1975

Influence of Digging Rodents on Primary Production in Rock Valley

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1974 PROGRESS REPORT

THE INFLUENCE OF DIGGING RODENTS ON PRIMARY PRODUCTION IN ROCK VALLEY

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US/IBP DESERT BIOME
RESEARCH MEMORANDUM 75-19

in

REPORTS OF 1974 PROGRESS
Volume 3: Process Studies
Vertebrate Section, pp. 27-36

1974 Proposal No. 2.3.2.2

Printed 1975

Citation format: Author(s). 1975. Title.
US/IBP Desert Biome Res. Memo. 75-19.
Utah State Univ., Logan. 9 pp.

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ABSTRACT

The objective of this study was to evaluate the impact of rodent burrowing upon soil conditions and plant growth. Recent burrowing activity affects less that 5% of the ground surface. However, signs of old, weathered activity suggest that, over the long term, burrowing affects a considerably larger percentage of the ground surface. Over one-third of the perennials were found to have burrowing activity beneath them. Rodents tended to prefer larger shrubs, with open bases as sites for burrows. There was a slight trend for finer soil particles and lower bulk density in burrowed soils than found in unburrowed soils. This trend was much less than expected from the literature. Water infiltration into the soil was increased by burrowing activity and by the presence of a shrub. In the open, burrowing activity doubled the infiltration rate. Burrowing had little effect beneath shrubs. Evaluation of the effects of rodents upon plant growth was hindered by the poor growth during the study period. *Ambrosia dumosa* was the only shrub that exhibited even a slight response to the rodents: growth was lower than in control plants. This response may have been due to browsing by gophers and ground squirrels. Artificial burrowing resulted in no inhibition or enhancement of growth. It is quite evident that when plant growth is low, rodent activity has little influence.

INTRODUCTION

Interest in the predation interactions of rodents and primary producers has led to the neglect of other potential interactions. Most desert rodents are semifossorial and yet little attention has been paid to the effects of burrowing upon plant growth. Grinnell (1923) and Hall (1946) speculate that burrowing activities develop a more hospitable soil for plant growth. Vorhies and Taylor (1940) noted that wood rat activities increase the organic content in the soil. Greene and Reynard (1932) and Greene and Murphy (1932) describe changes in soil chemical and physical factors due to burrowing activity. Greene and Reynard (1932) found increased nitrates, soluble salts and carbonates due to rodent activity. Greene and Murphy (1932) indicate that burrowed soils have a higher water-holding capacity than nonburrowed soils because of a shift of finer soils to the surface. All of these modifications of soils by burrowing should lead to the enhancement of plant growth. Thus desert rodent activity may figure significantly in regulating primary productivity.

OBJECTIVES

1. Evaluation of the extent of burrowing activity in Rock Valley.
2. Evaluation of the influence of burrowing activity upon chemical and physical properties of soil.
3. Evaluation of the influence of rodent activity upon plant growth.
4. Evaluation of the influence of artificial burrowing upon plant growth.

METHODS

Study Site

The study site was located in Rock Valley, Nye County, Nevada. The Rock Valley facility is operated by the UCLA Laboratory of Nuclear Medicine and Radiation Biology. The general vegetation, soil and climatology of this area have been previously described by Wallace and Romney (1972) and by Turner et al. (1973). The enclosures utilized for evaluating the impact of burrowing rodents were located on a bajada about 0.5 km southeast of enclosure 3 (Turner et al. 1973) and 1 to 2 km south of the IBP validation site described in Turner et al. (1973). Measurements of the extent of burrowing activity were made on the validation site as well as on the bajada.

Measurement of the Extent of Burrowing Activity

The nature of perennial vegetation and the extent of burrowing activity on the bajada and the validation site were estimated using 30-m line intercepts. The base of each shrub encountered was examined for evidence of fairly recent burrowing activity. Burrowing activity that appeared to have occurred within the last few months was recorded. Deciding which burrows were too old to record was highly subjective and based upon the amount of weathering of the burrow. Very recent activity was usually obvious but the boundary between older burrows and very old burrows is arbitrary and the judgments are probably conservative. These observations were then used to estimate the percentage of shrubs of each of the major species associated with burrowing activity.

In the same line-intercept transects, the amount of ground surface influenced by burrowing activity was measured. Surface area affected by burrowing was expressed as a percentage of the total ground surface. Digging activity was categorized into two forms; burrowing and turned-over ground. The distinguishing factor was the presence of openings into burrow systems and the absence of any openings in turned ground. The latter form was associated with gopher activity (DSCODE A3USL03).

