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PLANT PRODUCTIVITY AND NUTRIENT INTER-RELATIONSHIPS OF PERENNIALS IN THE MOHAVE DESERT

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ABSTRACT

Various studies of aspects of perennial plant productivity, most of which relate to the carbon budget of the northern Mohave Desert, were continued in 1975. Respiration rates of the reproductive parts of plants were determined for five common Mohave Desert shrubs. They were determined at five different developmental stages and at four different temperatures for each (10, 20, 30, 40 C). The rates increased with temperature generally and varied from < 0.1 to > 5 μg C·g dry wt^{-1}·hr^{-1}. The late fruit stage usually, but not always, gave the lowest rate. Attempts were made to determine soil respiration by measurement of the efflux of CO_2 from the soil. For several days after watering of soil in August, the CO_2 efflux rate was greatly increased. The cloud-cover effect was measured on gas exchange rates. For *Larrea tridentata*, *Atriplex canescens* and *Ambrosia dumosa*, there was a very pronounced effect of cloud cover when the light intensity was in the range of 0.2 to 0.4 cal·cm^{-2}·min^{-1}. Distribution of ^{14}C in two *Larrea tridentata* plants was determined 16 months after exposure of the leaves to $^{14}CO_2$. After 16 months, 13.7 and 16.8% of the original ^{14}C was retained in the plants. More ^{14}C was in stems and leaves than in roots. The below-ground:above-ground ratio for ^{14}C was 0.56 as compared to 1.85 for biomass. The organic debris in the soil below the shrubs and which was floated out by $MgSO_4$ did not contain ^{14}C, but the very fine roots in the samples did in 90% of the cases. The results helped to determine what are to be considered as roots in this desert area. *Ambrosia dumosa* grown in solution culture were exposed to $^{14}CO_2$ to label photosynthate and distribution among leaves, stems and roots after 4, 24 and 48 hr. For all sampling periods, the highest levels of ^{14}C were found in leaves and the lowest in roots.

INTRODUCTION

This project is part of a continuing study to determine productivity and overall carbon budget of the major shrubs in a northern Mohave Desert ecosystem. The results of this study will be used to test and refine photosynthesis and whole ecosystem models which are now being developed by the US/IBP Desert Biome.

OBJECTIVES

The specific objectives were to:

1. Determine the effect of respiration of reproductive parts, as affected by age and temperature, on the carbon budget of five common Mohave Desert shrubs.
2. Develop a technique for measuring CO_2 evolution from the soil surface. It was also planned to determine changes in CO_2 efflux from the soil, specifically those resulting from addition of moisture.
3. Determine the effect of cloud cover on photosynthesis and transpiration of Mohave Desert shrubs.
4. Determine residence time and distribution of previously fixed ^{14}C and to determine if it would indicate an average respiratory turnover rate.
5. Determine root-shoot distribution of dry matter and ^{14}C when roots could not be lost in soil and to determine rate of ^{14}C movement to roots.

METHODS

REPRODUCTIVE STRUCTURE RESPIRATION

Respiration rates of reproductive structures were determined by methods similar to those of Cunningham et al. (1974).

Reproductive structures were grouped into five developmental stages as follows: 1) early flower buds -- *Lycium* *andersonii* and *L. pallidum*, corolla not extended past calyx; *Larrea tridentata*, buds small and sepals not split; *Ambrosia dumosa*, inflorescence compact and entirely closed; *Krameria parvifolia*, buds < 4 mm long and predominantly green; 2) late flower buds -- *Lycium* spp., corolla extending past calyx, but not open; *Larrea*, sepals split but corolla still closed; *Ambrosia*, flower heads separated but not open; *Krameria*, buds > 4 mm long and turning purple; 3) open flower -- corollas open; 4) early fruit -- smaller than mature size with flower parts still adhering or recently fallen; 5) late fruit -- maximum size with mature coloration developing.

