of 111.8 as given by Farr (1950) and used by Clark and Peech (1955) in their original construction of the calcium phosphate solubility diagram, was used in this study. Ionic strength was determined from the electrical conductivity of the solution by the method of Griffin and Jurinak (1973).

Equilibrium studies were conducted by shaking suspensions of 4.00 gm of calcite placed in 125 ml Erlenmyer flasks with a 50 ml volume of phosphate solution and equilibrated at various temperatures. The initial phosphorus concentrations ranged from 0.1 to 5.0 ppm. The tops of the flasks were covered with parafilm in which a small hole was made to allow equilibration with atmospheric carbon dioxide. The flasks were shaken for periods of 2 to 3 days at a given constant temperature. The pH was assumed constant due to the buffering ability of the calcite-carbon dioxide system.

Interpretation of the equilibrium adsorption data was aided by application of the familiar Langmuir (1918) and B.E.T. (Brunauer, Emmett and Teller, 1938) equations. Obtaining adsorption data at different temperatures allowed the differential isosteric heat of adsorption $\overline{\Delta H}$, to be determined by application of the Clausius-Clapeyron equation (Klotz, 1964).

Long term adsorption kinetic studies were carried out as described in the equilibrium studies except that flasks were removed from the water bath and filtered after periods of time varying from a few minutes up to two months. Reaction time in all cases is defined as the period between when solution was added until completion of filtration. Filtration time was approximately 10 sec.

Short-term kinetic studies were carried out by weighing 50 gm of calcite into a 2 liter Erlenmyer. One liter of distilled water was added and the flask shaken in a water bath. The pH was adjusted by manipulation of the carbon dioxide partial pressure in the flask until a constant value of 8.4 was reached. Fifty ml of 4.0 ppm phosphorus solution was then added and the flask vigorously stirred. At the appropriate time intervals, approximately 50 ml of the slurry was poured out onto a filter and an aliquot taken for phosphorus analysis.

Desorption kinetics were studied by weighing 5.00 gm samples of calcite into 250 ml Erlenmyer flasks. A 50 ml volume of distilled water was added to the flask and the flask shaken in a thermostated water bath for one day to allow equilibration with atmospheric carbon dioxide. To each flask was added 5 ml aliquots of 2.0 ppm phosphorus solution and shaken 2-3 days. One gm of 30-50 mesh Dowex 1-X8 anion exchange resin, which had previously been soaked in a saturated calcite solution and air dried, was then added. The flasks were vigorously shaken for various lengths of time and the resin separated from the calcite slurry on a 60 mesh sieve. The resin was then placed in a funnel with No. 1 Whatman filter paper and the phosphate exchanged off the resin with 1N Na_2SO_4 solution. The filtrate was collected in a 50 ml volumetric flask and analyzed for phosphate.

Anion exchange resin simulates a plant root which continually takes phosphate out of solution and thus maintains a steep chemical potential gradient between solid phase phosphate and solution phosphate. It was found that 92% of the phosphate added to a solution was recovered from the resin in less than two minutes.

RESULTS AND DISCUSSION

Fertility assay

The fertility assay consisted of comparing the response of corn and crested wheatgrass to application of various plant nutrients. Corn was chosen as a standard agronomic crop for comparison of response to the on-site species, crested wheatgrass. The response of both crops to N and P additions was quite dramatic and the response surface of the N and P interaction on the yield of corn and crested wheatgrass is illustrated in Figures 1 and 2 respectively. Data points of the incomplete factorial design are indicated by a solid circle and are the means of three replications. Statistical analysis by the F test, at the 5% level, is given in Table 1 and the complete raw data is recorded in Data Set A3UJD05.

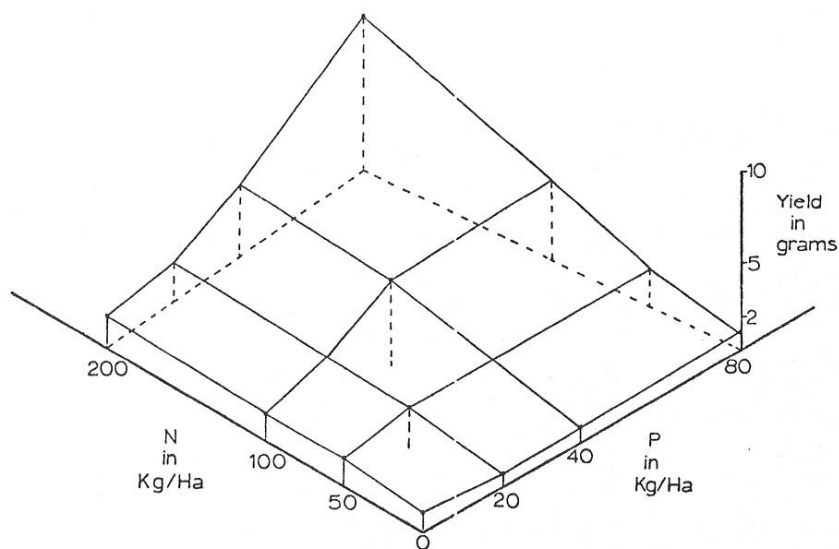


Figure 1. Response surface for corn growth showing N and P interaction. DSCODE A3UJD05

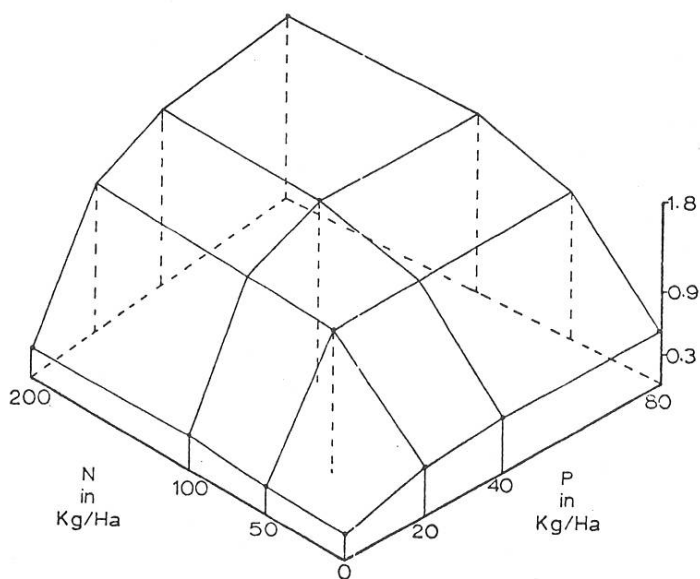


Figure 2. Response surface for crested wheatgrass growth showing N and P interaction. DSCODE A3UJD05

Table 1. Statistical analysis of N, P, and species interactions on yields of corn and crested wheatgrass. DSCODE—A3UJD05

	F 5%	Dry Wt. 1	Mg P/pot 2	Soil P ppm 3
Replications	3.74	0.25 NS	0.12 NS	2.13 NS
Species	4.60	202.5*	26.77*	0.44 NS
N	4.60	217.19*	736.03*	0.23 NS
P	4.60	143.65*	1004.75*	15.94*
SP x N	4.60	94.88*	130.91*	0.22 NS
SP x P	4.60	28.27*	148.49*	0.003 NS
N x P	4.60	125.48*	583.15*	1.01 NS
SP x N x P	4.60	33.80*	90.54*	0.62 NS

* F significant at the 5% level

2.3.5.6.-10

The results are clear and show that the differences in yield and phosphorus uptake are significant for all interactions of plant species, N and P. Soil test values for phosphorus are all non-significant except for phosphorus fertilizer levels, which is significant. For crested wheatgrass, an N level of 200 kg/ha and a P level of 80 kg/ha gave a 500% yield increase over the check pots. As little as 50 kg/ha N and 20 kg/ha and 20 kg/ha of P gave yield increases of 367% over the check. These yield increases were greater than expected from the soil test values obtained during the 1971 research. The reason is shown in Figure 3, which gives the yield of crested wheatgrass as a function of the soil test value, i.e. ppm of sodium bicarbonate soluble P, found for the Curlew Valley soil. For standard agronomic practices, it is found that soils which give phosphorus soil test values greater than 10 ppm seldom give economical yield increases to additions of phosphorus. The results shown in Figure 3 indicate that yields did not level off when adequate nitrogen was available until phosphorus soil test values were 20 ppm P. This illustrates the desirability of individual testing of non-agronomic soils and plants when yield performance predictions are required.

The polynomial found for these experimental conditions which predicts yield (Y) for any given phosphorus soil test value (X) when adequate N is available is:

$$Y = -2.83 + .418 X - .0091 (X)^2 \quad (1)$$

Similarly, the polynomial found which describes yield (Y) for a soil test value (X) when no nitrogen was added to the pots was:

$$Y = -.14 + .059 X - .0013 (X)^2 \quad (2)$$

An interesting facet of these fertility experiments was the difference between corn and crested wheatgrass in their growth responses to phosphorus additions. As can be seen in Figures 1 and 2, corn made no significant increase in growth when phosphorus alone was added while crested wheatgrass growth was increased by 67% over that of the check. This difference in phosphorus response was particularly evident during the early stages of growth and is illustrated in Figures 4 and 5 for corn and crested wheatgrass respectively. Figure 4 illustrates that when only P is added to the soil, no significant differences in growth of corn, when compared to the check, can be detected. Figure 5 illustrates that the pot with P added alone has grown approximately twice as fast as either the check or with N added alone.

The most obvious application of this result is in range improvement. Crested wheatgrass seedlings have been shown to respond markedly to phosphorus additions. It is concluded that, by addition of phosphorus at the time of seeding, seedling vigor could be improved thus insuring greater success in establishing new stands of crested wheatgrass.

