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PLANT PRODUCTIVITY AND NUTRIENT INTER­RELATIONSHIPS 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·h⁻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 CO₂ from the soil. For several days after watering of soil in August, the CO₂ 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 ¹⁴C in two Larrea tridentata plants was determined 16 months after exposure of the leaves to ¹⁴CO₂. After 16 months, 13.7 and 16.8% of the original ¹⁴C was retained in the plants. More ¹⁴C was in stems and leaves than in roots. The below-ground:above-ground ratio for ¹⁴C was 0.56 as compared to 1.65 for biomass. The organic debris in the soil below the shrubs and which was floated out by MgSO₄ did not contain ¹⁴C, 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 ¹⁴CO₂ to label photosynthate and distribution among leaves, stems and roots after 4, 24 and 48 hr. For all sampling periods, the highest levels of ¹⁴C 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 CO₂ evolution from the soil surface. It was also planned to determine changes in CO₂ 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 ¹⁴C and to determine if it would indicate an average respiratory turnover rate.
5. Determine root-shoot distribution of dry matter and ¹⁴C when roots could not be lost in soil and to determine rate of ¹⁴C 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 sepal 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, sepal 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 CO₂ 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 O₂ consumed per 30 min. This was converted to µl CO₂ 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 7.8 cm and enclosed an area of 0.05 m². 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 (~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·cm$^{-2}$·min$^{-1}$.

All results are reported on a tissue dry weight basis, i.e., photosynthesis as mg CO$_2$·g dry wt$^{-1}$·hr$^{-1}$; transpiration as g H$_2$O·g dry wt$^{-1}$·hr$^{-1}$.

**14C 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 14C 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$_2$/g dry wt$^-$hr$^-$1, as irradiance increased from 0.16 to 0.43 cal-cm$^-$2/hr$^-$1. At full sunlight there was a slight drop in net CO$_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$_4$ species, exhibited photosynthetic rates as high as those found in many C$_3$ plants. Yet the low light saturation value is characteristic of plants with the C$_4$ 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$_3$ plants, relative to the C$_4$ 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.

**$^{14}$C Assimilates in Larrea**

After 16 months, the amount of $^{14}$C remaining in *Larrea tridentata* tagged with $^{14}$CO$_2$ was about 15% of the total amount originally fixed. Of all plant parts, leaves contributed least to both biomass and $^{14}$C content, 9 and 12.5%, respectively. Roots and stems switched ranking between biomass and $^{14}$C amount. Roots made up 64% of the biomass while containing only 36% of the remaining $^{14}$C, while stems had 27.5% of the total biomass and 52% of the $^{14}$C (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 $^{14}$C 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 $^{14}$C. As stated earlier, only 10% of the organic debris samples contained $^{14}$C, 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 that 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 parvijolia* 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.

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

<table>
<thead>
<tr>
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<td><em>Ambrosia dumosa</em></td>
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<td>395</td>
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<td><em>Krasia servifolia</em></td>
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<td>668</td>
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<td>211</td>
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<tr>
<td>Totals</td>
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<td>250*</td>
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<td>1429</td>
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*Includes biomass of annuals.

Table 5. Distribution of ¹⁴C in *Ambrosia dumosa* grown in solution culture after tagging with ¹⁴CO₂ in photosynthesis

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<tr>
<th>After Labeling</th>
<th>Leaf</th>
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<td>time (hrs)</td>
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<td>642</td>
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<td>48</td>
<td>1215</td>
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<td>40.7</td>
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<td>Uptake/plant part (x 1000)</td>
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<td>48</td>
<td>366</td>
<td>147</td>
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<td>% of ¹⁴C in plant parts</td>
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GAS EXCHANGE, TRANSLOCATION, ROOT GROWTH AND
SOIL RESPIRATION OF GREAT BASIN PLANTS

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US/IBP DESERT BIOME
RESEARCH MEMORANDUM 76-7

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ABSTRACT

Refinement of gas exchange models for *Atriplex confertifolia* and *Ceratoides lanata* were undertaken in 1975. These refined models contributed to the third and final iteration of the community carbon balance schemes for the *Atriplex*- and *Ceratoides*-dominated communities. Studies were also continued on CO2 efflux from the soil surface in communities dominated by *Atriplex confertifolia*, *Artemisia tridentata* and *Ceratoides lanata*. Detailed information on community structure in the *Atriplex*- and *Ceratoides*-dominated communities was also collected during 1975 to contribute to the refined carbon balance schemes of these two communities. Relative root growth activity utilizing the below-ground root observation chambers was also continued in 1975 for *Atriplex confertifolia*. The labile carbon pool was also estimated for the *Atriplex*-*confortifolia*-dominated communities. Although the extent of the labile pool is large, there did not appear to be large fluctuations in the level of this pool during the season. A detailed time sequence of labile pool levels in the root systems of plots labeled with C14O2 was also conducted during this year. A new technique to estimate root system respiration in situ was tested in 1975. A two-year study was initiated in 1975 to determine the effects of partial foliage removal on elements of the carbon balance of the *Atriplex*-dominated community. During this first year, although no apparent differences were immediately detectable in below-ground turnover coefficients or CO2 efflux from the soil surface, changes in the accumulated above-ground litter production and also the seasonal timing of litter production were documented as a result of the foliage removal. The second year of this study is underway during 1976.

An additional study was initiated to assess the respiratory capacity of excised elements of the diffuse root system of *Atriplex confertifolia*. Changes in respiratory capacity during the sampling season suggested an adaptive scheme which would reduce the carbon requirement for maintaining the large, diffuse root system.

INTRODUCTION

This progress report for the year 1975 is reported in several component parts. Substantial effort was continued in several aspects of the carbon balance of the communities dominated by *Atriplex confertifolia* and *Ceratoides lanata*. Particular emphasis was directed towards a more refined photosynthetic model of these two communities.

Experimental work also continued this year on root respiration capacity, root growth activity, soil respiration, community structure and soil moisture extraction. New experiments were undertaken to assess the impact of partial foliage removal on above- and below-ground productivity and other elements of the carbon balance of *A. confertifolia*. Studies in labile carbon pools were also initiated.

OBJECTIVES

General goals of this project are to:

1. Relate gas exchange and other physiological processes of Great Basin plants to the productivity, water use and carbon balance of communities dominated by these plants.
2. Assess the effects of perturbations such as partial foliage removal on elements of the carbon balance of these plants.

During 1975 our specific objectives were to:

1. Design and execute more refined photosynthetic and respiratory models for *Atriplex confertifolia* and *Ceratoides lanata* to be used in predicting seasonal gas exchange.
2. Produce a third iteration of the general community carbon balance schemes for the communities dominated by *Atriplex* and *Ceratoides*.
3. Initiate studies of respiration capacity of root elements of *Atriplex* collected in the field.
4. Initiate studies analyzing the impact of partial foliage removal in *Atriplex*-dominated communities on elements of the carbon balance such as above- and below-ground production, soil respiration, litter production, etc.
5. Determine the extent of the labile carbon pools in the *Atriplex*-dominated community and determine time sequences in the labile carbon pools of below-ground plant parts.
6. Attempt a new technique for measurement of in situ root system respiration.
7. Continue monitoring relative growth rate activity in the soil observation chambers of the *Atriplex*-dominated community.
8. Determine precipitation and soil moisture content levels at several depths in the *Atriplex*-dominated community.
9. Determine soil respiration in the communities dominated by *Atriplex*, *Ceratoides* and *Artemisia*.

METHODS

Field studies conducted during 1975 were carried out as in previous years in our research area west of the Wildcat Hills in Curlew Valley.

GAS EXCHANGE MODELS

In order to greatly refine the interpolative models of plant gas exchange, a new approach was taken during 1975. The model of net photosynthesis was designed to operate on a 1-hr time-step and assumed the basic hyperbolic function:
\[
P = P_{\text{max}} \cdot \frac{2C}{C/(I/I_{\text{max}}) + 1}
\]

where \(I\) is solar irradiance (ly·min\(^{-1}\)); \(I_{\text{max}}\) is maximum irradiance at that time of the year; \(P_{\text{max}}\) is the maximum photosynthetic rate as measured in the field at a particular phenological stage and for prevailing water stress conditions; \(C\) is a relative conductance term expressing relative photosynthetic capacity at a particular temperature for a given phenological stage. This conductance term was derived from gas exchange measurements of these plants in the field. For these determinations, irradiance was held constant while temperature was varied. These temperature dependency relationships were determined in 1970 for phenological stages covering the period from April through October for both *Atriplex confertifolia* and *Ceratoides lanata* (see earlier reports of this project for detailed description of these data). From these data sets, a series of quadratic polynomial equations was derived using least squares techniques, where \(C\) is a relative conductance term relating photosynthetic capacity to temperature in the form:

\[
C = a + \beta T + rT
\]

\(a\), \(\beta\) and \(r\) are constants derived for a given species and phenological stage, and \(T\) is leaf temperature.

This model was validated using an independent data set where net photosynthesis of these two species was measured in the field with the gas exchange cuvette systems programmed to track ambient environmental conditions. Although there was considerable plant-to-plant variation in the populations sampled for the validation data set, the interpolative model appears to be a valid representation of a population of these two species and predicted values of photosynthesis during the season were within 5% of the total measured values.

Dark respiration was evaluated with a model of the form:

\[
R = A \cdot \exp B \cdot T
\]

where \(A\) and \(B\) are coefficients relating leaf temperature, \(T\), to dark respiration rates, \(R\), for particular species and phenological stages. These relationships were derived by least squares analysis from the 1970 data set collected in the field under controlled environmental conditions and, in turn, validated against the independent data set where field respiration rates were measured tracking ambient conditions.