A Gilson differential respirometer was used to determine the respiration rates. Branches were cut from plants in the field and placed in a cooler for transport to the laboratory. Reproductive structures were removed and placed into respirometer vessels to which 1 ml of distilled water had been added. Approximately 10 structures were placed in each vessel. The number of replicates ranged from 6 to 31 with most measurements replicated 10-20 times. Ten percent KOH was used to absorb CO_2 and respiration rates were measured at 10, 20, 30 and 40 C for 30 min. The amount of time that elapsed from field collection to end of the temperature runs was usually 5-6 hr. At the conclusion of an experiment, fresh and dry tissue weights were recorded. Respiration was measured in μl O_2 consumed per 30 min. This was converted to μl CO_2 by assuming a respiratory quotient equal to 1. Carbon loss was calculated as mg C per g dry weight of tissue per hour.

SOIL RESPIRATION RATES

In March 1975, five plots were established in Mercury Valley about 8 km southwest of Mercury, Nevada. This area was selected in lieu of Rock Valley because of the availability of line power. At each plot, a Plexiglas sleeve was placed into the soil. The sleeves extended into the soil 7.6 cm and enclosed an area of 0.05 m^2. Two plots were

located under *Larrea tridentata* plants and one under *Ambrosia dumosa*; the other two plots were situated in areas devoid of vegetation.

Evolution of CO_2 from the soil was measured using a differential infrared gas analyzer (IRGA), Beckman model 865, in an open-flow system. Similar systems have been used by previous workers to measure soil CO_2 flux (Reiners 1968; Kucera and Kirkham 1971; Kanemasu et al. 1974).

Our methods involved fixing the field chamber to a sleeve imbedded in the soil and passing compressed air into the chamber at 2 liters/min. Inside the chamber, the air was mixed with the aid of a circulating fan. Exhaust air was passed through a Drierite column and then to the IRGA. A plywood shield was placed over the chamber to prevent excess heat buildup inside.

The chamber was flushed for 10-20 min until the CO_2 level in the sampling line had stabilized. Measurements were then taken at 5-min intervals for a period of 20-40 min. An average CO_2 concentration was then determined.

Measurements of soil CO_2 flux were taken from mid-June through mid-August.

In August, two plots, one *Larrea* and one bare, were selected for a water-amendment study. Ten liters of water were sprinkled over a 1-m square, the equivalent of 1 cm of rain. The 0.05-m^2 plot was located in the center of the watered area. The plots were watered on August 8 and again on August 11. Watering was done in the afternoon and CO_2 measurements were started the next morning. This delay allowed the pulse in CO_2 evolution caused by the water reacting with the soil carbonate to be released (MacGregor 1972). These water amendments were designed to simulate summer thundershowers which are common in the Mohave Desert.

Cloud-Cover Effects on Gas Exchange Rates

All plants used were "healthy looking" and were well watered at or during the intervals at which measurements were taken. Three species were included: *Larrea tridentata*, *Atriplex canescens* and *Ambrosia dumosa*. The *Larrea* and *Atriplex* plants were growing in concrete beds at UCLA. The rates for *Ambrosia* were obtained from a plant growing in a 20-liter can at UCLA. The same plants were used for all measurements (when possible the same stem and leaves were used) to avoid introducing the plant as a variable. The measurements were made from September 5-11, 1975 (DSCODES A3UBD11, 12, 13).

With the exception of *Larrea*, all rates were obtained with actual cloud cover. For *Larrea*, cheesecloth was used to simulate cloud cover, with real clouds being used to determine how much shading was needed. An actual overcast point was, however, obtained for *Larrea* as a crosscheck with the simulated condition.

The chamber air temperature was maintained at 25 C, with a relative humidity of 28%. The control point for the

CO_2 concentration was set at 325 ppm ($\sim$ ambient). A 10-min interval was allowed for the shading to take effect. For this experiment, radiation in the 400-700 nm range was measured inside the chamber using a filtered photocell calibrated against an Eppley pyranometer. Maximum irradiance, or 100% sunlight, with the system was about 0.8 cal$\cdot$cm$^{-2}\cdot$min^{-1}.

All results are reported on a tissue dry weight basis, i.e., photosynthesis as mg $CO_2\cdot$g dry wt$^{-1}\cdot$hr^{-1}; transpiration as g $H_2O\cdot$g dry wt$^{-1}\cdot$hr^{-1}.