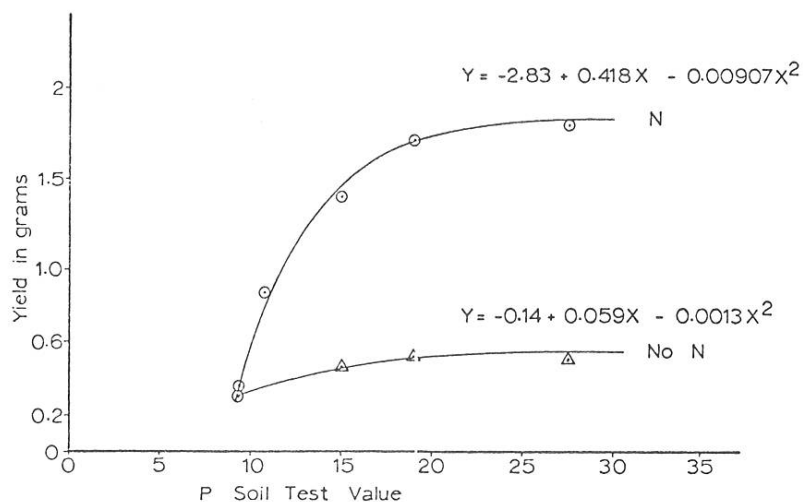


Figure 3. Relationship between phosphorus soil test value and yield of crested wheatgrass. DSCODE A3UJD05

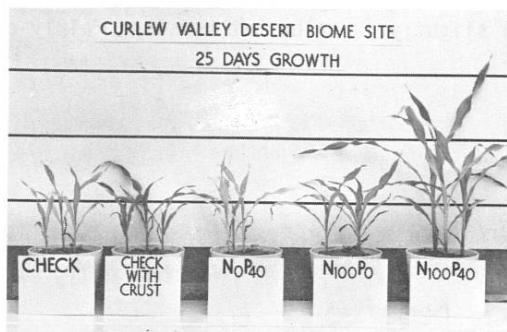


Figure 4. Growth of corn after 25 days on soil from the Curlew Valley site of the US/IBP Desert Biome.

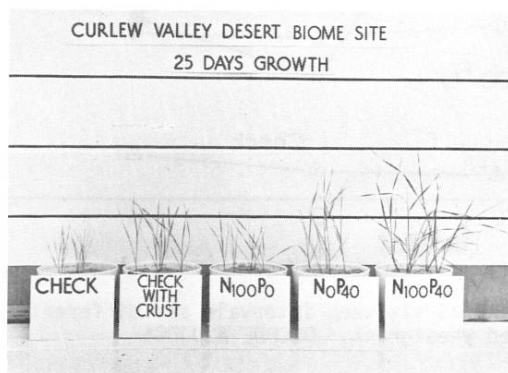


Figure 5. Growth of crested wheatgrass after 25 days on soil from the Curlew Valley site of the US/IBP Desert Biome.

2.3.5.6.-12

Results of the 1971 research indicated that a substantial fraction of the phosphorus in the soil profile was located in the surface crust (2 cm depth). The consequence of this on the phosphorus nutrition of the plant was that even though the available P content of the crust was high (25 ppm), when diluted down with the bulk soil to 10% crust, the value was only 2.5 ppm. Therefore the addition of crust merely acted as though a small amount of P fertilizer was added to the pot with a correspondingly small increase in yield. At higher P levels the effect of the soil crust was negligible. This result is illustrated in Figures 4 and 5 for corn and crested wheatgrass respectively. The increase in growth from the crust addition is a direct response to the slight increase in the fertility level. In the field situation, the effect of the higher P content of the crust on plant nutrition is considered small.

The long-term nutrient supplying capacity of the soil under continuous cropping was determined by harvesting the crested wheatgrass at six-week intervals. The results of four harvests are shown in Figure 6.

Yields of the check fell slightly in value but remained fairly constant for all harvests.

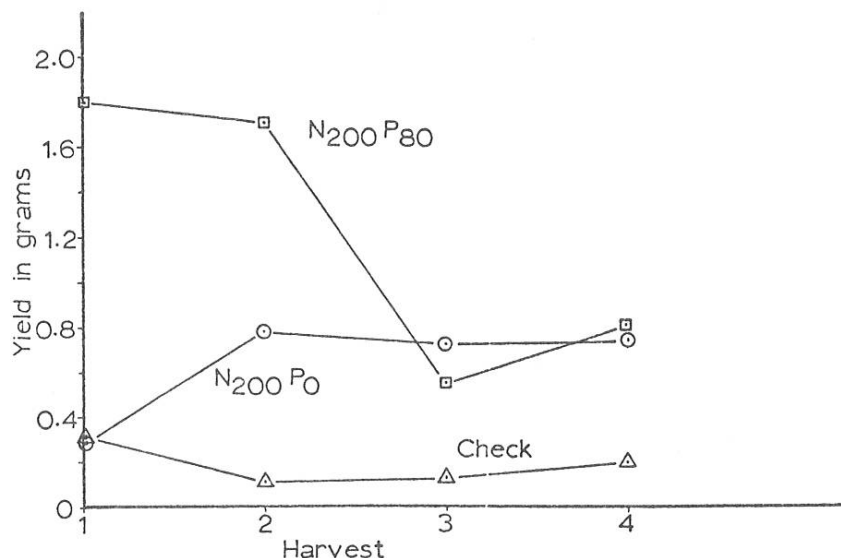


Figure 6. Effect of harvesting at six week intervals and different nutrient additions on yield of crested wheatgrass. DSCODE A3UJD05

When nitrogen alone was added, yields increased more than 50% between the first and second harvest but then remained fairly constant for the remainder of the harvests. This is presumed to be due to the development of the root system during the first harvest period and the plant being able to take advantage of it for growth during the following harvest periods. This further supports the contention that phosphorus is needed for good early growth of crested wheatgrass. Since phosphorus is known to stimulate root growth (Black, 1957), the probable mechanism is faster root proliferation.

The next significant aspect of Figure 6 is the sudden drop in yields between the second and third harvest when adequate levels of N and P were available for plant growth. The answer to this is shown in Figure 7. Treatments with micronutrients added at the start of the experiment yielded 391% more dry matter per pot than the same fertilizer level but without micronutrients added. It is speculated that the continued withdrawal of nutrients had depleted the soil of micronutrients by the end of the second harvest of crested wheatgrass.

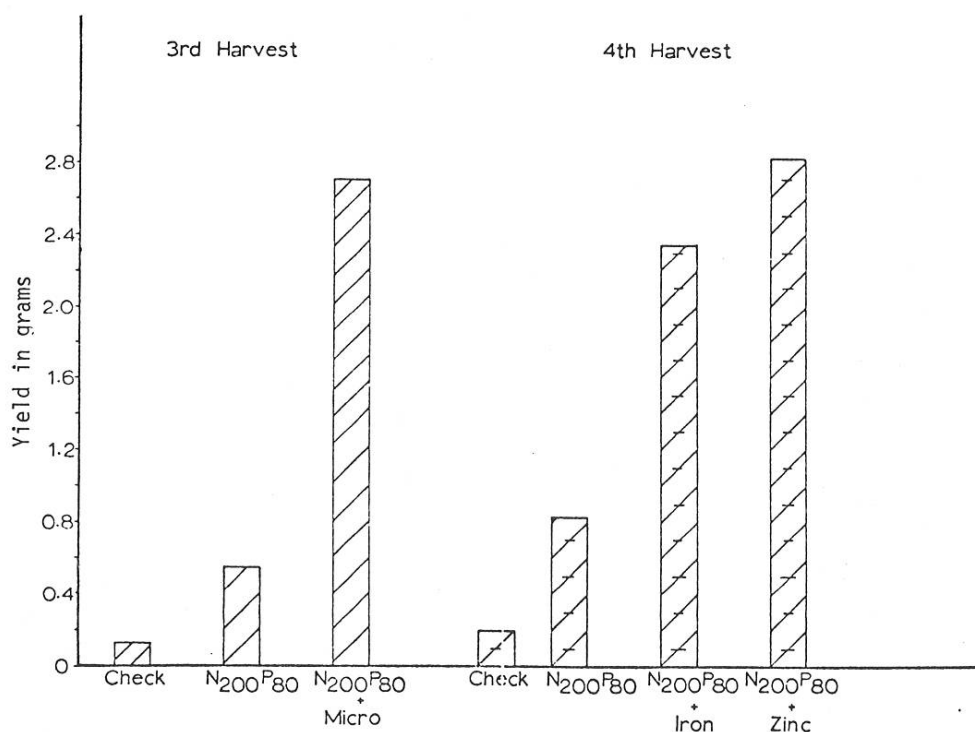


Figure 7. Effect of different nutrient additions on the yield of the third and fourth harvest of crested wheatgrass. DSCODE A3UDJ05

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Iron and zinc were considered the most likely micronutrients to be limiting growth. At the end of the third harvest, these two elements were added to one pot each and the results are also shown in Figure 7. Both iron and zinc gave large growth responses indicating both were in short supply. This result is an interesting facet of the experiments but the treatment had no replication. Further work is contemplated to determine the extent of micronutrient deficiencies at the Curlew Valley site. The effect of nutrient levels on the growth of crested wheatgrass, in the Curlew Valley soil, is further amplified by the remarkable statistic that when 200 kg/ha of N, 80 kg/ha of P, and micronutrients were added at the start of the experiment, the yield of biomass per pot for the third harvest was 2,043% greater than the check treatment.

The rate of phosphorus uptake by the plants was determined and is shown in Figure 8. The rate was found to be relatively constant after the first harvest. This was assumed to be due to a more developed root system which had expanded throughout the pot and allowed the rate of P uptake to be determined from analysis of tops only without regard to the amount present in the soil. The rate of P uptake by crested wheatgrass was found to vary between 10.6 $\mu\text{g P/day/pot}$ found in the check treatment and 44.2 $\mu\text{g P/day/pot}$ found at the maximum N and P levels.

Phosphorus inventory

The results of the phosphorus inventory of five plant species and the droppings of rabbits and cows is present in Table 2 and in Data Set A3UJD03. These data allow the amount of phosphorus cycled in the plants to be estimated by computation from biomass data. An interesting aspect of these data is the previous contention that a large fraction of the phosphorus would be tied up in rabbit droppings. From the data collected, it is estimated that less than 3% of the total phosphorus is cycled in rabbit droppings and the greater amount of the remaining 97% is cycled by the plants.

Figure 9 shows the seasonal variation in phosphorus content of crested wheatgrass and sagebrush. Sagebrush phosphorus contents remain relatively constant at roughly 1200 ppm throughout the year while crested wheatgrass varies in value from 175ppm for the dead grass in February to 1550 ppm for the viable grass during May. This points out the seasonal variation in species which will need to be taken in to account when modelling the flow of phosphorus in the ecosystem.