Transpiration rates were predicted from transpiration: photosynthesis ratios derived from the seasonal gas exchange data of 1970 when the cuvettes were programmed to track ambient conditions.

The models were run on a 1-hr time-step basis using temperature and radiation data from the Curlew Valley Validation Site. Since it was only practical to measure gas exchange in these species in the field over the entire season for one year (1970), the \(P_{\text{max}}\) terms for other years were based on water stress conditions and phenological progression for these species at various times during the other years. Also, photosynthetic capacity data using \(^{13}\text{C}O_2\) uptake in a technique reported in detail in last year's progress report was used to evaluate the \(P_{\text{max}}\) term during other years. This was particularly important in determining \(P_{\text{max}}\) for the March and early April period since this early spring period was not included in the 1970 field gas exchange measurements.

**Community Structure**

The model predicts rates of gas exchange per unit foliage weight. In order to convert this to a community ground area basis, the seasonal progression of foliage biomass is necessary for both species during years of contrasting moisture and growth conditions. Community biomass has been sampled for both of these species over the past several years, once or twice per season. This was continued in 1975 for the *Atriplex* community. However, this was of insufficient detail to document the seasonal progression of foliage biomass. Therefore, biweekly foliage:total above-ground biomass ratios were determined for both species during both the dry (1974) and a reasonably moist (1975) year. These foliage:biomass ratios were determined for three basic size classes of shrubs for each species. In order to determine the proportional contribution of biomass in the community for each of the three size classes of shrubs, line-intercept transects were measured during 1975. Fifteen 30-m transects were set out in the *Atriplex*- and *Artemisia*-dominated stands, and ten 30-m transects in the *Ceratoides* community. Along these transects, individual plants were counted and plant canopy projections in the four cardinal directions were determined. These gave relative volume estimates for individuals in each species in order to determine the proportion of individuals of various size classes represented in the population. Based on 20 individuals of each size class of each species, relationships were determined between relative volume based on canopy diameters, and above-ground biomass so that the biomass contribution of each size class constituent of the population could also be estimated. Since foliage:biomass ratios vary with the size class of the individual shrub, this method of weighting the proportionate contribution of foliage for each size class group in the population was felt to be a substantial refinement in estimates of the seasonal progression of foliage biomass. This could also be referenced against the occasional total biomass inventories when 70-m² plots within these communities were totally harvested, inventoried, and separated for foliage and stem above-ground biomass. The techniques for biomass sampling have been elaborated in earlier reports of this project.

**Root System Turnover**

Using the \(^{14}\text{C}/^{13}\text{C}\) dilution technique (reported in detail in last year’s progress report), further studies were undertaken in 1975 on *Atriplex confertifolia* in a series of sampling plots.

**Root Respiration Studies**

Rates of root respiration were determined from root segments excised from *Atriplex confertifolia* plants growing...
at the Curlew Valley study site. Segments were obtained by excavating meter-deep pits adjacent to *A. confertifolia* plants, and tunneling horizontally into the soil profile to locate suitable roots for excision. The segments chosen were generally less than 1 mm in diameter and were 8-15 cm in length.

Excised segments were lightly brushed to remove clinging soil and then placed in test tubes with a volume of 14 ml. The test tubes were flushed with water vapor-saturated ambient air, sealed with airtight screw stoppers, and then placed in a temperature-controlled water bath. Airtight syringes were used to take samples of the ambient air for later determination of CO₂ concentration. Gas samples were again taken from the test tubes containing root segments after a 90-min incubation period at the desired temperature.

The CO₂ concentration of all gas samples was measured using a Varian gas chromatograph with thermal conductivity detector and silica gel column. Total CO₂ evolved by the individual root segments was determined by subtracting the CO₂ concentration of ambient air from the CO₂ concentration in the test tubes at the end of the 90-min incubation period.

Diameter, length, color and morphological appearance of the roots were recorded, and they were then dried at 60°C for two days for dry weight determinations. Percent water content of the soil at the study site was determined periodically using a neutron probe.

This study was designed to test two major hypotheses concerning the functioning of *A. confertifolia* root systems. The first hypothesis was our expectation that roots from different depths in the soil would differ in their respiratory capacity on any given date. The second hypothesis was that roots from a given depth in the soil profile would show changes in their respiratory capacity as the growing season progressed.

In order to test the first hypothesis, roots from each 10-cm depth interval in the profile down to a depth of 1 m were excised and tested for respiration rate at a single temperature of 12°C. This procedure was repeated at approximately 2-week intervals from late June to late October in 1975. The second hypothesis was tested by taking roots from a single depth interval (40-50 cm) and assaying their respiration rates at three temperatures: 10, 15 and 20°C. Each individual root was assayed at only a single temperature, so it was necessary to use a number of replicates to derive a mean respiration rate for each temperature. This sampling procedure was also repeated at approximately 2-week intervals from early August to late October 1975.

**Community Biomass**

Biomass of the *Atriplex confertifolia*-dominated community was determined at two times during 1975 (May 29 and September 19). For above-ground biomass, twelve 4.8-m² plots were completely harvested and separated for various categories such as new shoot growth, tap roots, etc. As in past years, intensive soil coring was used to determine below-ground biomass for the *Atriplex*-dominated community. This was carried out in the spring (May 27) and in the fall (September 28) for three depth intervals of 8-30, 30-50 and 50-70 cm.

**Experiments on Effects of Foliage Removal**

In order to assess the effects of removing a large percentage of the above-ground foliage and shoot material on facets of the carbon budget of *Atriplex confertifolia*, an experiment was designed for the two-year period, 1975-76. In 1975, six pairs of 4.8-m² plots were selected and one of each pair was randomly chosen for foliage removal at a level of approximately 90% in early June. Below-ground turnover of three pairs of plots was evaluated for the growing season of 1975. In 1976 the remaining plots will be similarly analyzed. In addition, 20 pairs of individual shrubs of varying size classes were selected for monitoring of shoot and litter production. One member of each pair was randomly selected for similar foliage removal.

**Labile Carbon**

Labile carbon reserves were determined for various plant parts of *Atriplex confertifolia* at three times during the growing season. This involved both ethanol-soluble (sugars) and acid-hydrolyzable (starch) fractions.

To determine the sugar component (ethanol-soluble components), dried plant parts were ground to 40 mesh in a Wiley mill, subjected to further drying, weighed and extracted in 80% ethanol using a Soxhlet extractor. The residue was saved for starch extraction and analysis. The extract was evaporated to near dryness followed by dilution with water, addition of 5 ml concentrated lead acetate and decolorizing using 5 g carbon black. The mixture was then filtered through Whatman no. 42 filter paper. To convert sucrose into its constituents, 5 ml of 0.5 N HCl was added and the sample was hydrolyzed for 5 min. The sample was then brought to 25 ml volume and frozen until subsequent analysis for sugars. In assaying for sugars, the dinitrosalicylic method for reducing sugars was used (Miller 1959). To determine starch content, the residue from the ethanol extraction was hydrolyzed with 100 ml 1:20 HCl by refluxing for 10 min using the technique of Loomis and Shull (1937, p. 200). The hydrolyzed material was then processed and analyzed similarly to the ethanol extract with elimination of the evaporation step.

A time sequence of labile carbon components in a series of small plots (1 m²) was also undertaken. Series A was labeled with C¹⁴O₂ using the same technique as that employed in the below-ground turnover analysis on June 12, 1975. Series B was labeled on July 16, 1975, and Series 3 on August 4, 1975. There were three plots in each series. These were each harvested at three times for determination of sugars and starch (ethanol-soluble and acid-hydrolyzable fractions, respectively) and the relative radioactivity of C¹⁴ in each of these components. In addition, CO₂ efflux and C¹⁴O₂ efflux were collected at the soil surface in each of these plots using the normal techniques for soil respiration measurement.
In addition to the above measurement, soil respiration was measured in the Atriplex-, Artemisia- and Ceratoides-dominated communities as in previous years. The pattern of root growth was also followed in the root observation chambers in the Atriplex community. Soil moisture content and precipitation were also measured. Techniques were essentially the same as reported in earlier years of this project.

RESULTS

COMMUNITY BIOMASS PRODUCTIVITY AND STRUCTURE

Table 1 contains a summary of the 1975 above- and below-ground biomass determinations at two times during the year for the Atriplex-dominated communities (DSCORE A3UCB21). Table 2 contains a summary of the change in foliage:biomass ratios during the progression of the 1975 growing season for the three major shrub species (A3UCB31).

These data are representative for three size classes of shrubs of each of the three species. The percentage of individuals in each of the three basic size classes of shrubs in the communities dominated by Atriplex confertifolia, Ceratoides lanata and Artemisia tridentata are represented in Table 3 (A3UCB35). In Table 4 are biomass:canopy area ratios for each of the three size classes of shrubs in the communities dominated by these three species (A3UCB31).