^{14}C Assimilates in *Larrea*

Six naturally growing *Larrea tridentata* were exposed to $^{14}CO_2$ for 2 hr on the morning of May 14, 1974. Twigs were sampled at the end of this 2-hr period for use in estimating the total $^{14}CO_2$ fixed by the plants. Two of these plants were excavated 16 months later on September 17, 1975. All parts were then analyzed for ^{14}C content by methods reported previously (Bamberg et al. 1973; Wallace et al., in press).

Soil from a 2.5-canopy-sized area around the plants was sampled for use in fine root biomass determinations. Soil samples (10 cm^3) were added to a saturated MgSO$_4$ solution. Soil organic matter was separated by flotation and hand-sorted to obtain fine roots. These roots were prepared and counted for ^{14}C. The roots were dried and ashed and found to contain 60-75% noncombustible ash. This high ash content was due to soil and salt contaminants adhering to roots. Root weights were normalized to 25% ash. In about 90% of the cases the fine roots contained ^{14}C, while only 10% of the organic debris samples contained the isotope. The amount of roots in the soil surrounding the plants was estimated by extrapolating from small soil samples to the total volume of soils within the area encompassed by 2.5 canopies to a depth of 30 cm. This method is similar to that employed by Bamberg et al. (1974) and Vollmer et al. (1975).

Distribution of ^{14}C in *Ambrosia*

Ambrosia dumosa cuttings were grown for 30 days in solution culture at which time the shoots were about 15 cm tall. The shoots were then exposed to $^{14}CO_2$ (about 5 μCi) in plastic bags for about 2 hr. Two plants each were separated into leaves, stems and roots after 4, 24 and 48 hr. The methods generally were like those previously used (Bamberg et al. 1975).

RESULTS AND DISCUSSION

Reproductive Structure Respiration

The mean respiration rates and standard errors are presented in Table 1 (A3UBD25). There was a positive correlation between temperature and respiration rates of shrub reproductive structures.

Other obvious trends in the data exist for all five species. For the drought-deciduous species, *Ambrosia* and the two *Lycium* species, the flower buds exhibited the highest respiration rates, while late fruit showed the lowest rates.

Open flowers had the highest rates observed for the reproductive structures of *Larrea* and *Krameria*. Reasons for the interspecies differences in the respiration rates of the various developmental stages of reproductive structures are not apparent at this time.

The work of Cunningham et al. (1974) is directly comparable to this study. Cunningham's work and our work with *Larrea* showed similar relationships between the temperature curves for the different developmental stages; i.e., the rates increased from the early bud to the open flower stage and then declined as the fruit developed. A major discrepancy between our work and that of previous workers is that the rates given here are one-tenth those reported by Cunningham et al. (1974).

SOIL RESPIRATION RATES

During June and July, modifications of the sampling system were still being made. By the end of July we were satisfied that we were operating with a leak-proof system, capable of maintaining a constant flow rate through the chamber (A3UBD26). At that time of the year, soil CO_2 efflux was virtually nil both under shrubs and in interspaces. Table 2 shows CO_2 evolution rates from watered and unwatered plots located under *Larrea tridentata* and in interspaces. The addition of water promoted the release of CO_2 from the soil surface in both plot locations. However, the response to the second watering differed considerably. Soil CO_2 efflux from bare soil did not change with the addition of more water while there was almost a 30-fold increase in the rate at which CO_2 was released from under the *Larrea*. Biological activity would be expected to be higher under shrubs than in the open due to presence of roots (Vollmer et al. 1975), invertebrates (Edney et al. 1975; Freckman et al. 1975), microbes (Vollmer et al. 1976) and soil organic matter (Romney et al., in press). The small difference in CO_2 evolution between the two locations after the first watering is probably due to the shallow wetting zone (< 5 cm) that would result from the addition of only 1 cm of water. The second watering wet the upper part of the shrub root zone, thus stimulating a much larger response. Caldwell et al. (1974) obtained positive values for respiration every month of the year in Curlew Valley.