Soil Particle Size Distribution

Ten soil samples were collected from two different locations on the bajada; on open undisturbed ground and on open ground that had been burrowed. Collection sites were selected in the appropriate microhabitat nearest to randomly selected points along a 50-m tape. Soil samples were collected from a soil column measuring 10 x 10 x 30 cm. For analysis, the samples were subdivided into three depth intervals; 0-5, 5-20 and 20-30 cm.

Initial soil fractioning was carried out with Tyler sieves and fractioned into three size intervals; >2.0, 2.0-0.25 and <0.25 mm. Four subsamples were removed from the <0.25-

mm fraction and passed through a 0.05-mm sieve to determine the 0.25-0.05 mm fraction. The clay proportion in the < 0.05 fraction was determined using the pipette sedimentation technique of Black (1965). The technique was modified for a small sample size.

After the soil was fractioned, the < 2-mm fractions were reconstituted and ground in a ball-mill for 6 hr. This homogenized the sample for subsequent chemical analyses (A3USL03).

Water Infiltration

Water infiltration was estimated in 14 replicates for each of four locations on the bajada; on open undisturbed ground, in open burrowed ground, beneath a *Larrea* with no burrowing, and beneath a *Larrea* with burrowing. Open sites were at least 0.5 m from the nearest shrub canopy and sites beneath shrubs were 10 cm from the shrub base. Sites were selected in the same manner as were soil sampling sites. The infiltration rates were measured using a steel, cubical device, 10 x 10 cm square, that penetrated 1 to 2 cm into the soil. The infiltration of about 1 liter of distilled water was timed. A porous metal plate was placed at the bottom of the cube to prevent disturbance of the soil surface as the water was poured in. If gross lateral infiltration occurred, the sample was rejected (A3USL02).

Chemical Properties of the Soil

Organic content of the soil was determined by ashing of two 20-g subsamples of the milled soil per sample. Subsamples were ashed for 4 hr at 538 C and organic content was expressed as parts per million.

Soil pH was determined for a 1:1 suspension of milled soil in water. The sample was centrifuged and filtered. The supernatant was evaporated to determine total soluble salts in the soil. Total soluble salts was expressed as parts per million.

Nitrogen content of the milled soil was determined using the Kjeldahl technique of Black (1965) and expressed as parts per million (A3USL04).

Influence of Rodent Activity upon Perennial Growth

In order to evaluate the effects of rodents upon perennial shrub growth, enclosures were established upon the bajada south of the validation site. Each enclosure was an octagon with a diameter of 15 m. Enclosures were constructed from hardware cloth and metal flashing. The fence extended 0.5 to 1 m into the ground and 0.5 to 1 m above the ground. A strip of flashing across the top of each fence restricted climbing over the fence. The fence appeared impermeable to gophers and pocket mice. Some squirrels quickly learned to jump over the flashing and were difficult to contain. Squirrel activity was concentrated in the appropriate enclosures by removing them from the other enclosures.

Twelve enclosures were used for this experiment; three served as controls with no occupants, three contained pocket gophers (*Thomomys bottae*), three contained ground squirrels (*Ammospermophilus leucurus*), three contained pocket mice (*Perognathus formosus*). The rodents were supplied with oats and carrots in hopes of reducing the impact of their browsing upon the vegetation.

Within each of the experimental enclosures we tagged five shoot tips on two members of each of the following species of perennial shrub: *Ambrosia dumosa*, *Lycium andersonii*, *Larrea tridentata* and *Grayia spinosa*. Shoot tip growth was monitored from late April through September. Using the system of Romney and Wallace, the following were recorded for each shoot tip: length to the nearest millimeter; numbers of leaves, flowers, fruits and lateral shoots; total length of lateral shoots to the nearest millimeter (A3USL01).

Artificial Burrowing

In several empty enclosures similar to those described above, artificial burrowing was carried out. The "burrows" were created using a soil auger two inches in diameter. Burrows were placed under 12 *Larrea tridentata*. Six of the burrow systems were reamed out at monthly intervals after being established in April and six were not reamed after being established. Growth of shoots was measured as described above (A3USL01).