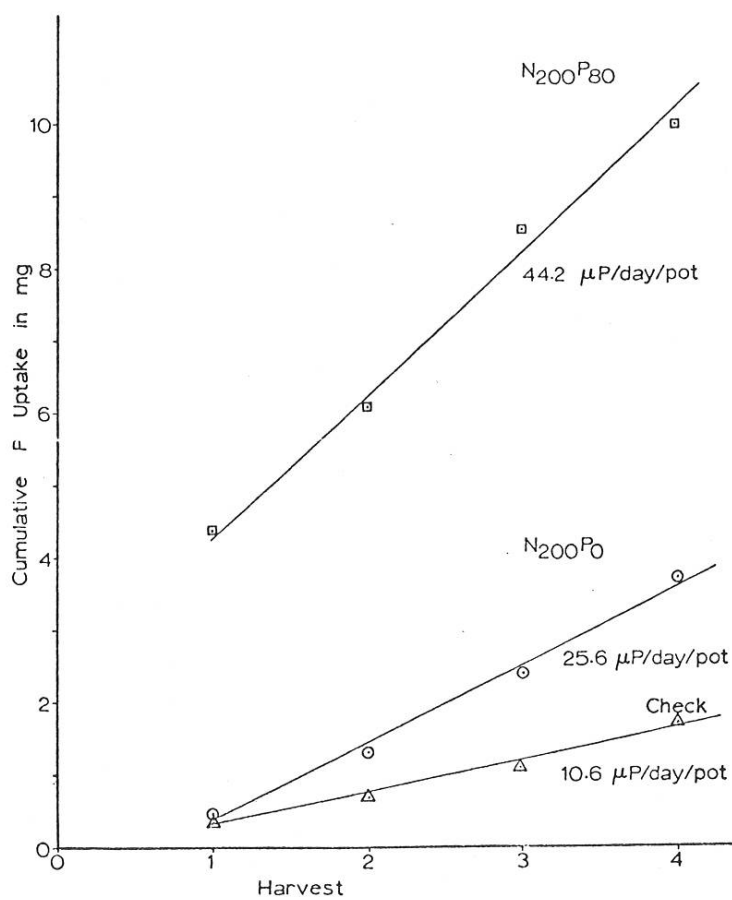


Figure 8. Effect of nutrient additions on the rate of phosphorus uptake by crested wheatgrass. DSCODE A3UJD05

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Table 2. Phosphorus content of vegetation, rabbit and cow droppings collected at the Curlew Valley site of the Desert Biome DSCODE—A3UJD03

Date	Site	Hectare	Sage	Grass	Rabbit- brush	Wheat- grass	Shadscale	Litter	Rabbit Droppings	Cow Droppings
5-12-71	1	39	Tops 1462 Roots 762	Tops 1600 Roots 837	Tops 1500 Roots 737				775	
5-12-71	2	42				Tops 1550 Roots 987	Tops 887 Roots 612		3750	1275
7-13-71	1	39	Tops 1143 Roots 717	Tops 885 Roots 974	Tops 1143 Roots 735			577	1100	
7-13-71	2	42				Tops 838 Roots 935	Tops 742 Roots 1085	448	1053	
2-24-72	2	6	Tops 1338 Roots 594			Tops 175				
3-28-72	2	6	Tops 737 Roots 545			Tops 1455 Roots 635	Tops 503 Roots 460			

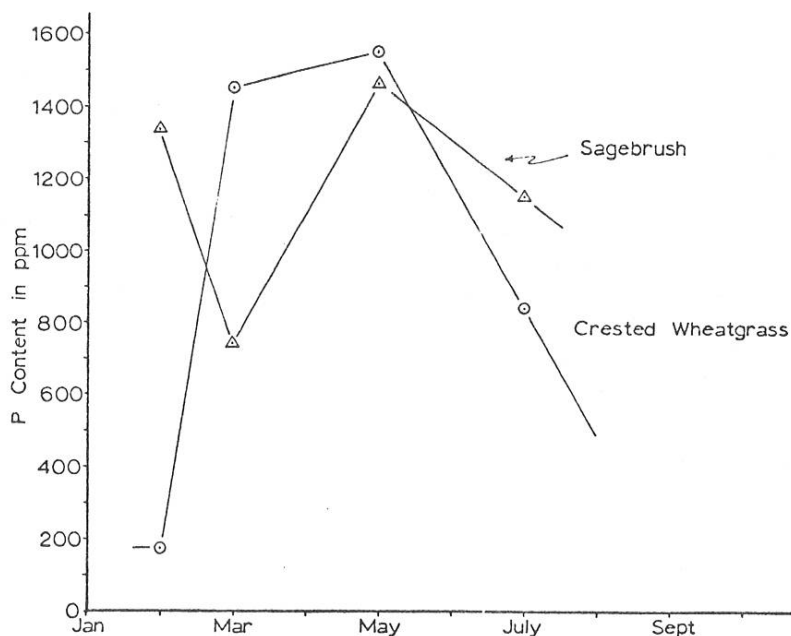


Figure 9. Seasonal variation in phosphorus content of crested wheatgrass and sagebrush. DSCODE A3UJD03

Chemical studies

The relationship between ionic strength and electrical conductivity (EC) of 27 Curlew Valley soil extracts and 124 river waters was found to be highly correlated, which corroborates the findings of Ponnamperna, et al. (1966). The total chemical analyses of the soil extracts are given in Table 3 and Data Set A3UJD02. Figure 10 shows the observed relationship between EC and the ionic strength. The ionic strength was calculated with the analytical data corrected for ion-pair formation. The linear regression for all natural waters and soil extracts was:

$$Y = .0127 X - .0003 \quad r = .996 \quad (3)$$

or $I \approx .013 \text{ EC} \quad (4)$

where ionic strength, I , is in moles/liter and EC is in millimhos/cm at 25 C. The linear relation shown in equation (4) differs from the findings of Ponnamperna, et al. (1966), who studied solutions considerably less saline. Correction of the computed ionic strength for ion-pair formation and extension of the data to systems of higher salinity had reduced both the slope and the scatter of data points around the regression line. These data modify the findings reported in the 1971 progress report (RM 72-38).

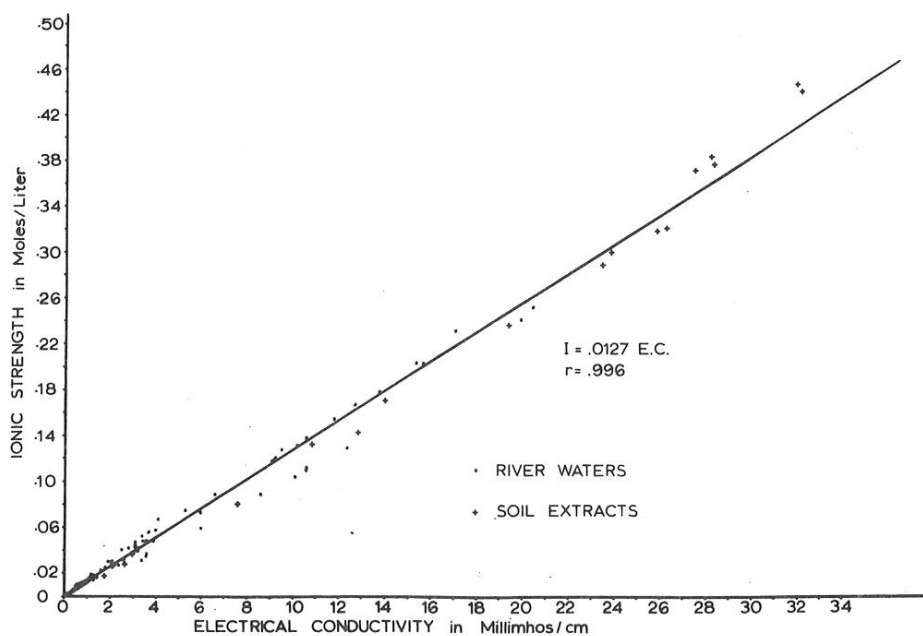


Figure 10. Relationship between ionic strength and electrical conductance of natural aqueous solutions. DSCODE A3UJD02

2.3.5.6.-18

In the Desert Biome work, the ionic strength was used in the formulation of the thermodynamic model for the calcium-phosphate mineral complex. However, the most widely used application of the ionic strength concept is in the calculation of the mean activity coefficient of an electrolyte in solution or the individual ion activity coefficient. To verify equation (4) experimentally, the individual Ca^{+2} ion activity coefficient was determined by five methods for the 27 soil extracts whose chemical analyses are shown in Table 3. The calcium ion activity coefficient data are shown in Table 4. The "actual" individual ion activity coefficients shown in column 2, Table 4, were computed using the Davies equation and the ionic strengths shown in Table 3. These ionic strength data are computed from the total chemical analyses which were corrected for the formation of ion pairs as previously described. The "experimental" calcium ion activity coefficients shown in column 3, Table 4, were calculated from the ionic strength determined by equation (4) used in conjunction with the Davies equation. The calcium ion activity coefficient data in column 4 and 5, Table 4, were computed as above except the Debye-Hückel equation was used in the calculations. The "electrode" ion activity, as measured by the calcium specific ion electrode, and the calcium ion concentration in the extract corrected for ion pair formation.

Table 4 shows that good agreement exists between the "experimental" calcium ion activity coefficient as calculated using equation (4) and the "actual" values determined using ion-pair corrected chemical analyses with both the Debye-Hückel and Davies equations. It is interesting that more difference was noted in the values of the ionic activity coefficient computed between the two theories than between the "actual" and "experimental" values computed by each theory. This suggests that a highly accurate ionic strength value estimate is less important than selecting the proper relationship with which to compute the activity coefficient after the ionic strength value has been obtained.

The Ca^{++} ion activity coefficient values calculated from the activity of Ca^{++} obtained by the calcium specific ion electrode were consistently higher than the values obtained by the other methods. Due to the lack of complete selectivity for the calcium ion by the electrode, it appears that a great deal of confidence cannot be placed in the calcium ion activity readings from a mixed salt system e.g., soil extracts.

The data in Table 3 indicate that the lower profile samples from sites 2 and 3 were gypsiferous. Consider, for example, the 137-157 cm sample of site 2. The "actual" or ion-pair corrected calcium and sulfate concentrations were computed to be 19.55 and 26.11 mM, respectively. The activity coefficients calculated using the Debye-Hückel equation and ionic strengths computed from EC data and equation (4) were 0.26 and 0.19 for calcium and sulfate ion, respectively. Calculating the ion activity product for $(\text{Ca}^{+2})(\text{SO}_4^{-2})$, gives $(.01955)(.26)(.02611)(.19)$ or 2.5×10^{-5} . The solubility product value obtained using activity coefficients computed by the Davies equation was 2.9×10^{-5} .