CLOUD-COVER EFFECTS ON GAS EXCHANGE RATES

As cloud cover decreased, net photosynthesis and transpiration of *Larrea tridentata* increased slowly (Fig. 1a; A3UBD07). A reduction of sunlight to 23% decreased photosynthesis to 47% of maximum, 33% of sunlight to 64% and a 40% drop in light to 80%. The net photosynthetic rates of *Larrea* did not appear to exhibit a light saturation response. Net photosynthesis increased at a very slow rate, however, and the maximum values found here are comparable to those reported previously (Bamberg et al. 1974, 1975).

With *Ambrosia dumosa* (Fig. 1b) the rate of photosynthesis doubled, 25 to 51 mg $CO_2 \cdot g$ dry $wt^{-1} \cdot hr^{-1}$, as irradiance increased from 0.16 to 0.43 $cal \cdot cm^{-2} \cdot hr^{-1}$. At full sunlight there was a slight drop in net CO_2 uptake. The low light saturation value for *Ambrosia* is indicative of the C_3 photosynthetic pathway found in this species.

The photosynthetic rates of *Atriplex canescens* increased sharply with higher light intensities (Fig. 1c). Decreasing the light by about 50% lowered photosynthesis to 79% of that at full sunlight. In 14% of full sunlight the net photosynthetic rate was only 12% of that at full light intensity. *Atriplex*, a C_4 plant, showed no signs of photosynthesis being limited by light saturation.

Each of the three species responded differently during this experiment. *Larrea*, which utilizes the C_3 pathway, had very low photosynthetic rates throughout, as might be expected. However, rates of photosynthesis did not level off at higher light intensities as is typical of C_3 plants. *Ambrosia*, another C_3 species, exhibited photosynthetic rates as high as those found in many C_4 plants. Yet the low light saturation value is characteristic of plants with the C_3 pathway. The C_4 plant used in this study, *Atriplex*, had fairly high rates of CO_2 uptake, although those of *Ambrosia* were greater, and did not appear to reach light saturation.

The water use efficiencies (photosynthesis-transpiration) were similar for the C_3 species, *Larrea* (9.5-14.0) and *Ambrosia* (10.0-15.0). *Atriplex* had similar values at higher light intensities (10.0-13.0) but dropped off to 4.5 under low light. The poor water use efficiency of the C_4 plants, relative to the C_3 species, may be due to the relatively mild environmental conditions under which the experiment was conducted. All the plants were well watered and chamber conditions were 25 C and 28% RH.

¹⁴C ASSIMILATES IN *Larrea*

After 16 months, the amount of ¹⁴C remaining in *Larrea tridentata* tagged with ¹⁴CO_2 was about 15% of the total amount originally fixed. Of all plant parts, leaves contributed least to both biomass and ¹⁴C content, 9 and 12.5%, respectively. Roots and stems switched ranking between biomass and ¹⁴C amount. Roots made up 64% of the biomass while containing only 36% of the remaining ¹⁴C, while stems had 27.5% of the total biomass and 52% of the ¹⁴C (Table 3). Since losses occur by both respiration and abscission, it is not possible to use the retention values alone to compute a respiration rate for the plants during the intervening 16 months (A3UBD11, 12, 13).

An offshoot of the ¹⁴C work has provided an insight into the accuracy of our $MgSO_4$ flotation technique used to determine fine root biomass. Previous observations of roots in all floated organic matter have yielded estimates of about 45% fine roots. This percentage was used to calculate fine root biomass. In this study, fine roots were hand-separated from the organic debris and both sample types analyzed for ¹⁴C. As stated earlier, only 10% of the organic debris samples contained ¹⁴C, while 90% of the root samples showed some activity. This indicates that the organic debris component, 55% of all floated material, is indeed relatively free of live roots. Ashing studies revealed even the separated fine roots were highly contaminated with noncombustibles (60-75%). If 25% ash is considered normal, previous estimates of fine roots were about three times too high.

This correction was applied to biomass data from 1973 and 1974 (Vollmer et al. 1975) and revised estimates are

presented in Table 4. Generally, the below-ground:above-ground ratios (B:A) were around 2.0. The large B:A values for *Krameria parvifolia* may be due in part to the large number of annuals which germinate under this species, since our root determination methods did not differentiate between annual and perennial roots.