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Table 1. Biomass determinations for the communities dominated by Atriplex confertifolia (A3UCB21)

<table>
<thead>
<tr>
<th>Collection Date</th>
<th>Plant Part</th>
<th>Biomass (gm⁻²)</th>
<th>σ</th>
</tr>
</thead>
<tbody>
<tr>
<td>5-10-75</td>
<td>Current year's growth</td>
<td>46</td>
<td>2.9</td>
</tr>
<tr>
<td></td>
<td>Old growth</td>
<td>240</td>
<td>27.3</td>
</tr>
<tr>
<td></td>
<td>Tap root</td>
<td>77</td>
<td>8.5</td>
</tr>
<tr>
<td></td>
<td>Standing dead</td>
<td>70</td>
<td>10.7</td>
</tr>
<tr>
<td>5-17-75</td>
<td>Diffuse root system</td>
<td>1755</td>
<td>190.3</td>
</tr>
<tr>
<td>9-19-75</td>
<td>Current year's growth</td>
<td>80</td>
<td>14.5</td>
</tr>
<tr>
<td></td>
<td>Old growth</td>
<td>221</td>
<td>24.8</td>
</tr>
<tr>
<td></td>
<td>Tap root</td>
<td>73</td>
<td>8.5</td>
</tr>
<tr>
<td></td>
<td>Standing dead</td>
<td>73</td>
<td>9.9</td>
</tr>
</tbody>
</table>

Table 2. Foliage:shoot dry weight ratios for Atriplex confertifolia, Ceratoides lanata and Artemisia tridentata of different size classes (A3UCB31)

<table>
<thead>
<tr>
<th>Date of Collection</th>
<th>Atriplex confertifolia</th>
<th>Artemisia tridentata</th>
</tr>
</thead>
<tbody>
<tr>
<td>Species and Size Class of Shrub</td>
<td>(small)</td>
<td>(intermediate)</td>
</tr>
<tr>
<td>3-3-75</td>
<td>0.11</td>
<td>0.08</td>
</tr>
<tr>
<td>3-10-75</td>
<td>0.03</td>
<td>0.03</td>
</tr>
<tr>
<td>3-17-75</td>
<td>0.13</td>
<td>0.09</td>
</tr>
<tr>
<td>4-4-75</td>
<td>0.021</td>
<td>0.03</td>
</tr>
<tr>
<td>4-11-75</td>
<td>0.29</td>
<td>0.13</td>
</tr>
<tr>
<td>5-1-75</td>
<td>0.03</td>
<td>0.04</td>
</tr>
<tr>
<td>5-18-75</td>
<td>0.31</td>
<td>0.26</td>
</tr>
<tr>
<td>5-25-75</td>
<td>0.05</td>
<td>0.05</td>
</tr>
<tr>
<td>6-2-75</td>
<td>0.38</td>
<td>0.28</td>
</tr>
<tr>
<td>6-9-75</td>
<td>0.07</td>
<td>0.05</td>
</tr>
<tr>
<td>6-16-75</td>
<td>0.36</td>
<td>0.30</td>
</tr>
<tr>
<td>7-3-75</td>
<td>0.08</td>
<td>0.04</td>
</tr>
<tr>
<td>7-10-75</td>
<td>0.32</td>
<td>0.33</td>
</tr>
<tr>
<td>7-17-75</td>
<td>0.07</td>
<td>0.05</td>
</tr>
<tr>
<td>7-24-75</td>
<td>0.30</td>
<td>0.27</td>
</tr>
<tr>
<td>8-1-75</td>
<td>0.07</td>
<td>0.05</td>
</tr>
<tr>
<td>8-8-75</td>
<td>0.30</td>
<td>0.29</td>
</tr>
<tr>
<td>9-15-75</td>
<td>0.05</td>
<td>0.04</td>
</tr>
<tr>
<td>9-22-75</td>
<td>0.31</td>
<td>0.20</td>
</tr>
<tr>
<td>10-19-75</td>
<td>0.04</td>
<td>0.06</td>
</tr>
<tr>
<td>10-26-75</td>
<td>0.28</td>
<td>0.21</td>
</tr>
</tbody>
</table>
LABILE CARBON

The percentage of labile carbon based on tissue dry weight is represented for Atriplex confertifolia at three times during the 1975 growing season. This is represented as two components: ethanol-soluble (sugars) and acid-hydrolyzable (starch) components (Table 5; A3UCB34). This is also represented on a community ground area basis utilizing the biomass information in Table 1. This is represented in Table 6 as glucose-equivalent carbon and starch-equivalent carbon on a ground area basis. Since most of the labile carbon pool is located below ground, a time series of labile carbon components in small plots exposed to C14 O2 was also undertaken. Table 7 shows the change in percent labile carbon in the sugar and starch components and the relative radioactivity of labile carbon (disintegrations per minute per gram carbon) for three plot series labeled at three times during the season (A3UCB34). Each of these plot series was harvested at three times for these determinations. Table 8 shows the carbon dioxide efflux and relative C14 O2 efflux (dpm·m⁻²·day⁻¹) from these plots taken during the course of the labeled series.

EXCISED ROOT RESPIRATION

Average respiration rates at 12 C for roots from the 0 to 30-cm depth increment on all sampling dates are shown in Figure 1 (A3UCB37). Rates for root segments from the 30 to 70- and 70 to 100-cm depth intervals are shown in Figures 2 and 3 (A3UCB37), while results from all three depth intervals are depicted in Figure 4. Figure 5 represents the average respiration rate at 12 C for all roots taken from the profile on each sampling date (A3UCB37). Temperature-dependent respiration curves for roots from the 40 to 50-cm depth interval on five sampling dates are shown in Figure 6 (A3UCB37).

EXPERIMENTS ON EFFECTS OF FOLIAGE REMOVAL

The seasonal progression of soil respiration represented as CO2 efflux per m² ground area in plots which were pruned and control plots is represented in Figure 7 (A3UCB25). In Figure 8 the ratio of accumulated litter production to above-ground standing crop (spring) for pruned and control plants is presented. The percent seasonal litter production, i.e., the relative distribution of litter fall from plants subjected to pruning and control plants during the course of the season, is represented in Figure 9. The below-ground turnover coefficients and corresponding productivities are represented in Table 9 for the pruned and control Atriplex plots (A3UCB27).

ROOT GROWTH, SOIL RESPIRATION, SOIL MOISTURE AND PRECIPITATION

The seasonal progression of root growth in the Atriplex-dominated community is represented in Figures 10 and 11. The seasonal progression of soil moisture content at several depths in the profile is depicted in Figure 12 (A3UCB36), and precipitation during the growing season is represented in Table 10 (A3UCB39). Soil respiration in the Ceratoides- and Artemisia-dominated communities is depicted in Figures 13 and 14 (A3UCB25).
Table 5. Percent labile carbon in ethanol-soluble (sugars) and acid-hydrolyzable (starch) components based on tissue dry weight for the *Atriplex*-dominated community (A3UCB34)

<table>
<thead>
<tr>
<th>Plant Organs</th>
<th>May 6, 1975</th>
<th>July 12, 1975</th>
<th>Sept. 19, 1975</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>% Sugar</td>
<td>% Starch</td>
<td>% Sugar</td>
</tr>
<tr>
<td>New leaves</td>
<td>0.9</td>
<td>6.81</td>
<td>0.75</td>
</tr>
<tr>
<td>Previous year's leaves</td>
<td>0.38</td>
<td>10.15</td>
<td>0.37</td>
</tr>
<tr>
<td>New leaves and stems</td>
<td>0.75</td>
<td>6.10</td>
<td>0.68</td>
</tr>
<tr>
<td>New fruits</td>
<td>-</td>
<td>-</td>
<td>0.21</td>
</tr>
<tr>
<td>Previous year's growth</td>
<td>1.20</td>
<td>8.25</td>
<td>1.04</td>
</tr>
<tr>
<td>Crown</td>
<td>0.32</td>
<td>4.21</td>
<td>3.12</td>
</tr>
<tr>
<td>Tap root</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>&gt;2 mm diam.</td>
<td>0.32</td>
<td>6.73</td>
<td>1.03</td>
</tr>
<tr>
<td>&lt;2 mm diam.</td>
<td>0.49</td>
<td>6.47</td>
<td>0.94</td>
</tr>
<tr>
<td>Diffuse root system</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>5-30 cm</td>
<td>0.28</td>
<td>10.20</td>
<td>0.13</td>
</tr>
<tr>
<td>30-50 cm</td>
<td>0.25</td>
<td>7.52</td>
<td>0.12</td>
</tr>
<tr>
<td>50-70 cm</td>
<td>0.15</td>
<td>7.68</td>
<td>0.05</td>
</tr>
</tbody>
</table>

Table 6. Estimated labile carbon pool in the *Atriplex confertifolia* community (A3UCB34)

<table>
<thead>
<tr>
<th>Date</th>
<th>Plant Part</th>
<th>Depth (cm)</th>
<th>Glucose-equivalent carbon (g·m⁻²)</th>
<th>Starch-equivalent carbon (g·m⁻²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Spring 75</td>
<td>New shoot growth</td>
<td>5-30</td>
<td>0.15</td>
<td>1.30</td>
</tr>
<tr>
<td></td>
<td>Previous year's shoot growth</td>
<td>5-30</td>
<td>1.01</td>
<td>6.60</td>
</tr>
<tr>
<td></td>
<td>Tap root</td>
<td>5-30</td>
<td>0.16</td>
<td>2.23</td>
</tr>
<tr>
<td></td>
<td>Diffuse root</td>
<td>5-30</td>
<td>0.32</td>
<td>17.3</td>
</tr>
<tr>
<td></td>
<td></td>
<td>30-50</td>
<td>0.32</td>
<td>10.5</td>
</tr>
<tr>
<td></td>
<td></td>
<td>50-70</td>
<td>6.20</td>
<td></td>
</tr>
<tr>
<td>Summer 75</td>
<td>New shoot growth</td>
<td>5-30</td>
<td>0.13</td>
<td>1.31</td>
</tr>
<tr>
<td></td>
<td>Previous year's shoot growth</td>
<td>5-30</td>
<td>1.07</td>
<td>8.20</td>
</tr>
<tr>
<td></td>
<td>Tap root</td>
<td>5-30</td>
<td>0.30</td>
<td>3.28</td>
</tr>
<tr>
<td></td>
<td>Diffuse root</td>
<td>5-30</td>
<td>0.48</td>
<td>25.20</td>
</tr>
<tr>
<td></td>
<td></td>
<td>30-50</td>
<td>0.25</td>
<td>16.40</td>
</tr>
<tr>
<td></td>
<td></td>
<td>50-70</td>
<td>0.06</td>
<td>16.85</td>
</tr>
<tr>
<td>Fall 75</td>
<td>New shoot growth</td>
<td>5-30</td>
<td>0.39</td>
<td>3.56</td>
</tr>
<tr>
<td></td>
<td>Previous year's shoot growth</td>
<td>5-30</td>
<td>1.04</td>
<td>7.93</td>
</tr>
<tr>
<td></td>
<td>Tap root</td>
<td>5-30</td>
<td>1.90</td>
<td>4.51</td>
</tr>
<tr>
<td></td>
<td>Diffuse root</td>
<td>5-30</td>
<td>12.27</td>
<td>31.60</td>
</tr>
<tr>
<td></td>
<td></td>
<td>30-50</td>
<td>3.68</td>
<td>18.46</td>
</tr>
<tr>
<td></td>
<td></td>
<td>50-70</td>
<td>3.23</td>
<td>11.71</td>
</tr>
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</table>