Table 3. Chemical analysis of saturation extracts from three profiles located at the US/IBP Great Basin Desert Biome site in Curlew Valley, Utah DSCODE—A3UJD02

Depth in cm	Concentration in mmol/L							Electrode Activity a _{Ca++}	Ionic Strength	E.C. mmhos cm
	Ca ⁺⁺	Mg ⁺⁺	Na ⁺	K ⁺	HCO ₃ ⁻	CO ₃ ⁼	SO ₄ ⁼			
Site 1										
0- 3	1.94	.42	2.21	2.49	6.12	.10	1.11	1.30	12	.78
3- 13	1.72	.42	1.68	1.13	4.48	.09	1.26	1.20	10	.62
13- 25	1.38	.48	2.45	1.34	3.97	.09	1.09	.90	10	.68
25- 33	.99	.38	3.24	1.78	4.10	.14	.92	.64	9	.66
33- 48	.53	.20	8.27	1.71	5.09	.13	1.53	.30	13	.91
48- 69	.30	.08	10.94	.95	7.01	.18	1.61	----	14	1.02
69- 94	.38	.26	30.15	1.45	4.43	.09	2.53	.19	35	3.02
94-137	2.46	.30	116.71	2.88	1.96	.04	3.34	.90	130	10.86
137-165	3.95	.49	150.00	3.23	1.86	.02	3.49	1.40	168	14.10
Site 2										
0- 3	2.26	.61	2.72	2.47	3.35	.23	.30	1.40	10	.90
3- 15	.59	.19	3.99	1.60	2.17	.23	.37	.35	7	.64
15- 28	.49	.22	12.40	3.22	2.17	.14	.84	.30	17	1.76
28- 41	3.09	2.73	116.86	6.16	1.80	.09	6.73	1.10	141	12.92
41- 71	7.32	8.80	265.55	4.45	2.03	---	15.43	2.00	319	26.38
71- 91	5.82	8.19	275.80	3.60	1.45	---	14.64	1.70	317	25.96
91-109	18.32	13.77	279.90	4.45	.99	---	39.01	4.20	376	28.54
109-137	25.31	18.74	335.28	5.21	.67	---	43.88	5.80	446	32.16
137-157	24.74	20.76	319.89	5.21	.55	---	42.48	5.80	440	32.40
Site 3										
0- 3	2.84	.52	1.89	1.04	3.44	.14	.53	1.80	10	.80
3- 15	1.13	.30	2.28	1.11	1.13	.09	.49	.84	7	.65
15- 28	1.52	.53	18.97	2.64	1.18	.09	.92	.88	27	2.72
28- 46	1.56	.77	69.93	3.79	1.62	.12	2.88	.76	79	7.58
46- 66	5.82	5.18	205.05	4.85	.99	.05	9.16	2.00	234	19.47
66- 89	7.04	7.79	260.42	4.51	.88	.05	12.02	2.30	299	24.02
89-112	6.68	6.93	246.06	4.15	.81	.05	12.20	2.20	287	23.57
112-132	22.22	14.66	267.60	5.32	.67	---	41.75	5.40	372	27.68
132-152	23.48	16.78	267.60	5.73	.67	---	41.87	5.60	384	28.39

Table 4. Comparison of calcium ion activity coefficients obtained by three different methods DSCODE—A3UJ302

Depth in cm	Davies		Debye Hückel		Electrode
	Actual	Experimental	Actual	Experimental	
	$\gamma \text{ Ca}^{++}$	$\gamma \text{ Ca}^{++}$	$\gamma \text{ Ca}^{++}$	$\gamma \text{ Ca}^{++}$	$\gamma \text{ Ca}^{++}$
Site 1					
0- 3	.64	.66	.66	.67	.76
3- 13	.67	.69	.68	.70	.79
13- 25	.67	.67	.68	.69	.73
25- 33	.68	.67	.68	.70	.72
33- 48	.63	.64	.64	.66	.69
48- 69	.62	.63	.63	.65	---
69- 94	.50	.49	.53	.52	.59
94-137	.34	.33	.37	.37	.40
137-165	.30	.30	.35	.34	.37
Site 2					
0- 3	.67	.66	.68	.67	.68
3- 15	.70	.69	.72	.70	.70
15- 28	.59	.57	.61	.59	.69
28- 41	.32	.31	.36	.35	.40
41- 71	.26	.25	.29	.28	.31
71- 91	.26	.26	.29	.29	.33
91-109	.25	.25	.27	.27	.29
109-137	.24	.24	.26	.26	.29
137-157	.24	.24	.26	.26	.29
Site 3					
0- 3	.67	.67	.67	.67	.67
3- 15	.70	.69	.71	.70	.78
15- 28	.54	.51	.56	.53	.60
28- 46	.39	.37	.43	.41	.54
46- 66	.28	.28	.31	.31	.54
66- 89	.26	.26	.29	.29	.38
89-112	.26	.26	.29	.29	.36
112-132	.25	.25	.27	.28	.32
132-152	.25	.25	.27	.28	.31

These data infer that the Debye-Hückel equation is superior to the Davies equation for predicting individual ion activity coefficients. This is in agreement with the view expressed by Adams (1971). However, at higher ionic strength values ($> .1$), the assumption was made that the activity coefficient of the calcium sulfate ion-pair is unity (Nakajama, 1971). If this assumption is not valid, the conclusions concerning the use of these two equations may be altered.

The good agreement between the "actual" activity coefficients and those computed in conjunction with equation (4), as shown in Table 4, coupled with the ability to closely approximate the solubility product of gypsum in a gypsiferous soil, supports the validity

of equation (4). This method is considered to be sufficiently accurate for estimating the ionic strength of mixed electrolyte solutions as to eliminate the need of laborious solution and analysis of natural waters.

Another application of the derived relationship is in the prediction of EC from ionic concentration data (McNeal, et al., 1970). Theoretically, correction of analytical data for ion-pair formation and use of equation (4) should yield more reliable EC values than those obtained from regression analysis based on non-corrected concentrations or relations based on linear-segment fitting of one particular data set.

The information presented here on the interaction of phosphorus with calcite is a condensation of a more complete treatise given by Griffin (1973). The results of phosphate adsorption on calcite plotted according to the Langmuir isotherm equation are presented in Figure 11. The data show two distinct linear portions which delineate two regions of adsorption.

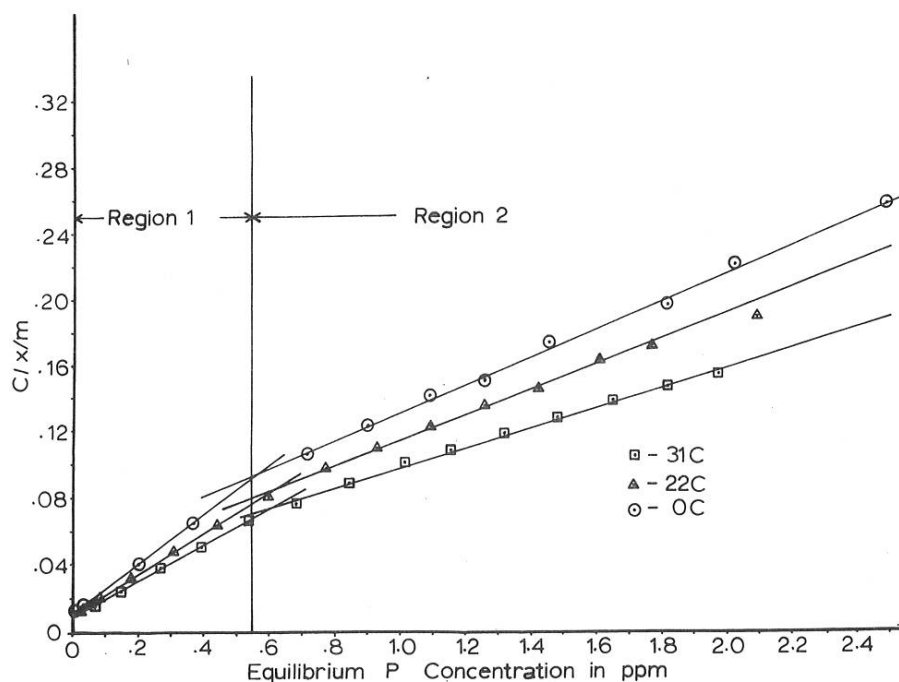


Figure 11. Phosphorus adsorption data for calcite plotted according to the Langmuir isotherm. DSCODE A3UJD02

Attempts to resolve the adsorption isotherms presented in Figure 11 into their component energy sites were unsuccessful and led to inspection of a second hypothesis, that of multilayer adsorption. The results are shown in Figure 12 and indicate that the data are linear throughout the entire applicable surface coverage range of the equation.

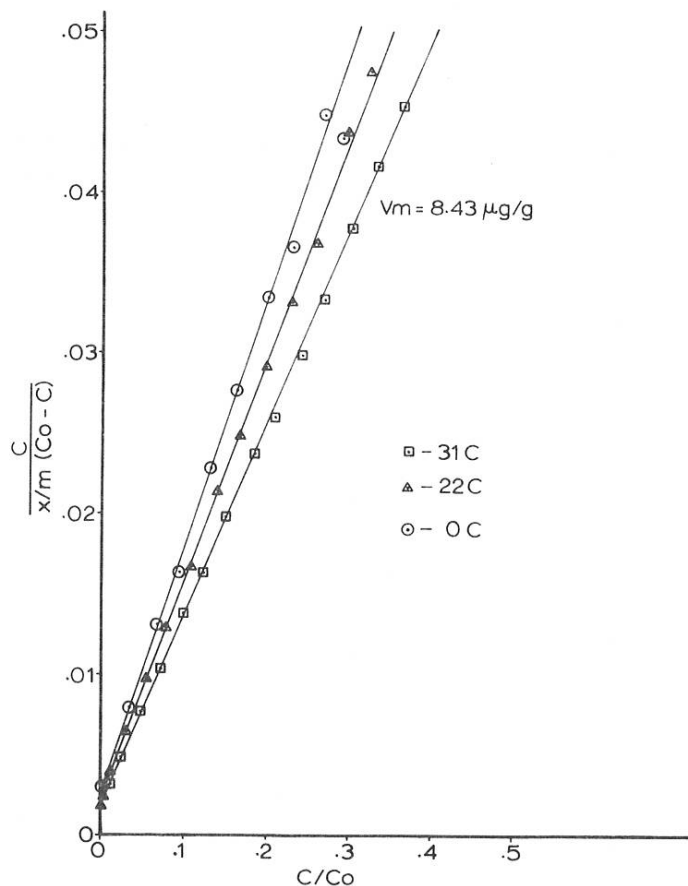


Figure 12. Phosphorus adsorption data for calcite plotted according to the B.E.T. equation. DSCODE A3UJD02

The monolayer capacity computed from the B.E.T. equation is shown in Figure 12 and agrees closely with the adsorption maximums obtained from the region 1 slopes of the Langmuir plot of Figure 11. Comparison of these monolayer capacities with the total surface area of the calcium carbonate indicate that only approximately 5% of the total surface is covered with phosphate ions. It appears that we do not have classical multilayer adsorption, but apparently have adsorption in layers at very specific sites on the surface. This leads to the hypothesis that this special kind of multilayer formation at

specific sites may be the critical cluster formation for heterogeneous nucleation of calcium phosphate on the surface of calcite.