RESULTS

Extent of Burrowing Activity

The vegetation description of the main study area, on the bajada on the southern edge of Rock Valley, is presented in Table 1 (A3USL03). The dominant shrubs are *Ambrosia dumosa* (AMBDUM), *Krameria parvifolia* (KRAPAR), *Lycium andersonii* (LYCAND), *Larrea tridentata* (LARTRI) and *Grayia spinosa* (GRASPI). On the IBP validation site (Table 2) *Ephedra* spp. (EPHSPP) replace *G. spinosa* as the fifth dominant species.

Table 3 (A3USL03) presents the percentage of sampled shrubs with indications of burrowing activity under them. On both the bajada and the validation site burrowing activity was found under more than one-third of the shrubs. The burrowing frequency varied from species to species. Of the species found in over 30% of the sample transects the shrubs least preferred for burrowing sites were KRAPAR (12%) on the bajada and AMBDUM (20%) on the validation site. The shrub species most preferred as a burrow site was LYCAND. On the bajada 56% of this species exhibited burrowing activity, and on the validation site, 75% of the shrubs exhibited such activity. A Spearman's Rank correlation test reveals no significant correlation between importance rank and frequency of burrowing ($P >> 0.05$). A chi-square analysis of the data reveals that the relative frequency of shrubs with burrowing does not have the same pattern as does the relative frequency of shrubs per sample ($P << 0.01$). AMBDUM and KRAPAR show much less burrowing activity than would be expected if burrowing sites were determined by the relative frequency of these species in the community.

The amount of ground surface covered by burrowing activity is quite small (Table 4; A3USL03). Only 4.5% of the ground surface on the bajada and 4.0% of the ground surface on the validation site were affected by burrowing activity. On the bajada site only 31% of this burrowing activity was associated with shrubs while 67% of the burrowing activity on the validation site was associated with shrubs.

Soil Structure

We have only analyzed soils from 10 locations on the bajada south of the validation site. All were located in open ground, more than 0.5 m from the edge of the nearest shrub canopy. Half of the samples were from sites of burrowing activity; the other half showed no signs of burrowing activity.

Soil particle size distribution is presented in Table 5 (A3USL05). There is perhaps a slight trend for 0.05 to 2 mm diameter particles to increase in the surface layer of the burrowed soil. These differences are not statistically significant. The bulk density of the burrowed soils tends to be less than the unburrowed soils although this difference again is not statistically significant.

Infiltration Rates

Infiltration rates are presented in Table 6 (A3USL01). Infiltration rates beneath shrubs are nearly twice that of the rates in open ground. Burrowing under shrubs increases infiltration by only about 4-5 cc min^{-1}. These trends are not statistically significant. In open ground burrowing activity nearly doubled the mean infiltration rate ($P < 0.05$).

Chemical Properties of the Soil

The chemical properties of the soil samples (A3USL04) have not been completely analyzed at this date.

Effects Upon Perennial Growth

Growth of perennial shrubs in 1974 was very poor (Figs. 1-4; A3USL01). Maximum growth for both LYCAND and GRASPI was only 6% of their original length, and total change in shoot length over the total period of sampling averaged less than 1 mm. This is less than the accuracy to which shoot length was measured. LYCAND in the control enclosures shed leaves faster than in the other enclosures (Fig. 5; A3USL01). For GRASPI there were no differences in the number of leaves per shoot that were associated with any of the four manipulations. LYCAND showed no signs of flowering or of lateral shoot addition in any of the enclosures. GRASPI in all enclosures showed peak flowering in mid-July but added no new lateral shoots.

Maximal increase in shoot lengths of LARTRI averaged from 43 to 64% of the original length, an increase of 5 to 6 mm (Fig. 3). Analysis of variance reveals no significant difference among the manipulations ($P > 0.25$). For AMBDUM shoot length increased 25 to 92% of the original length, 2 to 6 mm. Least growth occurred in the enclosures containing gophers or ground squirrels (Fig. 4). Analysis of variance reveals that the differences are not statistically significant ($P > 0.05$). The pattern of changes in number of leaves per shoot did not vary among the manipulations for either LARTRI or AMBDUM (Fig. 5). LARTRI and AMBDUM flowered on less than 10% of the shoots that were sampled. LARTRI in all plots showed an increase in the number of lateral shoots by 0.2 to 0.4 per shoot tip.

Effects of Artificial Burrowing on LARTRI Growth

Artificial burrowing under LARTRI individuals resulted in no pronounced changes in the growth of shoot tips (Figs. 3, 5, 6; A3USL01). Growth patterns of those LARTRI under which artificial burrowing took place paralleled the patterns of the other LARTRI.