Table 7. Percent labile carbon in ethanol-soluble (sugars) and acid-hydrolyzable (starch) components based on tissue dry weight and radioactivity of carbon in these components based on dpm per g carbon. These data are for the diffuse root system in the small plots (A3UCB34)
Table 8. Carbon dioxide efflux and relative C\textsuperscript{14} activity of CO\textsubscript{2} efflux from small plots (A3UCB34)

<table>
<thead>
<tr>
<th>Plot Series</th>
<th>Dates</th>
<th>mg CO\textsubscript{2}·m\textsuperscript{-2}·day\textsuperscript{-1}</th>
<th>dpm·m\textsuperscript{-2}·day\textsuperscript{-1}</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>5-29➔6-75</td>
<td>3.2 x 10\textsuperscript{3}</td>
<td>2.2 x 10\textsuperscript{7}</td>
</tr>
<tr>
<td></td>
<td>6-6➔6-12</td>
<td>3.4 x 10\textsuperscript{3}</td>
<td>1.3 x 10\textsuperscript{7}</td>
</tr>
<tr>
<td></td>
<td>6-12➔6-24</td>
<td>2.8 x 10\textsuperscript{3}</td>
<td>3.4 x 10\textsuperscript{6}</td>
</tr>
<tr>
<td></td>
<td>6-24➔7-3</td>
<td>1.9 x 10\textsuperscript{3}</td>
<td>2.5 x 10\textsuperscript{6}</td>
</tr>
<tr>
<td></td>
<td>7-3➔7-16</td>
<td>1.2 x 10\textsuperscript{3}</td>
<td>7.4 x 10\textsuperscript{5}</td>
</tr>
<tr>
<td></td>
<td>7-16➔8-4</td>
<td>1.9 x 10\textsuperscript{3}</td>
<td>1.8 x 10\textsuperscript{5}</td>
</tr>
<tr>
<td></td>
<td>8-6➔8-22</td>
<td>2.4 x 10\textsuperscript{3}</td>
<td>6.7 x 10\textsuperscript{4}</td>
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<td>2.4 x 10\textsuperscript{3}</td>
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</tr>
<tr>
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<td>7-3➔7-16-75</td>
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<td>7.1 x 10\textsuperscript{3}</td>
</tr>
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<td>7-16➔8-4</td>
<td>1.9 x 10\textsuperscript{3}</td>
<td>2.7 x 10\textsuperscript{3}</td>
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<td></td>
<td>8-6➔8-22</td>
<td>2.4 x 10\textsuperscript{3}</td>
<td>1.7 x 10\textsuperscript{3}</td>
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<tr>
<td></td>
<td>8-22➔9-5</td>
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<td>8.9 x 10\textsuperscript{3}</td>
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<tr>
<td></td>
<td>9-6➔9-19</td>
<td>2.3 x 10\textsuperscript{3}</td>
<td>3.9 x 10\textsuperscript{3}</td>
</tr>
<tr>
<td></td>
<td>9-19➔9-26</td>
<td>1.3 x 10\textsuperscript{3}</td>
<td>1.7 x 10\textsuperscript{4}</td>
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<td>7-16➔8-4-75</td>
<td>1.8 x 10\textsuperscript{3}</td>
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<tr>
<td></td>
<td>8-6➔8-22</td>
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<tr>
<td></td>
<td>8-22➔9-5</td>
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<td>4.7 x 10\textsuperscript{3}</td>
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<tr>
<td></td>
<td>9-6➔9-19</td>
<td>2.3 x 10\textsuperscript{3}</td>
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<td></td>
<td>9-19➔9-26</td>
<td>1.3 x 10\textsuperscript{3}</td>
<td>1.1 x 10\textsuperscript{3}</td>
</tr>
</tbody>
</table>

Figure 1. Respiration rates at 12 C for excised roots of *Atriplex confertifolia* from the 0 to 30-cm depth interval during the 1975 season. Results are shown plus or minus one standard error (A3UCB37).

Figure 2. Respiration rates at 12 C for excised roots of *Atriplex confertifolia* from the 30 to 70-cm depth interval during the 1975 season. Results are shown plus or minus one standard error (A3UCB37).

Figure 3. Respiration rates at 12 C for excised roots of *Atriplex confertifolia* from the 70 to 100-cm depth interval during the 1975 season. Results are shown plus or minus one standard error (A3UCB37).

Figure 4. Respiration rates at 12 C for excised *Atriplex confertifolia* roots taken from three depth intervals down to a depth of 100 cm. Results are for 1975 sampling season (A3UCB37).
Figure 5. Average respiration rate at 12°C for excised *Atriplex confertifolia* roots taken from all depth intervals down to 100 cm on each sampling date during 1975. Results are shown plus or minus one standard error (A3UCB37).

Figure 6. Respiration rates at three temperatures of excised *Atriplex confertifolia* roots taken from the 40 to 50-cm depth interval during the 1975 sampling season (A3UCB37).

Figure 7a

Figure 7b

Figure 7. Carbon dioxide efflux at the soil surface during the 1975 season for *Atriplex confertifolia*-dominated communities; (Fig. 7a) plots subjected to foliage removal in June, and (Fig. 7b) control plots. This is represented for CO₂ collected both in the canopy interspace and under the canopy of shrubs (A3UCB25).
Figure 8. Ratio of accumulated litter production to above-ground standing crop for *Atriplex confertifolia*. This is represented for plants which were subject to intense foliage removal and control plants (A3UCB38).

Figure 9. The seasonal distribution of above-ground litter production for *Atriplex confertifolia* subjected to foliage removal compared with control plants (A3UCB38).

Figure 10a

Figure 10. Relative growth rate of roots at different depths during the course of the 1975 season for *Atriplex confertifolia*. This is represented for two observation chambers (Figs. 10a and 10b) as well as the average for these chambers (Fig. 10c).
Figure 10, continued

Figure 10b

Figure 10c

Table 9. Turnover coefficients, biomass and productivity of root systems for communities dominated by *Atriplex confertifolia* subjected to foliage removal (A3UCB27)

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Turnover Coefficient</th>
<th>Biomass (g m⁻²)</th>
<th>Root Productivity</th>
</tr>
</thead>
<tbody>
<tr>
<td>Partial foliage removal</td>
<td>0.164</td>
<td>1778</td>
<td>292</td>
</tr>
<tr>
<td>Control</td>
<td>0.187</td>
<td>1719</td>
<td>321</td>
</tr>
</tbody>
</table>
Figure 11. Progression of maximum root growth activity with depth in the profile as a function of time during the 1975 season for *Atriplex confertifolia*. These data were plotted from Figure 10.

Table 10. Average precipitation in the *Atriplex confertifolia* and *Ceratoides lanata* study plots (A3UCB39)

<table>
<thead>
<tr>
<th>Collection dates</th>
<th>Precipitation (mm)</th>
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</thead>
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<tr>
<td>12-3-74-1-22-75</td>
<td>40.6</td>
</tr>
<tr>
<td>1-21-19</td>
<td>30.5</td>
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<td>3-19+4-14</td>
<td>22.9</td>
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<td>4-21-5-6</td>
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<tr>
<td>11-19+12-8</td>
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</tr>
</tbody>
</table>

Figure 12. Progression of soil water content at several depths down to 100 cm in the *Atriplex confertifolia* study site during 1975 (A3UCB36).

Figure 13. Carbon dioxide efflux from the soil surface in 1975 for the *Artemisia tridentata*-dominated community. This is represented for CO₂ collected both in the canopy interspace and under the canopy of shrubs (A3UCB25).
DISCUSSION

Gas Exchange Models

Results of the refined photosynthesis and respiration models for *Atriplex confertifolia* and *Ceratoides lanata* are represented in Figures 15 through 18 for the years 1973 and 1974. These two years were chosen because of available abiotic data from the Curlew Valley Validation Site and the fact that these were years of contrasting moisture regimes. Furthermore, other data such as foliage:biomass ratios of the principal species were available for these years. The seasonal progression of foliage per unit ground area for these two species was derived from information in Tables 1 through 4 and from similar information collected in earlier years of this process study. The compilation and calculation of this information has been explained in the methods section. The total yearly values from these simulations were incorporated into the third iteration of the community carbon balance schemes for the *Atriplex-* and *Ceratoides*-dominated communities (Figs. 19 and 20). These two carbon schemes now represent synthesized information for the two-year period of 1973-74. All values are represented as carbon fluxes (g C·m⁻²·yr⁻¹). The results of earlier iterations of these carbon schemes are explained in earlier reports of this project. The refined gas exchange models have, however, presented reasonably balanced carbon schemes where annual carbon fixation by photosynthesis is approximately equal to the summation of carbon incorporated into new shoot growth, shoot respiration and CO₂ efflux from the soil surface which should provide some indication of the summation of below-ground turnover activity and respiration of roots. None of the values in Figures 19 and 20 was derived by subtraction.