The interpretation of heterogeneous nucleation is corroborated by electron microscope studies. Figures 13 and 14 show electron-micrographs of single calcite crystals which have been reacted with water and with phosphate solution respectively. The surface of the crystal reacted with water is relatively smooth while the crystal that has been reacted with 0.19 ppm phosphorus solution has developed surface growths which cover only a small percentage of the surface. Further support of a heterogeneous nucleation interpretation of the data presented up to this point comes from the isosteric heat of adsorption calculations.

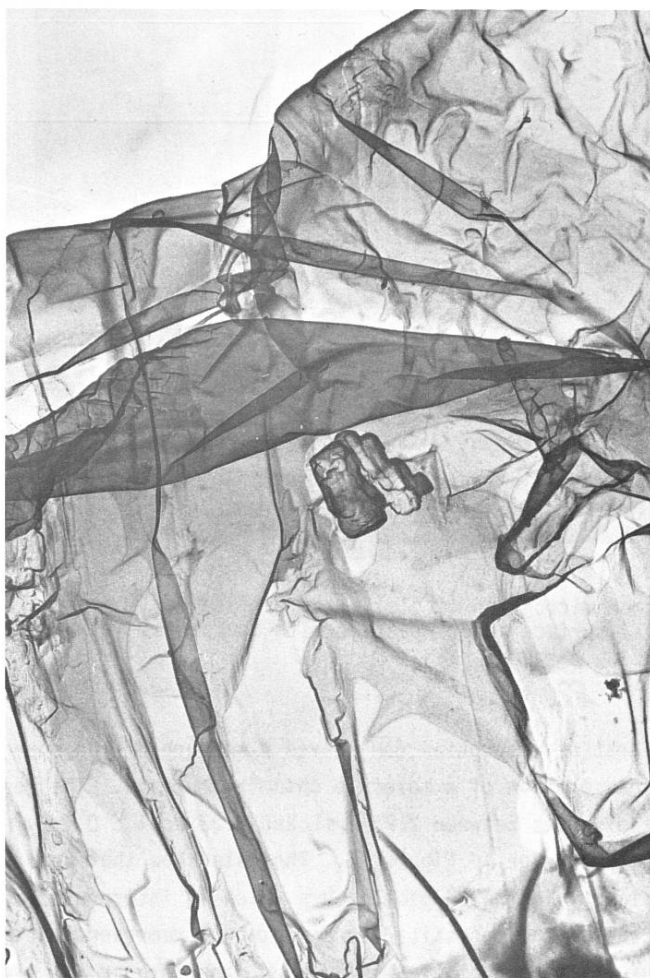


Figure 13. Electron micrograph of platinated surface replica of unreacted calcite single crystal surfaces at 18,000 x.

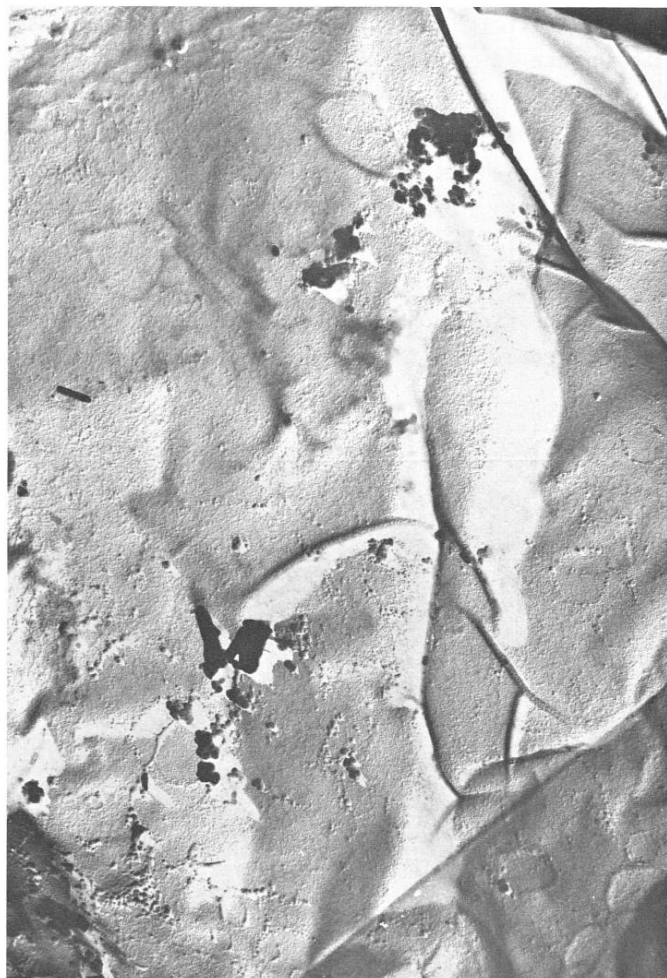


Figure 14. Electron micrograph of platinized surface replica of calcite single crystal surface after reaction with phosphorus at 18,000 x.

The isosteric heat of adsorption ($\overline{\Delta H}$) gives a measure of the energy released or adsorbed during the adsorption of a molecule onto the surface. The results indicate the $\overline{\Delta H}$ is endothermic and varies between 7.73 kcal and 9.33 kcal \pm 0.4 kcal and is plotted as a function of surface coverage in Figure 15. The data show that upon completion of region 1, a discontinuity in the $\overline{\Delta H}$ plot occurs which is interpreted as being due to the energy barrier created by the necessity for an internal rearrangement of the molecules on the surface. Further, after completion of a layer, the interaction energy of the surface becomes masked and the multilayer or cluster becomes less stable. This instability then allows rearrangement or nucleation and the epitaxial growth of the new calcium phosphate crystalline phase on the surface of the calcite.

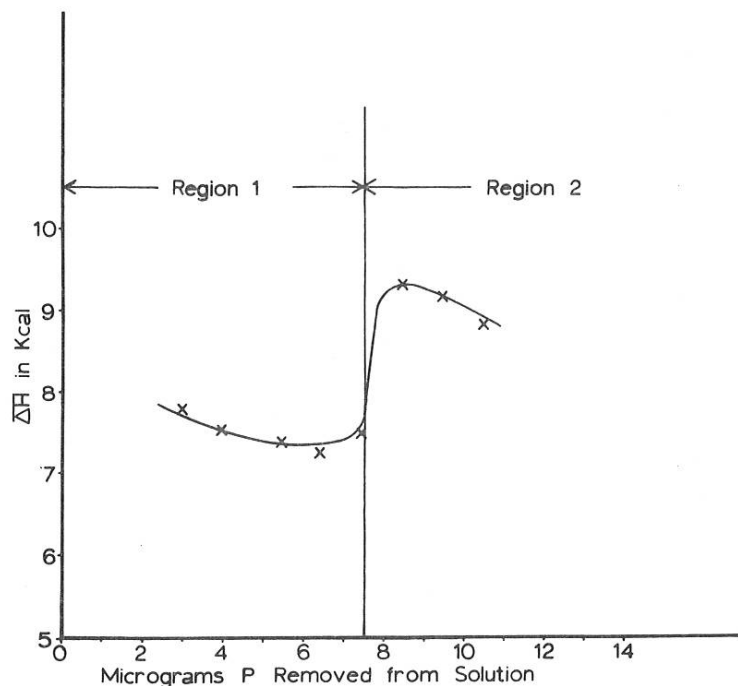


Figure 15. Isosteric differential heat of adsorption as a function of surface coverage.

To be consistent with heterogeneous nucleation theory, heats of adsorption values indicating chemisorption would be expected (Stumm and Morgan, 1970). The values for ΔH obtained in these experiments are consistent with a chemisorption mechanism.

Using solubility criteria, region 1 and 2 can be differentiated as belonging to two different calcium phosphate mineral species. The solubility diagram for the calcium phosphates and calcium carbonate is shown in Figure 16. Selected adsorption data points are plotted on the solubility diagram. The results indicate that the calcium ion concentration is being governed by the calcite-carbon dioxide system. The results further show that the solutions in region 1 are supersaturated with respect to hydroxylapatite and that solutions from region 2 are in equilibrium with or supersaturated with respect to a second mineral species, octocalcium phosphate. These data are further support of a heterogeneous nucleation hypothesis.

Adsorption kinetics

The data obtained from long-term kinetic experiments are presented in Figure 17. The interpretation of these data are consistent with and give strong support to the heterogeneous nucleation hypothesis. The interpretations of the kinetic results provide a

2.3.5.6.-26

summary of the interpretation given the previous data. The first important feature of the graph is the sharp initial drop in concentration which is interpreted as corresponding to the initial surface adsorption which is the precursor to the critical cluster formation. The second feature is the relatively flat portion of the graph which corresponds to the induction period prior to crystal growth. This portion is regulated by the chemical potential gradient established by the relative supersaturation of the initial solution. The higher the initial concentration, the faster the multilayer or critical cluster becomes unstable and the shorter the induction period. The third portion of the graph, where the concentration falls off to low values, may be interpreted as corresponding to the epitaxial growth of the calcium phosphate mineral species on the surface of the calcite.