DISTRIBUTION OF ^{14}C IN *Ambrosia*

Table 5 shows the distribution of ^{14}C in various structural components in *Ambrosia dumosa* plants at 4, 24 and 48 hr after labeling. Most of the label was confined to the leaves and stems with only 4.7-7.4% going to the roots, even though they composed 15-19% of the biomass. Changes in the percentage of ^{14}C in the different plant parts with time were not readily apparent, although the proportion of root ^{14}C may have increased slightly. As the experiment progressed, the amount of ^{14}C by weight decreased due to both dilution by new growth and respiratory loss. Roots maintained a relatively constant ^{14}C:weight ratio, while that of leaves and stems dropped sharply. This seems to indicate that most of the gains and losses of carbon during this 48-hr period occurred in the latter two structures.

EXPECTATIONS

In 1976, studies will be continued on 1) soil respiration; 2) ^{14}CO$_2$ translocation and respiration; 3) below-ground dynamics; 4) death of stems; 5) *Larrea* stem growth; 6) synthesis of the previous five years of data.
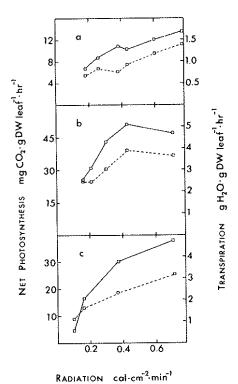

Figure 1. The effect of light intensity on net photosynthesis (solid line) and on transpiration (dashed line) of *Larrea tridentata* (a), *Ambrosia dumosa* (b) and *Atriplex canescens* (c).

Table 1. Respiration rates of reproductive structures at various developmental stages for five Mohave Desert shrub species at different temperatures

Species	Stage	Respiration rate (mg C g·dry wt^{-1}·hr^{-1})			
		10 C $\bar{x} \pm$ SE	20 C $\bar{x} \pm$ SE	30 C $\bar{x} \pm$ SE	40 C $\bar{x} \pm$ SE
Ambrosia dumosa	1	0.94 ± 0.06	2.28 ± 0.12	3.80 ± 0.24	3.44 ± 0.35
	2	0.59 ± 0.06	1.62 ± 0.17	3.45 ± 0.42	2.85 ± 0.32
	3	0.15 ± 0.01	0.67 ± 0.04	1.33 ± 0.35	1.66 ± 0.18
	4	0.04 ± 0.01	0.10 ± 0.01	0.21 ± 0.01	0.27 ± 0.01
	5	0.06 ± 0.01	0.11 ± 0.02	0.08 ± 0.02	0.13 ± 0.04
Krameria parvifolia	1	0.22 ± 0.07	0.95 ± 0.25	1.19 ± 0.36	1.40 ± 0.45
	2	0.21 ± 0.02	0.35 ± 0.05	0.42 ± 0.09	0.42 ± 0.09
	3	0.35 ± 0.02	1.09 ± 0.09	1.97 ± 0.13	2.12 ± 0.17
	4	0.16 ± 0.07	0.49 ± 0.03	1.10 ± 0.10	1.63 ± 0.16
	5	0.13 ± 0.02	0.42 ± 0.04	0.91 ± 0.07	1.37 ± 0.14
Larrea tridentata	1	0.07 ± 0.01	0.17 ± 0.03	0.37 ± 0.06	0.54 ± 0.09
	2	0.15 ± 0.01	0.58 ± 0.05	0.94 ± 0.04	1.12 ± 0.06
	3	0.20 ± 0.03	0.60 ± 0.05	1.29 ± 0.08	2.26 ± 0.13
	4	0.09 ± 0.02	0.50 ± 0.03	0.99 ± 0.08	1.32 ± 0.11
	5	0.05 ± 0.02	0.25 ± 0.02	0.45 ± 0.03	0.78 ± 0.04
Lycium andersonii	1	0.89 ± 0.17	1.63 ± 0.21	3.53 ± 0.45	3.69 ± 0.56
	2	0.69 ± 0.02	1.57 ± 0.06	3.01 ± 0.21	3.73 ± 0.12
	3	0.43 ± 0.04	1.12 ± 0.05	2.35 ± 0.13	2.72 ± 0.14
	4	0.46 ± 0.04	1.07 ± 0.08	2.29 ± 0.17	2.84 ± 0.27
	5	0.50 ± 0.04	0.82 ± 0.05	1.29 ± 0.10	1.40 ± 0.10
Lycium pallidum	1	0.66 ± 0.08	1.73 ± 0.13	3.64 ± 0.24	5.43 ± 0.25
	2	0.51 ± 0.02	1.56 ± 0.03	2.74 ± 0.05	3.25 ± 0.07
	3	0.36 ± 0.02	1.13 ± 0.08	2.00 ± 0.08	2.34 ± 0.10
	4	0.48 ± 0.02	1.26 ± 0.05	2.40 ± 0.10	2.42 ± 0.11
	5	0.21 ± 0.03	0.53 ± 0.06	0.91 ± 0.11	1.16 ± 0.15