Labile Carbon

The estimated labile carbon pool in *Atriplex confertifolia*, while sizable (73 to 100 g carbon equivalent·m⁻²), did not show particularly great changes between the three basic samples taken in this study. The maximum difference in the total estimated labile carbon pool of 22 g carbon · m⁻² is equivalent to the net carbon gain during five days of photosynthesis in late May. In the time sequence study (Table 7), there was much less change in sugar and starch components of the labile pool in the root systems.

A technique designed to utilize the information in Tables 7 and 8 to derive an in situ measure of root system respiration independent of rhizospheric respiration was also attempted in 1975. Briefly, the concept is to utilize the relative specific activity of the labile carbon pool (weighted for constituents and proportionate contribution by depth in the profile) along with the efflux of C¹⁴O₂ from the soil surface to derive a measure of CO₂ coming from the root system. This assumes that the labile pool components constitute the immediate respiratory pool for the root system and that during the rather short period of time involved in this sequence, root death and decay, and hence rhizospheric evolution of C¹⁴O₂, would be minimized. By using an overlapping sequence of labeled plots it is anticipated that it might be possible to arrive at a reasonable estimation of root system respiration. An evaluation of this technique is underway in 1976.

Soil Respiration and Root Growth

As in previous years, CO₂ efflux from the soil surface in the three communities (see Figs. 7, 13 and 14) indicated the small differences between communities and also between locations within these communities, i.e., canopy interspaces versus the soil surface immediately below the shrub canopies.

The progression of relative root growth activity with depth in the profile during the growing season was also very similar to that of previous years (see Figs. 10 and 11).
Figure 15. Seasonal progression of photosynthesis, foliage displayed per unit ground area, carbon fixation per unit ground area, water loss in transpiration and carbon lost in dark respiration in the Atriplex confertifolia community in 1973.

Figure 16. Seasonal progression of photosynthesis, foliage displayed per unit ground area, carbon fixation per unit ground area, water loss in transpiration and carbon lost in dark respiration in the Ceratoides lanata community in 1973.

Figure 17. Seasonal progression of photosynthesis, foliage displayed per unit ground area, carbon fixation per unit ground area, water loss in transpiration and carbon lost in dark respiration in the Atriplex confertifolia community in 1974.

Figure 18. Seasonal progression of photosynthesis, foliage displayed per unit ground area, carbon fixation per unit ground area, water loss in transpiration and carbon lost in dark respiration in the Ceratoides lanata community in 1974.
Figure 19. Third iteration of the carbon balance of the *Atriplex confertifolia*-dominated community based on 1973 and 1974 measurements and calculations. Carbon fluxes are shown in g C·m⁻²·yr⁻¹. No state quantities are contained.

**Foliage Removal**

The two-year experiment to determine the effects of foliage removal in an *Atriplex confertifolia*-dominated community was initiated during 1975. Results during 1975 did not reveal immediate differences in CO₂ efflux from the soil surface in treated versus control areas (see Fig. 7). Nor was there evidence of any difference in below-ground turnover coefficients for the plots subjected to foliage removal as opposed to the control plots (see Table 9). There were, however, differences in accumulated litter production, and correspondingly also in the timing of litter fall during the course of the year (see Figs. 8 and 9).

**Excised Root Respiration**

Carbon use by below-ground plant parts is one of the least-studied components of plant carbon balance. In the case of *A. confertifolia*, this component assumes great importance because of extremely high root:shoot biomass ratios. These ratios reach an observed value of 7:1 on the study site in Curlew Valley (Caldwell and Camp 1974). The magnitude of root biomass suggests that an entire *A. confertifolia* root system, respiring at maximal rate, would seriously deplete the plant's available carbon supplies. Thus, it seems reasonable that portions of the *Atriplex* root system would display less than maximal respiration rates at certain times during the year.

Such a change in root respiratory capacity throughout the course of a growing season has been demonstrated by Shiroya et al. (1966) for *Pinus strobus*. Other studies (Osman 1971; Jensen 1960; Wardlaw 1968; Huck et al. 1962; Szaniawski and Adams 1974) have shown that soil temperature, soil moisture and shoot photosynthetic activity can all have both an immediate and a preconditioning effect on root respiratory capacity. Since environmental conditions in the soil vary with both depth and time of year, the following two hypotheses were proposed: 1) At any point in time, segments of the root system at different depths in the soil profile will display different respiration rates; 2) During the course of the year, each segment of the root system undergoes an adaptive acclimation of its respiration rate which allows it to function actively when conditions are favorable and to conserve the plant's energy resources when conditions are unfavorable.

As implied by these hypotheses, the major objective of this research was to elucidate the adaptations which allow *A. confertifolia* to maintain its large perennating root mass. Therefore, respiration rates of young growing tips were ignored. However, other difficulties prevent this from being a study of true maintenance respiration as defined by Penning de Vries (1975) and others. The respiration rates of structural, apparently suberized, roots may contain a component associated with diameter growth. The magnitude of this component is unknown but is assumed to be small. Also, excision of the roots may induce some damage respiration. Some preliminary tests have been run to check for damage respiration, and they suggest that it may be a small portion of total respiration, but more exhaustive testing is needed before firm conclusions can be drawn.

Despite these concerns, we believe that the results obtained in this study are good comparative values for the carbon costs of maintaining different parts of the root system during the growing season.
Changes in Temperature-Dependent Respiration Curves

During the growing season, roots from the 40 to 50-cm depth interval displayed changes in their respiratory response to temperatures of 10, 15 and 20 C. As shown in Figure 6, respiration rates at each of these temperatures decreased markedly between August 9 and September 19, and then showed a general increase through the end of October. Rates at 10, 15 and 20 C on September 19 can be shown to be significantly different from those on both August 9 and October 29. Q_{10} values associated with these results range from 1.48 to 3.53.

Comparison of these changes in respiration rate to soil temperature data collected from Curlew Valley (Fig. 21) suggests that changes in root respiratory response to any fixed temperature are not always correlated in a straightforward manner to changes in soil temperature during the same period. Thus, while soil temperatures in the 30 to 70-cm zone generally remain fairly stable from early to late August, root respiratory response to the three test temperatures apparently declined during this same period. Soil temperature then continually declined after early September, while root respiratory response declined until mid-September and then increased through the end of October.

The question of whether these changes in respiratory response represent true acclimations of root respiration is difficult to answer since acclimations are usually assumed to have adaptive value. We could speculate that the decline in respiratory response between August 9 and August 29 results in a beneficial reduction of carbon use by the roots during the time when soil temperatures are at a maximum. The continued decline until September 19 could represent a further beneficial reduction in carbon demand necessitated by a critical function such as fruit development, or it could simply represent a lag period in the plant's response to the now decreasing soil temperatures. From September 19 until the end of the sampling period there was apparently a homeostatic response which permitted the roots to continue functioning at a moderate rate despite decreasing soil temperatures.

It is impossible to state definitively the adaptive values of the observed changes in respiratory response, but the directions of these changes strongly suggest some adaptive value. There is, thus, good evidence for concluding that A. confertifolia roots demonstrate acclimation in their respiratory response to temperature during the course of the growing season.

Dynamics of Excised Root Respiration at 12 C

Since it was not feasible to test the respiration rates of individual excised roots at current soil temperatures, roots from all depths throughout the profile were assayed at a temperature of 12 C (with the exception of temperature-dependent respiration tests described in the preceding section). These assays are accurate reflections of changes in root respiratory capacity, but it is recognized that changes in respiration at 12 C are not necessarily equal to changes in respiratory capacity at other temperatures. These results also do not reflect changes in actual root activity in the field since changes in soil temperatures are not taken into account.

In order to get an idea of actual field respiration values, the respiration rates at 12 C were projected onto a temperature-dependent respiration curve, and respiration was then evaluated at current field soil temperatures. The temperature-dependent respiration curve was derived from means of the values presented in Figure 6. The curve described by these values is represented by the equation \( X_T = X_{10} + 0.0098(T-10)^3 \), where \( X_T \) is respiration rate at the temperature of interest, \( T \). The results of these calculations are shown in Figure 22.
Respiration of roots from the 0 to 30-cm depth layer—On June 22, roots from the 0 to 30-cm depth layer had a high respiratory rate of .7 mg CO₂·g dry wt⁻¹·hr⁻¹ at 12 C. This was the highest respiratory rate observed for any sample of roots during the summer field season. The water content in much of this soil layer was quite high during the June-early July as shown by the figure of 14% water content by volume at 20-cm depth on July 1 (Fig. 12). Soil temperatures were also relatively high at this time (Fig. 21). We would expect that high root metabolic activity during this period of favorable soil conditions would be advantageous to the plant.

The roots in this part of the profile then displayed a rapid reduction in respiratory capacity resulting in an observed respiratory rate of .2 mg CO₂·g dry wt⁻¹·hr⁻¹ at 12 C on July 26. Soil temperatures increased during the time period from June 22 to July 26, but the magnitude of the reduction in respiratory capacity would actually cause a reduction in root respiration under field conditions as shown in Figure 22. This reduction in carbon demand by the roots in the 0 to 30-cm depth interval occurred during a period when soil temperatures were rapidly increasing and soil water content was being rapidly depleted. The adjustment in respiratory capacity appears to have the effect of reducing carbon use by the roots at a time when a high level of metabolic activity would not be particularly advantageous.