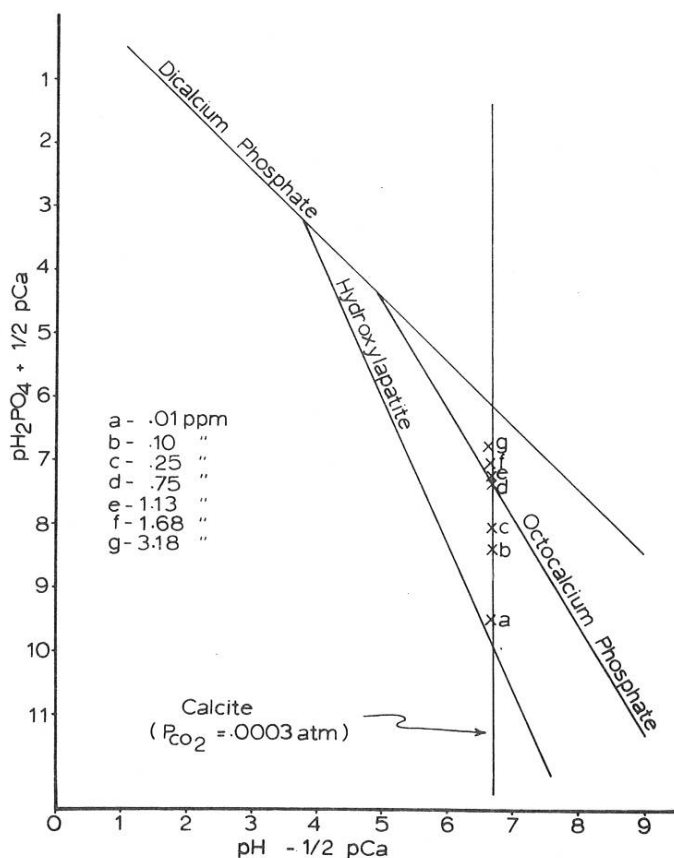


Figure 16. Solubility diagram of the calcium phosphates with selected adsorption data plotted. DSCODE A3UJD02

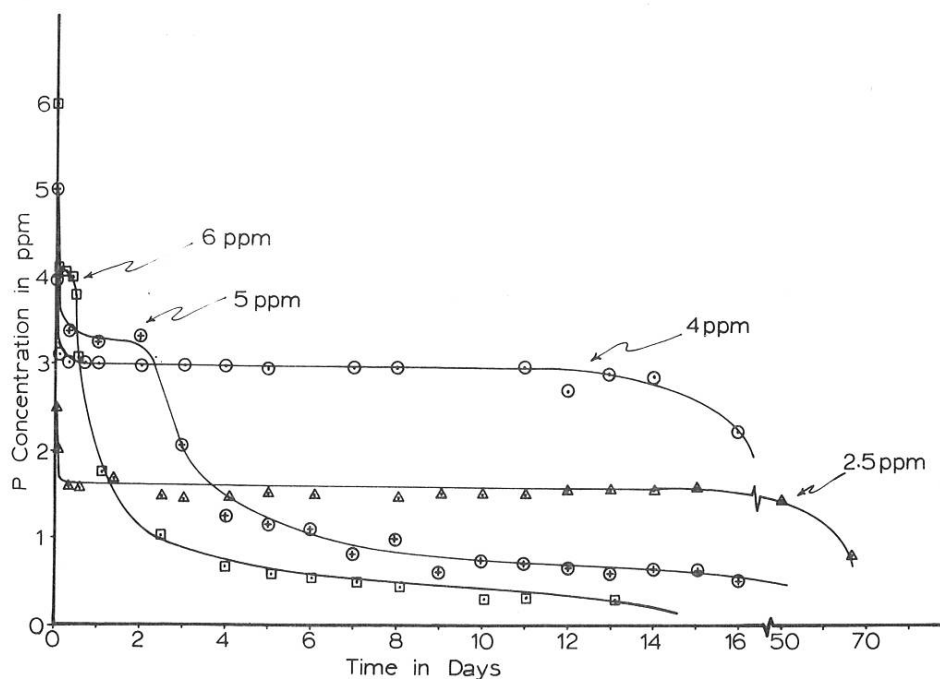


Figure 17. Long term kinetics of phosphorus interaction with calcite at 23 C and different initial phosphorus concentrations.

In order to study the initial stages of the reaction, experiments were set up to obtain data at short reaction times. It was also desired to verify if the reaction was surface-mediated or precipitation type reaction. To accomplish this later objective, an identical reaction system (see Methods section) was set up with the calcite carefully filtered out by gravity so as not to disturb the calcite-carbon dioxide equilibrium which had been established. The phosphorus was then added to the saturated solution and monitored at various times. The results of these experiments are shown in Figure 18. They indicate that the reaction is indeed surface-mediated since when no calcite was present, the concentration of phosphorus remained essentially constant during the entire four-hour reaction period. The phosphorus concentration in the samples containing calcite fell rapidly to low values within 10 to 20 min after the initiation of the reaction. If the reaction had been a precipitation of calcium phosphates, the presence of calcite should have had no influence on the reaction rate since both systems were equally supersaturated with respect to hydroxylapatite. Therefore, the conclusion was reached that the calcite surface was an important factor in the observed reaction kinetics.

2.3.5.6.-28

The shape of the kinetic curve shown in Figure 18 made it apparent that the reaction could not be described by simple kinetic relationships. Complex reaction kinetics involving two or more simultaneous reactions were suggested by the shape of the plots.

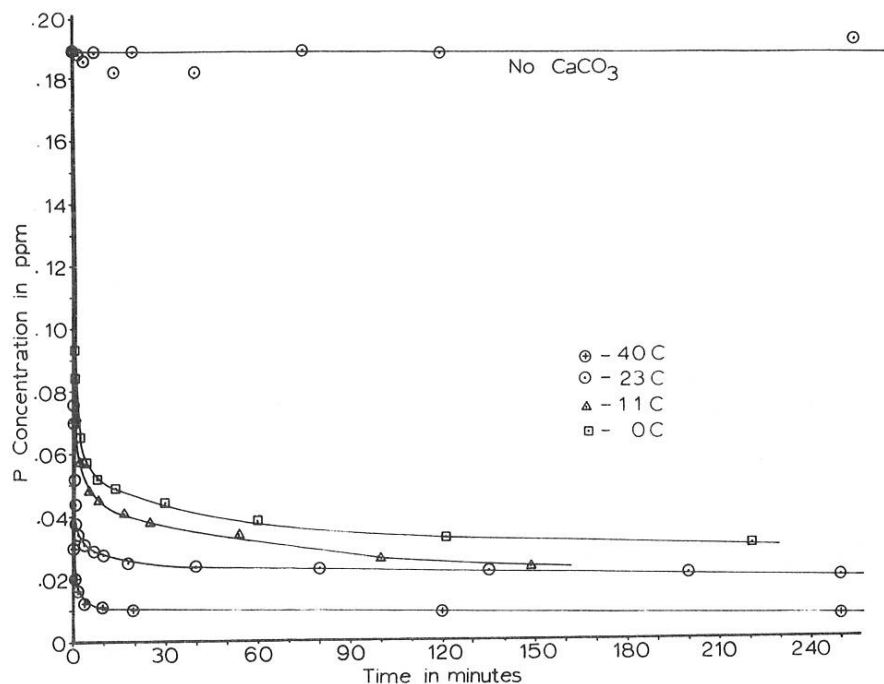


Figure 18. Kinetics of phosphorus interaction with and without calcite and at different temperatures.

The data were analyzed according to simultaneous second-order and first-order kinetics. The results are shown in Figures 19 and 20 for the first-order and second-order plots respectively. The results of these kinetic data add further support and are consistent with the postulated mechanism of a heterogeneous nucleation of calcium phosphate mineral species mediated by the surface of calcite. The postulated mechanism is the second-order adsorption of phosphorus on the surface of the calcium carbonate, that is, the rate of adsorption is regulated by the solution concentration of phosphorus and the number of empty surface sites. This is followed by a first-order reaction which is interpreted as corresponding to the surface rearrangement of the heteronuclei into the calcium phosphate crystal which supercedes crystal growth.

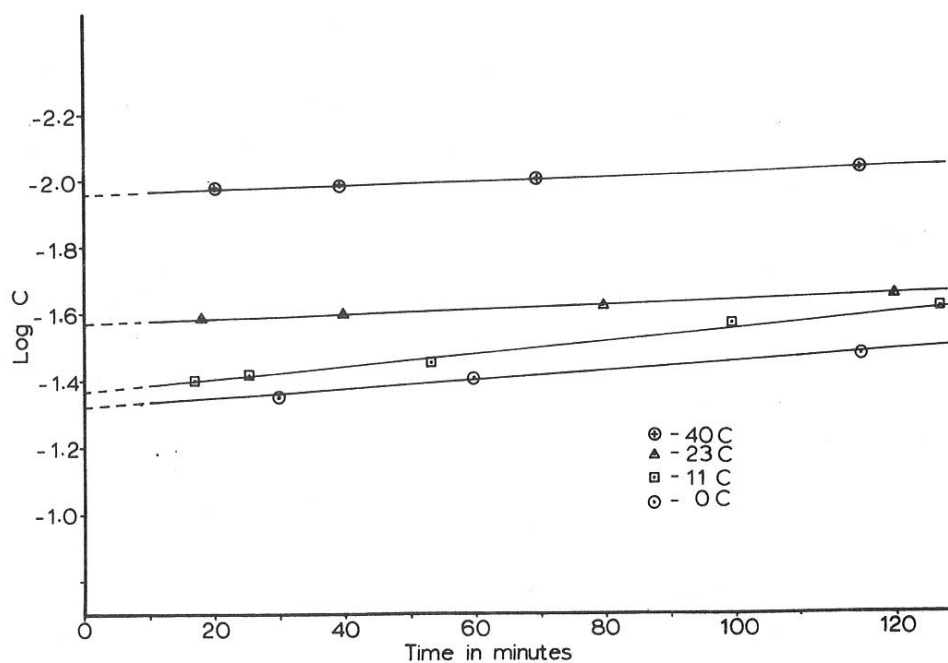


Figure 19. First-order rate plot for phosphorus interaction with calcite at reaction times greater than 10 minutes.