DISCUSSION

Extent of Burrowing Activity in Rock Valley

In order to evaluate the potential impact of burrowing, it is necessary to know the amount of burrowing activity in the Rock Valley area. The amount of ground affected by active or recent burrowing activity averaged only 4 to 4.6% of the ground surface on both the validation site and the bajada to the south (Table 5). From these observations, major short-term effects upon the soil by burrowing would appear to be small. However, there were numerous sites on the bajada where old, weathered burrow sites were evident. Quantification of this old activity was not carried out because of the increasing indistinctness of such activity as it weathers. It certainly appears that over an extended period of time much of the soil has been worked by burrowing rodents, so that the estimates of current and recent activity underestimate the effects of burrowing over an extended time period.

The distinction between burrowed and turned ground was an arbitrary categorization. Burrow systems were those areas with obvious openings to the surface while turned ground lacked such openings. The latter were predominantly mounds of earth shoved to the surface by pocket gophers. The differences in the proportion of ground devoted to burrow systems and turned ground (Table 5) probably reflect differences in pocket gopher activity. On the validation site, only about 18% of the identifiable activity was attributed to gophers, while 33% of the activity on the bajada was attributed to gophers. This correlates with population density figures; 1-2 gophers ha^{-1} on the validation site, 4-5 gophers ha^{-1} on the bajada (Turner et al. 1973, Dingman and Byers 1974).

Although the total ground surface affected by recent or current burrowing is small, over one-third of the perennial shrubs have recent burrowing beneath them (Tables 3 and 4). The percentage of each perennial species influenced varied considerably. Thus, while 75% of the LYCAND on the validation site were affected, only 20% of the AMBDUM were affected. If burrowing does affect shrub growth, a sizable proportion of the shrubs will be affected, and in some species the majority of individuals will be affected.

The dominant shrubs most preferred as sites for burrowing were LYCAND and LARTRI, both of which tend to be somewhat open at the base but have moderately large canopies. The shrubs least preferred as burrow sites were AMBDUM and KRAPAR, which tend to have canopies low to the ground, restricting access to the base of the plant.

Table 1. Vegetation parameters from 30 line-intercept samples on the bajada in Rock Valley (DSCODE A3USL03)[a]

Species	Taxon Code	% Coverage	Number per sample	Fidelity[b]	Relative Frequency	Relative coverage
Ambrosia dumosa	AMBDUM	3.99	4.2	0.87	0.25	0.20
Krameria parvifolia	KRAPAR	2.73	3.0	0.90	0.20	0.16
Lycium andersonii	LYCAND	3.22	2.3	0.90	0.14	0.19
Larrea tridentata	LARTRI	2.64	1.8	0.83	0.13	0.17
Grayia spinosa	GRASPI	2.53	1.9	0.80	0.12	0.14
Ceratoides lanata	EURLAN	1.19	1.1	0.60	0.06	0.06
Ephedra spp.	EPHSPP	1.00	1.0	0.47	0.06	0.06
Lycium pallidum	LYCPAL	0.73	0.4	0.27	0.02	0.04
Atriplex confertifolia	ATRCON	0.07	+[c]	0.03	+	+
Coleogyne ramosissima	COLRAM	0.03	+	0.03	+	+
Dalea fremontii	DALFRE	0.02	+	0.03	+	+
TOTALS		18.16	15.2			

[a]Species are ranked in decreasing order of relative dominance. Relative dominance was quantified as the mean value of the fidelity, relative frequency and relative coverage.

[b]Fidelity=frequency of samples with this species.

[c]Present in a frequency of less than 0.01.

Table 2. Vegetation parameters from 30 line-intercepts on the validation site in Rock Valley (DSCODE A3USL03)[a]

Species	Taxon code	% Coverage	Number per Sample	Fidelity[b]	Relative Frequency	Relative Coverage
Ambrosia dumosa	AMBDUM	4.27	3.5	0.93	0.24	0.21
Krameria parvifolia	KRAPAR	4.07	3.3	0.90	0.22	0.24
Lycium andersonii	LYCAND	4.49	2.3	0.93	0.18	0.23
Larrea tridentata	LARTRI	4.65	2.7	0.90	0.19	0.23
Ephedra spp.	EPHSPP	2.17	1.5	0.70	0.13	0.10
Grayia spinosa	GRASPI	0.42	0.5	0.37	0.04	0.02
Lycium pallidum	LYCPAL	0.23	0.2	0.13	0.01	0.02
Ceratoides lanata	EURLAN	0.12	0.2	0.10	0.01	0.01
Atriplex confertifolia	ATRCON	0.17	0.1	0.07	0.01	0.01
Coleogyne ramosissima	COLRAM	0.05	+[c]	0.03	+	+
Dalea fremontii	DALFRE	0.02	+	0.03	+	+
TOTALS		20.71	14.3			

[a]Ranked according to descending relative dominance as in Table 1.