Between July 26 and August 8, respiration rates for roots from this part of the profile showed no significant change. A second significant decrease in respiratory capacity then occurred between August 8 and August 20, producing a rate of .1 mg CO₂·g dry wt⁻¹·hr⁻¹ at 12 C. This respiratory rate was the minimum value observed at 12 C for roots from this layer, and it occurred at a time when soil water content had reached a minimum value and soil temperature was at, or near, maximum. This suggests a disadvantageous period for root activity, and a reduction in root respiration probably did occur in the field at this time (Fig. 22).

Root respiratory capacity measured at 12 C showed small fluctuations around this minimum value from August 20 to October 17, but decreasing soil temperatures probably resulted in further decreases in respiration in the field during this period. Between October 17 and October 31, a significant increase in respiratory capacity occurred. This increase in respiratory capacity appeared to more than offset decreases in soil temperature at this time, thus resulting in a probable increase in respiration in the field. This increase in activity occurs at a time when soil water content has increased, so the timing of the increase seems to permit continued root activity during a period of ameliorating soil environmental conditions.

Respiration of roots from 30 to 70-cm depth layer—On June 22, excised roots from this depth interval showed a moderately high respiration rate of approximately .4 mg CO₂·g dry wt⁻¹·hr⁻¹ at 12 C. There was then an apparent increase in respiratory capacity between June 22 and July 26 which corresponded with a period of rapidly increasing soil temperatures and probably resulted in increased respiration in the field (Fig. 22). This change in respiratory capacity was clearly not homeostatic, and it actually occurred during a period of slowly decreasing soil water content. This suggests that the timing of changes in root activity is not simplistically controlled by changes in soil environmental conditions.

Following the peak of activity observed on July 26, respiratory capacity of roots from this layer showed a continual decline until a minimum value of approximately .1 mg CO₂·g dry wt⁻¹·hr⁻¹ was observed on September 3. Soil temperatures changed little during this period, so respiration under field conditions probably declined at about the same rate as observed respiratory activity at 12 C. This minimum respiratory rate at 12 C occurred shortly after minimum soil water content values had been observed at 40- and 60-cm depth, thereby suggesting once again that a reduction in carbon use by the roots occurs when soil environmental conditions are unfavorable.

After September 3 there was little change in the respiratory capacity of roots from the 30 to 70-cm depth layer as indicated by their response at 12 C. This period was marked by nearly stable soil water conditions, but soil temperatures showed continual decline so respiration rates in the field probably decreased proportionately. This obviously would result in decreased carbon demand by roots in the 30 to 70-cm depth interval.
Respiration of roots from 70 to 100-cm depth interval—Respiration of roots from the 70 to 100-cm depth interval was first observed at a low rate of about .1 mg CO$_2$ g dry wt$^{-1}$ hr$^{-1}$ at 12 C on June 22. There was then a rapid increase in respiratory capacity to a rate of .35 mg CO$_2$ g dry wt$^{-1}$ hr$^{-1}$ at 12 C on July 28. This increase in respiratory capacity was accompanied by increasing soil temperatures so there clearly must have been a marked increase in root respiration in the field.

Following the observation of the peak rate on July 26, respiratory capacity of roots in this soil layer declined gradually and eventually reached a minimum observed value of approximately .05 mg CO$_2$ g dry wt$^{-1}$ hr$^{-1}$ at 12 C on October 17. The decline in root respiration in the field over the time interval from July 26 to September 3 was probably more gradual than the decline in respiratory capacity measured at 12 C because temperatures in this part of the soil profile increase throughout August.

It should be noted that soil water content reached minimum observed values at depths of 80 and 100 cm on October 9, and this was followed closely by observation of minimum respiratory capacity for roots in this zone on October 17. This again suggests that periods of minimum root respiratory capacity may coincide with periods of least favorable soil environmental conditions.

After October 17 there was an apparent small increase in root respiratory capacity which probably allowed the roots from the 70 to 100-cm zone to continue functioning at moderately low levels despite declining soil temperatures.

Dynamics of root respiratory capacity throughout the entire profile—In late June, respiration at 12 C was greater for roots from the 0 to 30-cm layer than for roots from the 70 to 100-cm layer, and respiration of roots from the 30 to 70-cm layer was intermediate between these two values. Since soil temperatures during this period were highest near the soil surface, it is clear that the portion of the root system in the 0 to 30-cm layer was more active at this time than parts of the root system at greater depth.

Between late June and late July there was a change in these functional relationships. Respiratory capacity decreased significantly for roots in the 0 to 30-cm zone; showed an apparent slight increase for roots in the 30 to 70-cm zone; and increased significantly for roots in the 70 to 100-cm zone. As a result, respiratory response at 12 C was significantly higher for roots from the 30 to 70-cm zone than for roots from the 0 to 30-cm zone, and roots from the 70 to 100-cm zone had rates that were apparently intermediate between the other two. Thus, as soil temperatures increased throughout the whole profile in early summer, the respiratory capacity of roots near the soil surface decreased, while the respiratory capacity of roots from depths below 30 cm increased. The projected field respiration rates in Figure 22 show that the bulk of root zone activity shifted away from the surface layers to greater depths in the profile at this time.

The respiration values of roots from these first two sampling dates demonstrate that roots from different parts of the soil profile reached peak activity at different times. The frequency of sampling does not permit precise identification of periods of peak activity, but it is clear that roots from the 0 to 30-cm soil layer attained maximum respiratory capacity before roots from greater depths. Projected field respiration rates for the whole profile (Fig. 22) also show that the differential timing of maximum activity resulted in an apparently homeostatic condition for the profile as a whole. Average whole profile respiration rate changed very little from June 25 to July 26. This homeostatic condition was achieved by shifting the bulk of root respiratory activity away from the upper 30 cm of soil, where water and temperature conditions were becoming increasingly unfavorable, down to the lower soil profile with more moderate environmental conditions.

Relationships among activities of excised roots from the three zones showed little apparent change from late July to late August. Roots from the 30 to 100-cm zone still had higher respiration rates at 12 C on August 20 than did roots from the 0 to 30-cm layer, and values for roots from the 70 to 100-cm layer were still apparently intermediate. However, respiratory capacity of roots from all three layers showed a significant decrease from July 26 to August 20, obviously resulting in reduced whole profile root respiration during this period. This reduction in respiration would clearly have the advantageous effect of reducing carbon usage by the root system during the portion of the summer when soil temperatures are at a maximum at most depths.

Respiratory capacity of roots from the 0 to 30-cm layer had reached their minimum value by August 20, but roots from greater depths continued to show gradual decreases in respiratory capacity. Roots from the 30 to 70-cm zone reached a minimum value during early September, while roots from the 70 to 100-cm zone did not decline to minimum respiratory capacity until mid-October. Thus, roots from these three zones in the soil profile very clearly differed in timing of both maximum and minimum respiratory capacity. Also, as was pointed out in preceding sections, the observations of minimum respiratory capacity of roots from each depth layer occurred shortly after the observation of minimum water content in that layer. Thus, there is a strong suggestion that periods of minimal respiratory capacity coincide closely with periods of least favorable soil environmental conditions.

The decline in respiratory capacity of roots from below 30 cm in the period from August 20 to October 17, coupled with reductions in soil temperatures throughout the profile, produced a minimum value in whole-system respiration projected to field temperatures on October 17 (Fig. 22). This calculated value was .08 mg CO$_2$ g dry wt$^{-1}$ hr$^{-1}$, about 20% of the calculated maximum values for June and July.

By late October, respiratory capacity of roots from both the 0 to 30-cm and the 70 to 100-cm zones appeared to be increasing. Respiratory capacity of roots from the 40 to
50-cm zone also showed an increase when measured at 10, 15 and 20°C, but this increase was not apparent in the root segments from the 30 to 70-cm zone assayed at 12°C. The increase in respiratory capacity observed at this time apparently had a homeostatic effect, allowing the roots to maintain a moderate level of activity despite decreasing soil temperatures.

In summary, it is clear that Atriplex confertifolia roots show changes in their respiratory capacity during the course of a year. Also, roots from different depths in the soil profile clearly differ in the timing of their periods of maximal and minimal activity. At two times during the sampling season, between June 22 and July 26 and again between October 17 and October 31, these differential changes in respiratory capacity appeared to have a homeostatic effect on respiration in the whole root system. During the remainder of the sampling season, changes in respiratory capacity had the apparent effect of reducing root respiration under field conditions. The projected values for root respiration under field conditions declined continually as soil environmental conditions became increasingly unfavorable. There is a strong suggestion that changes in respiratory capacity are timed to produce maximum respiration at times when soil conditions are favorable and minimum activity when soil conditions are least favorable. This strategy for root respiration in A. confertifolia would clearly minimize the cost of maintaining the large amount of biomass present in the root system.

EXPECTATIONS

During 1976, the second year of the two-year experiment on the effects of partial foliage removal in the Atriplex-dominated community will be concluded. This will include investigations into the labile carbon pool as affected by foliage removal, above-ground litter production, below-ground turnover, soil respiration, etc.

Aspects of relative root growth dynamics are being continued in 1976 as well as the concluding year of the studies on respiration capacity of root elements of Atriplex confertifolia. Since 1976 is the final year of this project, emphasis will also be placed on synthesis and evaluation of the results of this project.

ACKNOWLEDGMENTS

Although this 1975 study was conducted largely under the support of the US/IBP Desert Biome, additional financial support from the Utah Agricultural Experiment Station has been invaluable in this work.