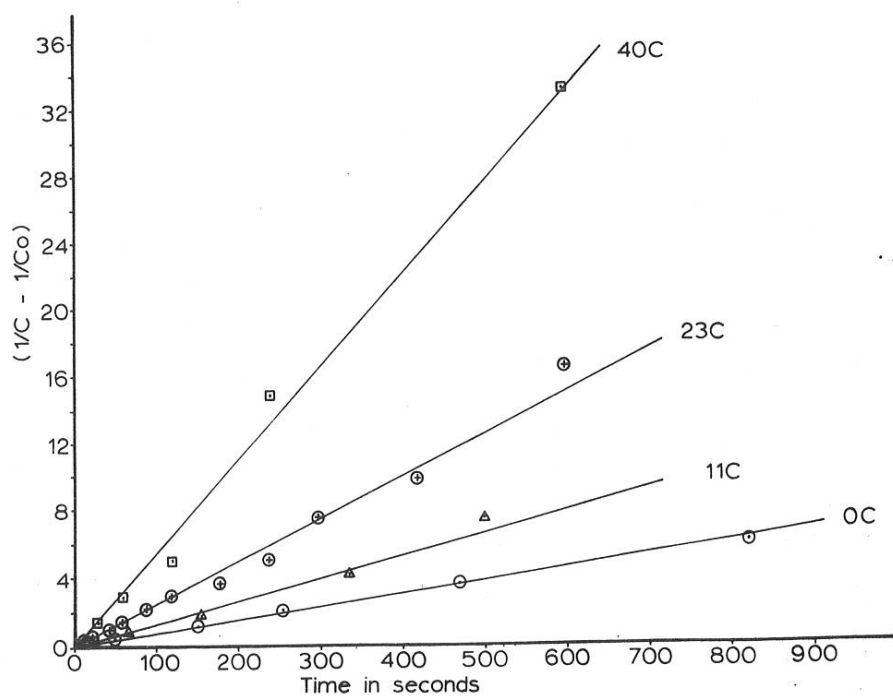


Figure 20. Second-order rate plot for initial phosphorus interaction with calcite.

2.3.5.6.-30

The adsorption rate constants for the simultaneous reactions at various temperatures were computed from the slopes of the lines and are presented in Table 5. These rate constants were then used in the computation of activation energies, which are also given in Table 5, and will be discussed in the section on the thermodynamic parameters.

Table 5. Kinetic parameters for the adsorption and desorption process at different temperatures

Temperature in Deg. C	Adsorption	Nucleation	Adsorption			
	k_1	k_1	E_a	ΔH^\ddagger	ΔS^\ddagger	ΔG^\ddagger
	1/mole-sec	1/sec	Kcal/mole	Kcal/mole	Calories deg.mole	Kcal/mole
0	$.72 \times 10^{-2}$	$.22 \times 10^{-4}$	9.0 + 1.8 adsorp. < 1 Nuc.	8.46	-37.2	18.62
11	$.14 \times 10^{-1}$	$.32 \times 10^{-4}$		8.44	-37.2	19.00
23	$.26 \times 10^{-1}$	$.10 \times 10^{-4}$		8.41	-37.6	19.61
40	$.55 \times 10^{-1}$	$.12 \times 10^{-4}$		8.38	-37.6	20.15
	Desorption	Dissolution	Ed	Desorption		
	1/sec	1/sec				
11		$.59 \times 10^{-4}$	1.4 ± 1 Diss < 1 Desorp. 0.41			
23	$.33 \times 10^{-6}$				-66.0	20.1
40		$.74 \times 10^{-4}$				

To determine if the calcium phosphate mineral nucleating on the surface was the thermodynamically stable hydroxylapatite or one of the metastable calcium phosphates, some of the kinetic data (shown in Figure 18) were plotted on the calcium phosphate solubility diagram and the results are presented in Figure 21. The data for 40 C indicate that the solution reaches equilibrium with hydroxylapatite within 24 hr. At the lower temperature (11 C) the equilibrium is approached, but not reached, during the four-hour reaction time represented on the diagram. This data leads to the conclusion that the calcium phosphate mineral species nucleating on the surface is indeed hydroxylapatite. However, predicting which species will nucleate on the surface requires caution since the results of data plotted in Figure 16 indicate that the mineral species which is nucleated on the surface depends on the initial phosphorus concentration, i.e. the Ca/P ratio.

The solubility diagram gives further support to the conclusion that the relatively flat portions of the kinetic curves correspond to amorphous or semi-crystalline clusters of ions on the surface which slowly change and/or nucleate into hydroxylapatite. The rate of this crystallization or nucleation depends on the relative supersaturation of the solution to the crystal form in question. It should be noted that at low phosphate concentrations the induction period may last an indefinite period of time. This may account for

2.3.5.6.-32

the calcium phosphate mineral which was nucleated on the calcite surface and desorption of phosphate ions from the calcite surface.

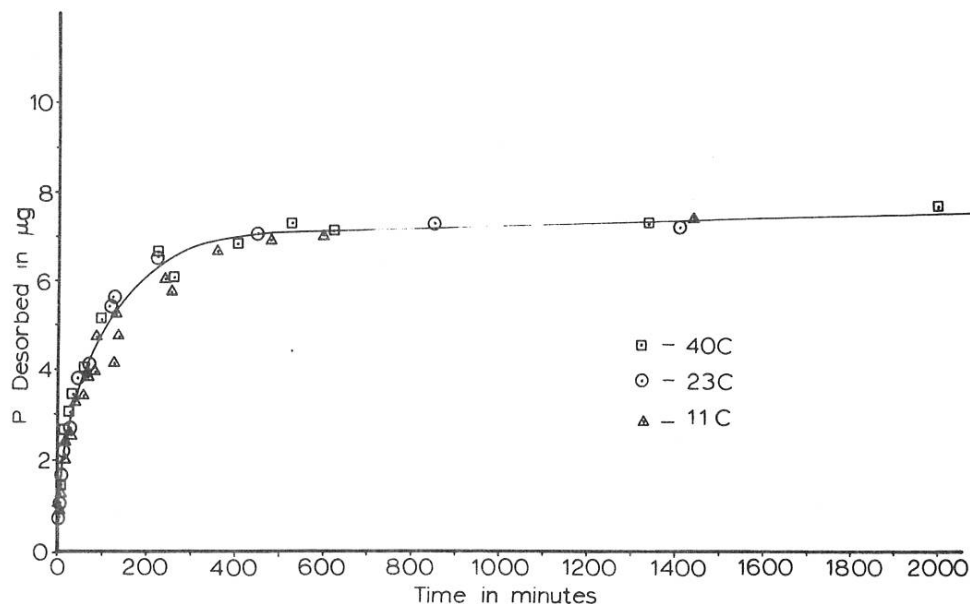


Figure 22. Kinetics of phosphorus desorption from calcite by the resin method.

To investigate the possibility that one of the mechanisms was dissolution of a mineral on the surface, the data were plotted according to the "parabolic diffusion law" given in Figure 23. The results indicate that during the initial stages of desorption (times less than 100 min) the data were found to follow the diffusion rate expression with a very slight temperature dependence.

The data for the entire 24 hr reaction period were analyzed according to simultaneous first-order reaction kinetics. The results are presented in Figure 24 and show the data to be broken into two distinct linear segments. The initial portion of the data are linear up to reaction times of 400 min. This is interpreted as corresponding to the first-order dissolution of the phosphate mineral from the surface of the calcite. The second portion of the plot also follows a first-order expression but is a much slower reaction. These data are interpreted as corresponding to a desorption of the phosphate ions from the surface of the calcite. The desorption rate constants computed from the slopes of the lines are given in Table 5.

the fact that hydroxylapatite is not found in many natural systems. It is the thermodynamically stable form, but the kinetics are very slow.

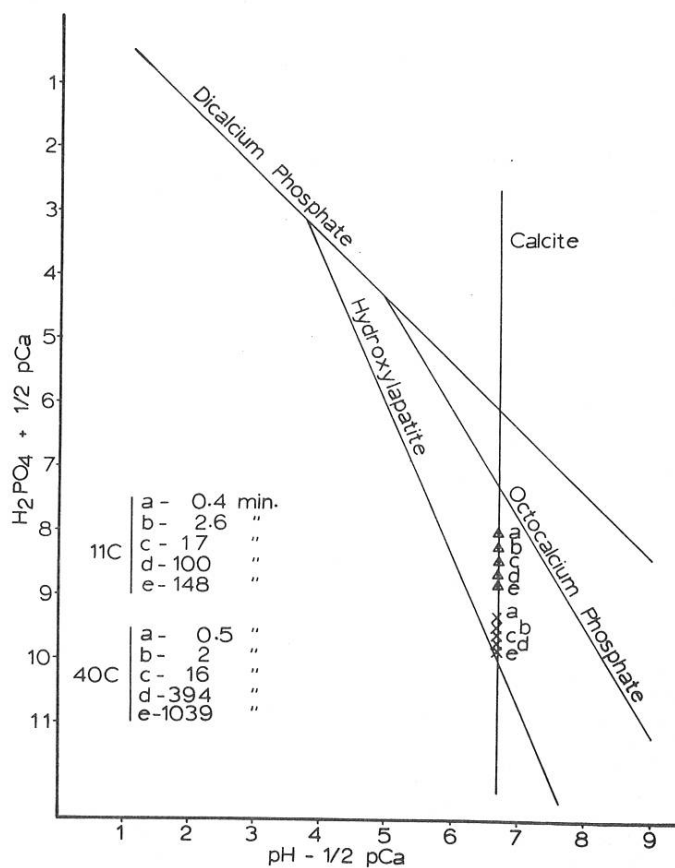


Figure 21. Solubility diagram for the calcium phosphates with kinetic data for two temperatures plotted.

Desorption kinetics

The results of desorption experiments using anion exchange resin are presented in Figure 22. The data show that between the temperatures of 11 C and 40 C there is only a small temperature dependence on the desorption of phosphorus from the calcite surface. Except for the small temperature dependence, the desorption kinetic curves are approximately the inverse of the adsorption kinetic plots. This led to the supposition that the desorption mechanism was approximately the inverse of the postulated adsorption mechanism, i.e., the desorption is the result of two simultaneous processes: that of dissolution of

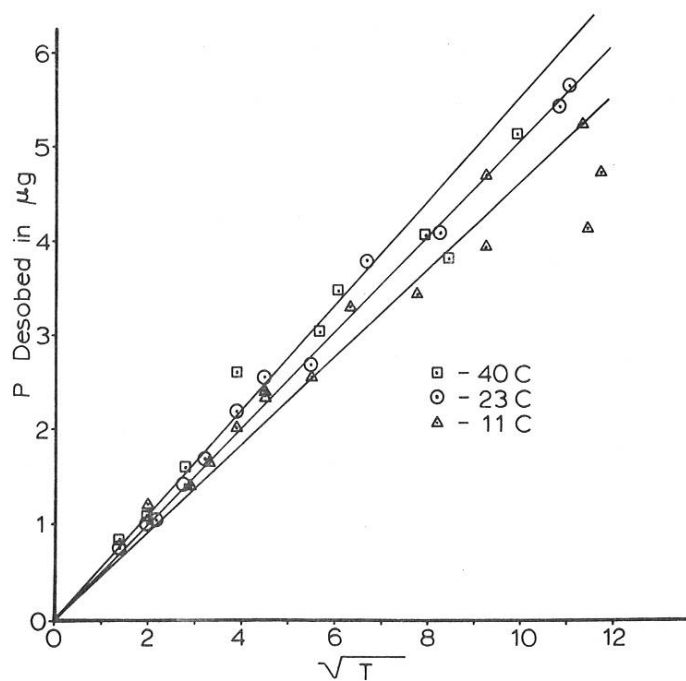


Figure 23. Phosphorus desorption data plotted according to the "parabolic diffusion law."