[b]Fidelity=frequency of samples with this species.

[c]Present in a frequency of less than 0.01

Table 3. Frequency of burrowing activity beneath perennial shrubs on the validation site and bajada, Rock Valley (DSCODE A3USL03)

	Validation Site		Bajada	
Taxon Code	Absolute Frequency [a]	Relative Frequency [b]	Absolute Frequency	Relative Frequency
AMBDUM	0.20	0.13	0.24	0.18
KRAPAR	0.23	0.14	0.12	0.07
LYCAND	0.75	0.32	0.56	0.24
LARTRI	0.48	0.24	0.41	0.13
EPHSPP	0.40	0.11	0.33	0.06
GRASPI	0.47	0.04	0.44	0.15
LYCPAL	0.00	0.00	0.67	0.05
CERLAN	0.17	0.01	0.45	0.09
ATRCON	0.00	0.00	1.00	0.01
COLRAM	1.00	0.01	0.00	0.00
DALFRE	0.00	0.00	0.00	0.00
TOTAL	0.37	1.00	0.36	1.00

[a] Absolute frequency is the proportion of individual shrubs of a given species with signs of burrowing.

[b] Relative frequency is the proportion of individual shrubs with signs of burrowing that belong to a given species.

Table 4. Percentage of ground surface affected by burrowing activity and percentage of burrowing activity under shrubs (DSCODE A3USL03)

	Percentage ground surface	Percentage under shrubs
Validation Site		
Burrow systems	2.93	77
Turned ground	1.04	42
Total	3.97	67
Bajada		
Burrow systems	2.09	43
Turned ground	2.53	20
Total	4.62	31

Table 5. Soil particle size distribution and bulk density from five open, unburrowed sites on the bajada, $\bar{X} \pm$ S.D. (DSCODE A3USL05)

	Particle Size					
depth	>2mm	2-0.25mm	0.25-0.05mm	0.05-0.002mm	<0.002mm	bulk density
0-5	50.9% ±6.73	9.4% ±2.11	24.2% ±3.05	15.5% ±4.65	0.3% ±0.9	2.024g/cc ±0.257
5-20	58.6 ±4.51	9.9 ±1.96	20.9 ±2.84	10.4 ±1.65	0.2 ±0.05	2.75 ±0.375
20-30	62.0 ±5.91	12.3 ±3.67	17.8 ±2.07	7.8 ±2.60	0.1 ±.05	3.74 ±.321

Table 6. Soil particle size distribution and bulk density from five open, burrowed sites on the bajada, $\bar{X} \pm$ S.D. (DSCODE A3USL05)

	Particle Size					
depth	>2mm	2-0.25mm	0.25-0.05mm	0.05-0.002mm	<0.002mm	bulk density
0-5	47.3% ±7.73	14.3% ±2.95	26.9% ±4.68	12.6% ±5.33	0.3% ±.23	1.825g/cc ±.228
5-20	57.9 ±8.04	11.5 ±3.06	20.0 ±4.00	10.3 ±1.83	0.3 ±0.07	2.577 ±.137
20-30	62.1 ±11.89	10.1 ±3.35	19.3 ±6.54	8.2 ±2.85	0.2 ±.08	2.995 ±0.385

Table 7. Infiltration rates on the bajada above the Rock Valley Validation Site, $\bar{X} \pm$ S.D. (DSCODE A3USL02)

	no. samples	rate $cc \cdot min^{-1}$
open ground no burrow	14	15.1±6.14
open ground burrow	14	28.3±24.31
under shrub no burrow	14	53.8±24.98
under shrub burrow	14	58.3±39.84

Influence of Burrowing on Soil Properties

Soil particle size distribution does show a slight trend for soil particles between 0.05- and 2-mm diameter to be moved to the surface by burrowing activity (Tables 6 and 7), and the bulk density of the soil tends to be less in the burrowed soil than in the unburrowed soil. This means the soil is more loosely packed and water should penetrate the soil more readily after it has been burrowed. The changes in soil texture and in soil packing resulting from burrowing activity in Rock Valley do not seem as pronounced as such changes described elsewhere (Greene and Murphy 1932, Hansen and Morris 1968).