Table 2. Diurnal CO$_2$ evolution from soil surface under *Larrea tridentata* and in bare areas

Date	Larrea tridentata		Bare Soil	
	Plot 13	Plot 15	Plot 11	Plot 12
	mg CO$_2$/m^2/hr			
4-7 August	0.0 (6)	0.0 (6)	0.0 (3)	0.0 (6)
8 August	unwatered	watered	unwatered	watered
9-11 August	0.0 (5)	7.2 (3)	0.0 (1)	21.2 (4)
11 August	unwatered	watered	unwatered	watered
12-16 August	0.0 (1)	194.4 (12)	0.0 (1)	18.0 (5)

Table 3. Plant biomass and ^{14}C content within a 2.5-canopy area* on September 17, 1975, for two previously tagged *Larrea tridentata*

	Plant #1		Plant #4		
	Biomass (dry weight)				
	grams	%	grams	%	
Small roots (< 1 mm)	52.1		80.1		
Medium roots (1 < 3mm)	109.0		164.0		
Other roots	43.4		52.4		
Total roots	204.5	58	296.5	70	
Stems	118.5	34	90.9	21	
Leaves	30.3	9	38.2	9	
Total	353.3		425.6		
	^{14}C content				
	cpm	%	cpm/gDW	cpm	%	cpm/gDW
May 1974	1,583,000			3,200,000		
September 1975	265,300	751		448,500	1054	
Roots (% of 9/75)	91,500	35	447	165,100	37	557
Stems (% of 9/75)	150,500	57	1270	211,400	47	2326
Leaves (% of 9/75)	23,100	9	762	72,100	16	1887

*Ground area: Plant 1 = 1.65m^2; Plant 4 = 1.79m^2.

Table 4. Revised estimates of below-ground:above-ground biomass ratios in Rock Valley for 1973 and 1974. Biomass expressed in kg dry wt/ha

	Above-ground biomass		Below-ground biomass		B/A ratio	
	1973	1974	1973	1974	1973	1974
Ambrosia dumosa	345	395	661	825	1.9	2.1
Krameria parvifolia	280	211	668	913	2.4	4.3
Larrea tridentata	467	511	1096	953	2.3	1.9
Lycium andersonii	551	515	871	937	1.6	1.8
Others	1361*	890*	1134	1213	0.8	1.4
Totals	3004*	2522*	4430	4929	1.5	2.0

*Includes biomass of annuals.

Table 5. Distribution of ^{14}C in *Ambrosia dumosa* grown in solution culture after tagging with $^{14}CO_2$ in photosynthesis

After Labeling hrs	Leaf	Stem	Root	Whole Plant
	dry weight, mg			
4	642	409	252	1303
24	1025	429	254	1708
48	1215	616	376	2207
	% plant parts by weight			
4	49.3	31.4	19.3	100.0
24	60.0	25.1	14.9	100.0
48	55.1	27.9	17.0	100.0
	cpm/plant part (X 1000)			
4	424	159	25.2	608
24	437	145	35.3	617
48	366	147	51.0	554
	% of ^{14}C in plant parts			
4	69.7	26.2	4.1	100.0
24	70.8	23.5	5.7	100.0
48	66.1	26.5	7.4	100.0
	cpm/g (X 1000)			
4	660	389	100	467
24	427	339	139	362
48	301	240	109	251

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