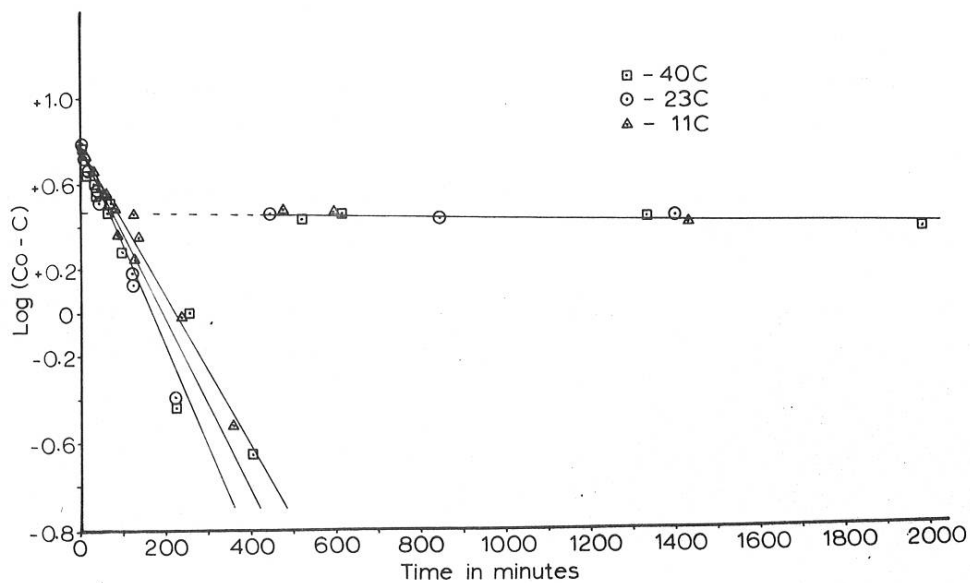


Figure 24. Phosphorus desorption data plotted according to simultaneous first-order rate expressions.

It is concluded that phosphorus desorption from calcite using anion exchange resin can be described by simultaneous first-order rate expressions. These two reaction rates are postulated to correspond to: 1. dissolution of calcium phosphate mineral nucleated on the surface with the rate-limiting step being diffusion, presumably through a static water film, and 2. desorption of phosphorus ions from the calcite surface.

Using the rate constants determined from the above study, the phosphorus desorption rate was computed to be 10.4 $\mu\text{g P/day/Pot}$. This compares to the value of 10.6 $\mu\text{g P/day/Pot}$ obtained for the rate of P uptake by crested wheatgrass in the check treatment of the nutrient assay. This demonstrates that realistic rate values for phosphorus uptake by roots are estimated by resins in laboratory experiments.

Thermodynamic parameters

The activation energy of adsorption and desorption were determined from the rate constants and are given in Table 5.

The enthalpy, entropy, and free energy of activation were also computed and are given in Table 5.

Results of 1971 research pointed out that the preponderate form of soil phosphorus was the calcium-phosphate mineral complex. Now that study of the kinetics and energetics of pure calcium-phosphate mineral system is completed, study of the phosphorus flux in the more complicated soil system can proceed from a strong theoretical base.

Determination of the kinetic rate constants for the Curlew Valley soil using the concepts and techniques developed for the pure calcite system is on-going. Preliminary results using the soil indicate that the interpretation of the phosphate adsorption mechanism is nearly identical to the pure calcite system. As an example, the Langmuir adsorption isotherm for the Curlew Valley soil is given in Figure 25 and can be compared with the nearly identical-shaped isotherm shown for pure calcite in Figure 11.

The phosphorus adsorption maximum computed from Figure 25 yields a value of approximately 500 kg/ha. Experience has shown that maximum plant growth does not occur until the available phosphorus level of the soil is around 20% of the adsorption maximum. Even with 80 kg/ha of added phosphorus, this only brings the phosphorus level to 16% for the Curlew Valley soil. The effect of the percentage of the adsorption maximum on yield of crested wheatgrass is illustrated in Figure 26. This result helps explain why unusually high soil test values were required for maximum yields. This soil from the Curlew Valley site has an unusually high phosphorus adsorption capacity and bonds phosphorus more tenaciously than soils with lower adsorption capacities.

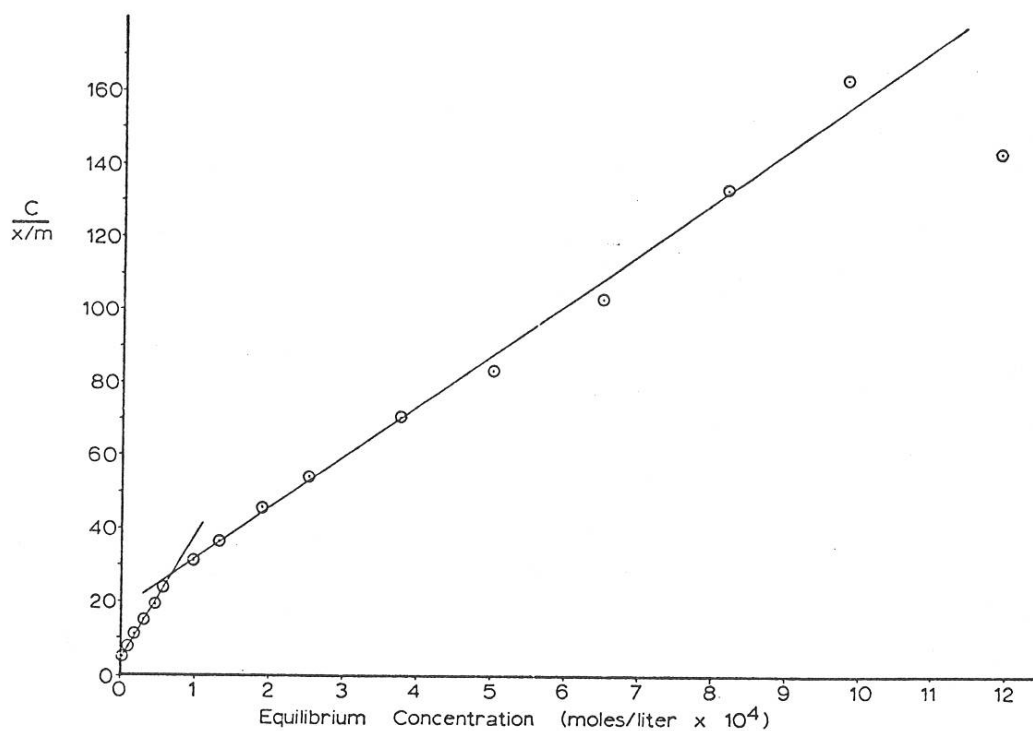


Figure 25. Phosphorus adsorption data for soil from the Curlew Valley site plotted according to the Langmuir isotherm.

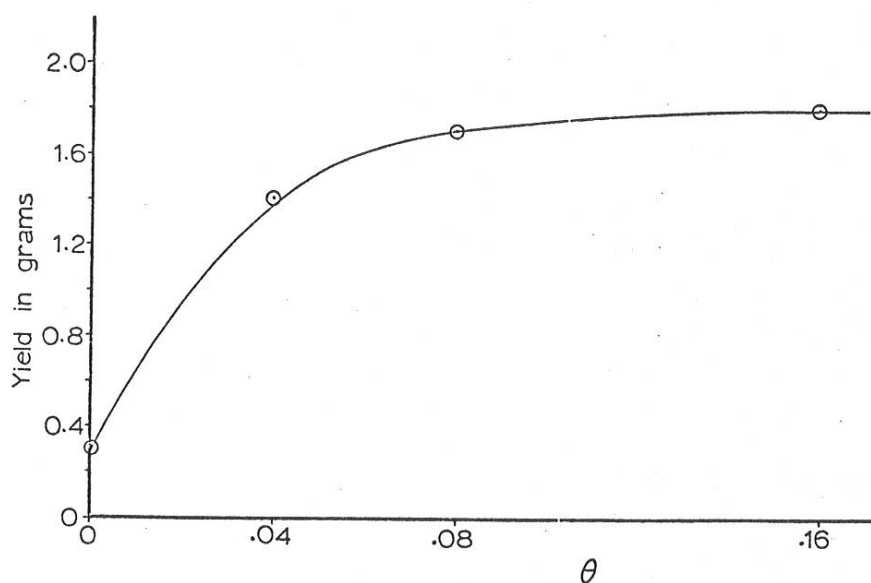


Figure 26. Yield of crested wheatgrass as a function of the percentage of the phosphorus adsorption maximum (θ) of the soil from the Curlew Valley site.

EXPECTATIONS

The research conducted during 1972 yielded data which indicated a growth response in crested wheatgrass to minor elements additions. In 1973 the growth chamber work will emphasize this aspect of plant nutrition in the soil of the Curlew Valley site of the Desert Biome. Preliminary results indicated large growth responses to both iron and zinc. The experimental design will emphasize this as an incomplete factorial of phosphorus and zinc with interlocking subsets to evaluate the added effects of zinc-iron and zinc-manganese. Nitrogen will be added at a uniform level for adequate growth as determined from the 1972 results. It is expected that in the absence of nutrient cycling, micro-nutrient deficiency will be a major factor in biomass production.

Chemical characterization of soil phosphorus will be completed in 1973 with the determination of the phosphorus flux values for the soil of the Curlew Valley site. The theory and techniques developed in 1972 enhance the possibilities for successful completion and interpretation of the soil phosphorus flux data during the 1973 project year. It is expected that the phosphorus flux rate for the soil will be similar to that obtained from the pure calcite system.

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