As expected, the burrowing activity does tend to increase the rate of water infiltration into the soil (Table 7). In the open, burrowing activity nearly doubled the rate of water penetration into the soil. Under shrubs the increase in infiltration is much smaller. The impact of the shrub itself upon the soil seems to increase infilterability to such an extent that burrowing activity has little influence. This suggests that although a large number of shrubs may have burrowing beneath them, this activity will have little effect upon water availability.

Effects of Burrowing upon Shrub Growth

The low rainfall in the winter of 1973-74 resulted in very poor growth. By late April, when the enclosures were completed and measurements initiated, the major portion of the growing season was over. Thus comparisons of growth rates among the manipulations show no significant correlations with either natural or artificial burrowing activity (Figs. 1-6). The only striking differences among manipulations were found in AMBDUM where shoots on shrubs in the gopher and ground squirrel enclosures grew much less than the controls or those in the presence of pocket mice. This may have been the result of browsing by the gophers and ground squirrels. AMBDUM did show signs of being browsed more frequently than other shrubs.

The only conclusion that can be drawn from this year's data is that with little or no rainfall, burrowing has an insignificant effect upon plant growth.

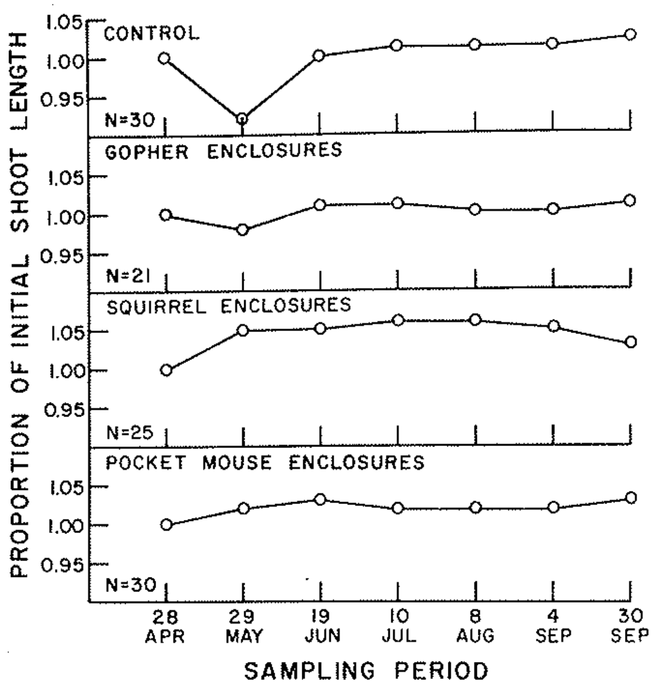

Figure 1. Mean growth of shoot tips of *Lycium andersonii* during the study period.

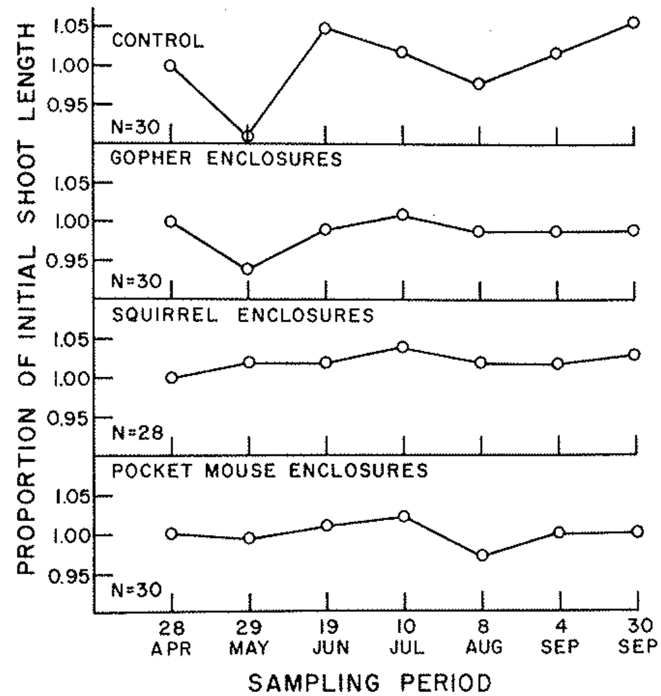

Figure 2. Mean growth of shoot tips of *Grayia spinosa* during the study period.