LITERATURE CITED


GAS EXCHANGE AND PRODUCTIVITY OF SONORAN DESERT SHRUBS

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ABSTRACT

The primary objective of this study is to investigate the interrelationship between abiotic environmental parameters, plant water relations and gas exchange patterns of the dominant plants of the Silverbell Validation Site. The secondary objective was to determine the retention of $^{14}$C photosynthate in the different plant components as an estimate of net carbon accumulation. Plants of Ambrosia deltoidea (bursage) and Cercidium microphyllum (bursage) demonstrate a large annual variation in plant water potential: -6 to -98 bars. Leaf shedding throughout the year is initiated whenever water potentials decrease below -40 bars. This shrub was capable of maintaining low diffusive resistances, 6 sec/cm, with concomitant predawn water potentials of -28 bars, and did not terminate gas exchange until water potentials had decreased to -60 bars. The photosynthesis pattern was regulated by plant water potential, although $^{14}$CO$_2$ assimilation was restricted below -50 to -60 bars. Despite relatively high predawn water potential values of -5 bars, the mean daily photosynthesis rate was only 12 mg CO$_2$·dm$^{-2}$·hr$^{-1}$. Leaf material of A. deltoidea is the main photosynthetic plant part, and $^{14}$C photosynthate is translocated into stem and fruit material. When fruits are present $^{14}$C translocation from leaf material is more rapid than translocation into stem material. Photosynthate translocation is severely reduced whenever plant water potentials are below -60 bars.

Plant water potentials for Cercidium microphyllum (paloverde) and Olneya tesota (ironwood) were relatively constant throughout the entire year, ranging between -10 to -36 bars. During periods of high soil water availability, the maxima water potential values are usually lower than the maxima values measured in plants of A. deltoidea. Both tree species are deciduous during some time of year, although C. microphyllum remained in a leafless state from mid-April to December. Leaf production in this species occurs whenever predawn water potentials are greater than -10 bars. Leaf shedding in plants of O. tesota was significant during flower and fruit development, despite maintaining plant water potentials favorable for leaf growth and photosynthesis. Minimum stomatal diffusive resistances in O. tesota were seldom less than 5 sec/cm, and maxima values of 20 sec/cm were observed with -35 bar plant water potentials. Photosynthesis persists throughout the entire year in response to maintaining a favorable plant water balance. Leaf material in both tree species is the main photosynthetic plant part, although the magnitude of stem photosynthesis in C. microphyllum is near 27% of the magnitude of leaf photosynthesis. Stem photosynthesis in C. microphyllum persists throughout the entire year. Fruit material in both species is photosynthetically active, and is an important carbon source for fruit development as both species are usually leaf deciduous during this period. The translocation of $^{14}$C photosynthate is reduced during the summer and fall months whenever plant water potentials are near minima values.

INTRODUCTION

Validation studies conducted within each of the four American deserts have provided extensive information on the biomass and net primary production of their dominant plants. These studies have documented the variability of vegetation production between the four desert types throughout a single year. Additionally, these studies have documented the variability of vegetation production within each desert type over a period of years. In order to further understand the mechanisms responsible for vegetation production, numerous plant process studies dealing with gas exchange parameters have been conducted on the dominant plants of the validation study sites. The objective of the gas exchange studies has been to integrate seasonal variations of abiotic environmental components, photosynthetic carbon assimilation and seasonal carbon balance contributing to biomass and net primary production.

Desert perennials -- cacti, grasses, shrubs and trees -- account for a significant portion of the biomass and net primary production for each of the four desert types. Gas exchange studies on the dominant perennial plants have been conducted in: a) the Chihuahuan Desert (Cunningham and Balding 1972, Cunningham et al. 1973, Cunningham et al. 1974); b) the Great Basin Desert (Caldwell et al. 1971, Hironaka and Tisdale 1971, Caldwell et al. 1972, Hironaka and Tisdale 1972, Caldwell et al. 1973, Hironaka and Tisdale 1973, Caldwell et al. 1974; c) the Mohave Desert (Bamberg and Wallace 1972, Bamberg et al. 1974); and d) the Sonoran Desert (Patten 1972, Ting et al. 1972, Patten and Nisbet 1973, Ting et al. 1973, Ting et al. 1974). However, previous US/IBP Desert Biome studies have not investigated the gas exchange of shrubs and trees of the Sonoran Desert.

Perennial plants of the Sonoran Desert possess a variety of adaptations which permit growth and survival in hot, arid conditions. The purpose of this study is to investigate the interrelationship between abiotic environmental parameters, plant water relations and gas exchange patterns of the dominant plants of the Silverbell Validation Site. The study reports the seasonal pattern of water potentials for Ambrosia deltoidea, Cercidium microphyllum and Olneya tesota, and the seasonal pattern of gas exchange for A. deltoidea and O. tesota. Only preliminary information is reported for C. microphyllum, which remained in a deciduous state throughout most of 1975. A. deltoidea (bursage) is a drought-deciduous shrub which is restricted to the Sonoran Desert. C. microphyllum (paloverde) is a deep-rooted, drought-deciduous tree, with chlorophyllous stems
which are photosynthetically active. *O. tesota* (ironwood) is a deep-rooted, drought-deciduous tree, which lacks chlorophyllous stems. Both species of trees are restricted to the Sonoran Desert.

This study will be expanded during 1976 to include the other dominant perennials of the Silverbell Validation Site—*Acacia constricta* (white thorn) and *Simmondsia chinensis* (jojoba). Additionally, emphasis will be placed on continuing the work with *C. microphyllum* due to the paucity of information collected throughout 1975. All species will be monitored on a regular monthly basis to establish the diurnal and seasonal patterns of water relations and \(^{14}\)C photosynthesis, and their interrelationship with abiotic parameters of the Sonoran Desert.

**OBJECTIVES**

The main objectives of this study are to determine the following:

1. The relationship between abiotic components of the desert environment and the gas exchange of the hot desert shrubs and trees. The abiotic components include solar radiation, air and leaf temperatures and soil water potentials. Both diurnal and seasonal patterns of \(^{14}\)CO\(_2\) photosynthesis and transpiration were monitored regularly throughout 1975.

2. The relationship between short-time measurements of \(^{14}\)CO\(_2\) assimilation and \(^{14}\)C retention in photosynthate. The retention of \(^{14}\)C products in leaf, petiole and stem components was monitored regularly throughout 1975. These data will be related to the seasonal patterns of net carbon accumulation.

Some of the original objectives proposed for 1975 were not completed. These include:

1. Photosynthate redistribution between the different plant organs. The proposed techniques did not permit distinction between the loss of \(^{14}\)C photosynthate due to translocation or respiration. Root material was not sampled for \(^{14}\)C-product translocation.

2. The biomass or above-ground standing crop at the study area was undetermined. Additionally, biomass increments during 1975, which would permit determination of net primary production, were not completed. Since this type of information is available from the Silverbell Validation Site, our research effort was centered upon the ecophysiology of the Silverbell vegetation.

**METHODS**

The research methods are listed below according to the three data sets proposed for the 1975 study period: 1) A3USZ01, Environmental Analysis; 2) A3USZ02, Gas Exchange; and 3) A3USZ03, \(^{14}\)C-Photosynthate Distribution.

**ENVIRONMENTAL ANALYSIS**

**Air Temperature**

The temperature of the air was measured with a portable, battery-powered thermistor (Atkins) at a height of 2 m.

**Relative Humidity**

The atmospheric water vapor concentration was measured with a portable, battery-powered psychrometer (Atkins). This instrument has a ventilated, shielded set of thermistors. The wet-bulb and dry-bulb temperatures were determined at a height of 2 m.

**Soil Water Potential**

The soil water potential was measured in situ with the thermocouple psychrometer technique. Soil psychrometer probes (Wescor, Inc.) were positioned horizontally at soil depths of 5, 10, 20, 30 and 60 cm. The soil water potential was measured directly with a dewpoint microvoltmeter (Wescor, Inc.). At the end of 1975 the calibration of all probes was rechecked by equilibration with standard molal solutions of NaCl (Lang 1967).

One set of probes was positioned in a vegetated area which did not receive additional water from horizontal drainage (open site). A second set of probes was positioned in a channel area which received additional water from horizontal drainage or runoff (vegetated site). The two sites were selected to represent contrasting soil water profiles in a vegetated area.

**Solar Radiation**

The solar radiation was measured directly with a pyranometer (Eppley). The pyranometer was positioned horizontally with the ground at a height of 2 m. Since the instrument measures total solar radiation by the radiometric technique, the pyranometer voltage was measured with a portable, battery-powered temperature potentiometer (Leeds and Northrup).

**GAS EXCHANGE**

**Leaf Temperature**

The temperature of leaves was measured directly with the infrared thermometry technique (Barnes Engin.). A set of leaves which would be used for subsequent gas exchange studies was sampled to determine the mean leaf temperature for each hourly sampling interval.

**Diffusion Resistance**

The diffusion resistance of individual leaves was measured directly with a nonventilated diffusion porometer (Ennis and Assoc.). The diffusion resistance was measured by recording the time required to change the water vapor concentration within the porometer sensor, between two predetermined concentrations. The transpiration rate was calculated by assuming the water vapor concentration within the leaf was saturated at the leaf surface.
exposed sides of each plant.

plants used concurrently for the gas exchange studies.

samples of stems for each species were labeled concurrently.

potential with a disc of leaf tissue.

thermocouple psychrometry were discontinued. The tech­

was measured directly with a Scholander-type pressure

The stem material was harvested after 0, 7 and 21 days. The

containing "CO, generated from Ba "CO,. Triplicate

transpiring, were exposed to 100 microcuries of "CO, for 30

were included due to the long

time between exposure to "CO, and storage on dry ice did not

The radioactivity in the leaf sample was

determined by liquid scintillation techniques, and the

counting efficiency determined by the internal standard

technique.