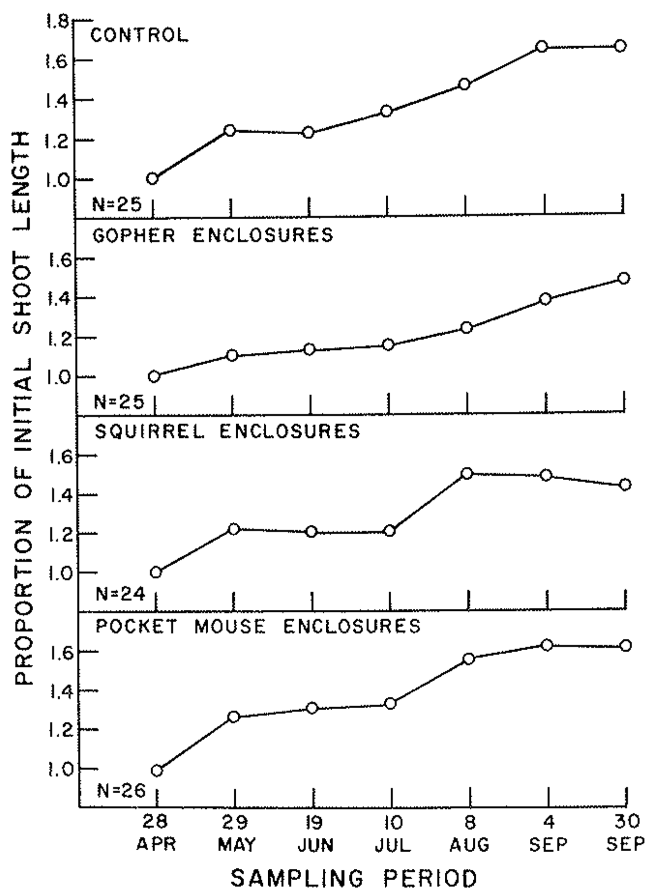

Figure 3. Mean growth of shoot tips of *Larrea tridentata* during the study period.

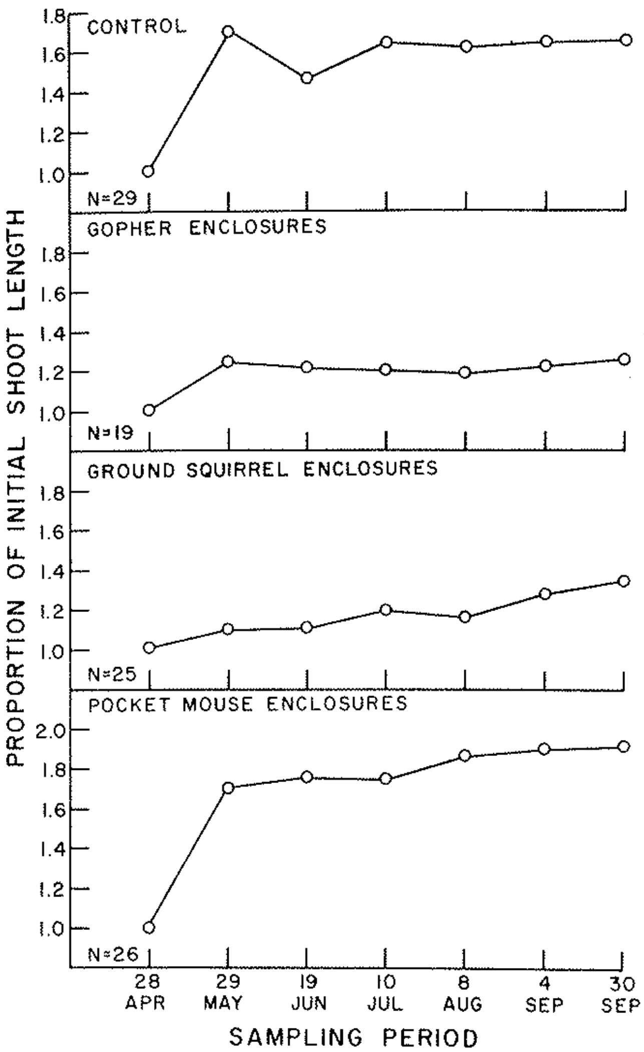

Figure 4. Mean growth of shoot tips of *Ambrosia dumosa* during the study period.

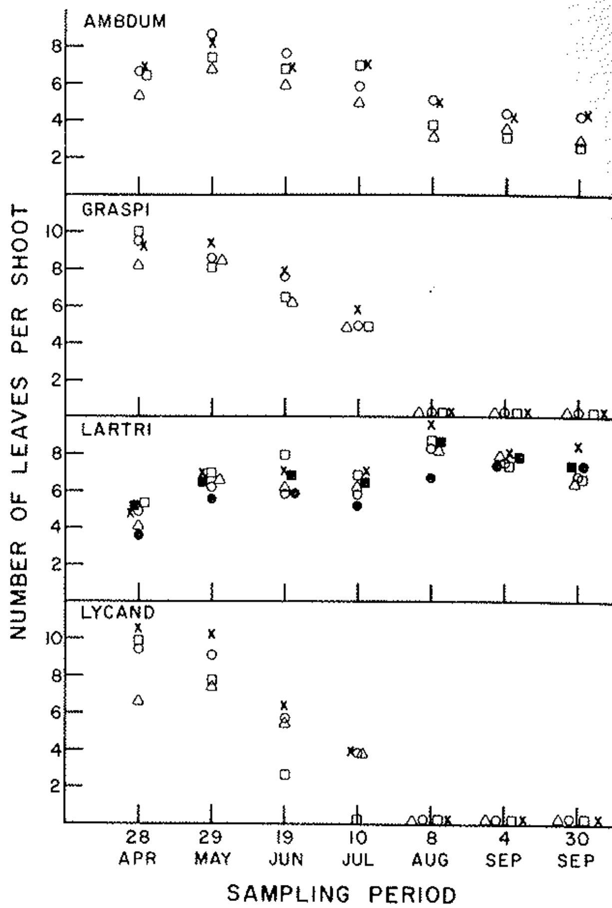

Figure 5. Patterns of leaf addition and fall for the four dominant shrubs on the bajada. Open circles represent control plots; open squares represent plots containing gophers; open triangles represent plots containing ground squirrels; X's represent plots containing pocket mice; closed circles represent plots with maintained artificial burrowing; closed squares represent plots with unmaintained artificial burrowing.

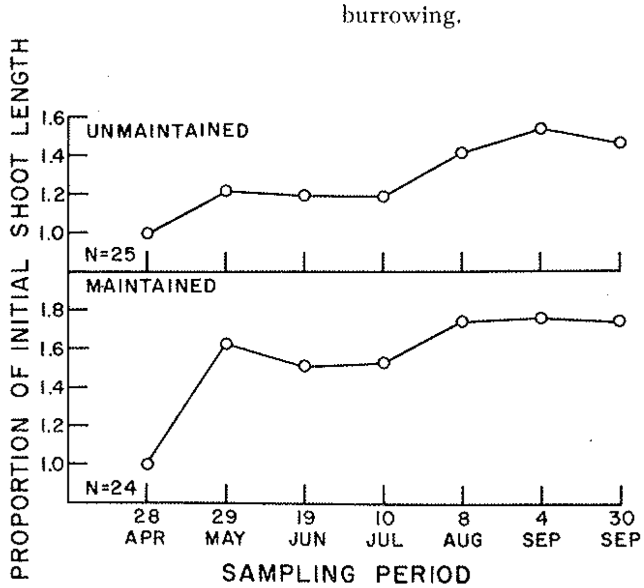

Figure 6. Mean growth of shoot tips of *Larrea tridentata* under which artificial burrowing was carried out.

EXPECTATIONS

The excellent rainfall in the winter of 1974-75 has provided for what should be a good growing season for both perennials and annuals in 1975. We shall increase sample sizes to counter the large variability within most of the parameters that we are measuring. This has been made feasible with the acquisition of a full-time field technician for 1975. If there is a significant influence on soil and plant parameters by burrowing activity it should become apparent in the spring of 1975.

ACKNOWLEDGMENTS

This study would have been impossible without the cooperation of the UCLA Laboratory of Nuclear Medicine and Radiation Biology and the Civilian Effects Testing Organization.

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