Plant Water Potential

The plant water potential (xylem pressure potential) was measured directly with a Scholander-type pressure

bomb. Terminal portions of stems were selected from plants used concurrently for the gas exchange studies. Terminal portions of stems were selected on the sun-
exposed sides of each plant.

Leaf Water Potential

Measurements of leaf water potentials by the technique of thermocouple psychrometry were discontinued. The tech­
nique, as originally proposed, was omitted due to the long

equilibration times required to attain a steady-state water

potential with a disc of leaf tissue.

14C PHOTOGRAPHATE DISTRIBUTION

Terminal portions of intact stems, which were actively transpiring, were exposed to 100 microcuries of 14CO, for 30

min. The stems were enclosed in clear polyethylene bags and the radioactive gas introduced with a syringe

containing 14CO2 generated from Ba14CO3. Triplicate samples of stems for each species were labeled concurrently.

The stem material was harvested after 0, 7 and 21 days. The oven-dried material was separated into leaf, petiole, stem,

flower and fruit components and combusted in an oxygen

atmosphere following the technique of Oliverio et al.

(1982). The radioactivity was determined by liquid scintillation techniques. The counting efficiency was determined by

the internal standard technique.

RESULTS AND DISCUSSION

USERY MOUNTAIN STUDY AREA

The study area is located in the Usery Mountains, which are approximately 45 km east of Phoenix, Arizona. The field

studies are being conducted at an elevation of 460 m, and

the vegetation is similar to the Silverbell Validation Site, i.e., upper Sonoran Desert scrub. The monthly mean
temperatures recorded adjacent to the study area (Table 1) are characteristic of a hot desert habitat. However, during

the interval from January to June 1975, the monthly mean temperatures were below the long-term temperature

average. Winter and spring daytime temperatures are generally above 15 C and few nighttime temperatures below

freezing are observed. The monthly mean temperatures for July to December 1975 were similar to the long-term

temperature averages, although December 1975 was warmer than normal. Summer daytime temperatures in

excess of 40 C occur during June, July and August, with July

1975 having the highest monthly mean temperatures. Summer nighttime temperatures remain high throughout

this interval. The persistent high temperatures, coupled with a scant, biseasonal precipitation, contribute to the arid

conditions of the study area.

The long-term precipitation regime is characterized by a

biseasonal pattern of rainfall (Table 2). Drought conditions

normally occur from April to June, and the rainfall is

reduced during the months of February and November. During 1975, the total annual rainfall was similar to the

long-term average from 1944 to 1974. Despite the similarity

in absolute amounts of rainfall, the monthly rainfall totals

during 1975 appear to be more irregular, and contributed

to the arid conditions of the habitat during the study year.

The distribution of rainfall throughout 1975 suggests a

triseasonal, alternating pattern of rain and drought condi­
tions (Fig. 1). The periods of rainfall were mid-February

through mid-April, July and early September, and late

November and December.

Soil Water Potential

Soil water potentials were measured with thermocouple

psychrometer probes at soil depths of 5, 10, 20, 30 and 60

cm. The annual pattern of average soil water potentials at

30- and 60-cm depths is presented in Figure 2. The data

were selected as representative of the soil water status within

the major rooting zones of A. deltoides, C. microphyllum and O. tesota (Thames et al. 1974). Data for the interval

from January to April are missing, since the soil probes were

overdue in shipment and were not placed at the study area

until April 1, 1975.

Soil water potentials decreased progressively following

the termination of rainfall in early April, becoming very low

during the summer drought period. Minimum soil water

potentials were -57 and -87 bars at the 60- and 30-cm

depths, respectively. The effectiveness of the July rains (34.8

mm total) in recharging the soil with water was only

moderate, due to the high air and soil temperatures

throughout this month. Soil water potentials reached

maxima values of -27 and -48 bars at the 30- and 60-cm

depths, respectively. The most extreme period of drought, as

evidenced by soil water status, occurred in the fall drought

period. Soil water potentials were very low at both soil

depths, -78 and -86 bars, preceding the initiation of the
Table 1. Monthly temperature record at the Usery Mountain study area

<table>
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<tr>
<th>Year</th>
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<th>F</th>
<th>M</th>
<th>A</th>
<th>H</th>
<th>N</th>
<th>J</th>
<th>J</th>
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<th>S</th>
<th>O</th>
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<td>1944-1974</td>
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<td>16.3</td>
<td>19.4</td>
<td>24.3</td>
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<td>30.3</td>
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<td>22.8</td>
<td>15.5</td>
<td>9.2</td>
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</tr>
<tr>
<td>1975</td>
<td>12.8</td>
<td>11.8</td>
<td>13.9</td>
<td>15.5</td>
<td>22.5</td>
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<td>30.7</td>
<td>27.8</td>
<td>21.4</td>
<td>15.4</td>
<td>12.2</td>
<td></td>
</tr>
</tbody>
</table>

1 The 1944-1974 data are monthly mean temperature averages for 3 decades at adjacent weather stations: Apache Junction, Falcon Field and Granite Reef Dam. The temperature data are presented in °C.

Table 2. Monthly precipitation record at the Usery Mountain study area

<table>
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<th>F</th>
<th>M</th>
<th>A</th>
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<th>A</th>
<th>J</th>
<th>J</th>
<th>A</th>
<th>S</th>
<th>O</th>
<th>N</th>
<th>D</th>
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<tr>
<td>1944-1974</td>
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<td>6.4</td>
<td>35.1</td>
<td>3.5</td>
<td>1.1</td>
<td>0.9</td>
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<tr>
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<td>0</td>
<td>34.8</td>
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<td>1.6</td>
<td>31.3</td>
<td>24.5</td>
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</tbody>
</table>

1 The 1944-1974 data are the monthly averages for 3 decades at adjacent weather stations: Apache Junction, Falcon Field and Granite Reef Dam. The total monthly precipitation data are presented in mm of rainfall.

Figure 1. Top. Annual pattern of precipitation occurring at the study area during 1975. Precipitation events of less than 1 mm omitted. Precipitation in millimeters.

Figure 2. Bottom. Annual pattern of soil water potentials at the study area during 1975. Soil depths of 30 cm (solid line) and 60 cm (dashed line). Each value is the average of two measurements, one taken in a flat, vegetation-covered area and one taken in an adjacent drainage area which was vegetation covered. Soil water potential in units of bars (A3USZ01).
winter rains. The effectiveness of the November rains (31.3 mm total) in recharging the soil with water was high, due to the lower air and soil temperatures of this period. Soil water potentials reached maxima values of -1 and -35 bars at the 30- and 60-cm depths, respectively.

**Plant Water Potential**

Plant water potentials were measured with a Scholander-type pressure bomb, and the measurements were completed before the plants were exposed to the direct solar radiation of dawn. Although this technique measures xylem pressure potential, the relationship between plant water potential and xylem pressure potential has not been determined using the three plant species of this study. Plant water potential is treated as synonymous with xylem pressure potential.

Data for the month of January are missing, since the pressure bomb measurements were not initiated until February. During this period the water potential of leaf discs was determined by the method of thermocouple psychrometry. Due to the long equilibration time required by this method, the method was replaced with the pressure bomb method, and the data were not reported.

Plant water potentials for the two trees, *C. microphyllum* and *O. tesota*, were relatively constant throughout the entire year, ranging between -10 to -36 bars (Fig. 3). The data contrast significantly with the greater annual variation in plant water potential of the shrub, *A. deltoidea*, which ranged between -6 to -98 bars (Fig. 3). The variability of water potential in this shrub species is similar in magnitude to the results of Halvorson and Patten (1974), while the lower variability of these tree species is similar in magnitude to the results of Klikoff (1967) and Halvorson and Patten (1974). The data indicate the tree species of the hot desert, relative to the shrub species, experience a smaller degree of plant water stress, which may be due to: a) a greater root biomass; b) a greater horizontal and vertical root distribution; or c) year-round water absorption despite high soil temperatures of the summer and low soil temperatures of the winter.

All three species demonstrate increased water potentials during periods of soil water availability, and decreased water potentials during periods of drought. The shrub species is most responsive to rainfall, as evidenced by the significant increase in water status following the July and November rains. The midsummer July rain increased the soil water potentials (see Fig. 2), and plant water potentials increased 12 bars in *O. tesota* and 45 bars in *A. deltoidea*. The shrub species was the most responsive to the November rains, during which time the water potential increased 7 bars in *O. tesota* and 86 bars in *A. deltoidea*.

**Phenology**

The annual pattern of the different phenological stages demonstrated by the three plant species is presented in Figure 4. All of the plants have a period of deciduousness during the year, and the reproductive stages are limited to the months of March through July. Additionally, the reproductive stage of all three species occurs when the plant water potentials are in the range of -20 to -30 bars (see Fig. 3).

Plants of *A. deltoidea* are continuously in leaf during the interval from January to May and initiate leaf shedding as plant water potentials fall below -40 bars. Some leaves persist on the plants despite summer drought conditions, until becoming completely deciduous by mid-June. Following the July rains and increased plant water potentials, leaf production begins shortly thereafter. However, these leaves are short lived and are gradually shed until the plants are completely deciduous by mid-November. Leaf production initiated a second time in 1975 following the winter rains. The deciduous nature of *A. deltoidea* is regulated more by water stress than by temperature regime, as the leafless state occurred during periods of high and moderate air temperatures (see Table 2).

Plants of *C. microphyllum* demonstrated the longest deciduous state throughout 1975. Despite slowly increasing plant water potentials from March to May, the plants initiated leaf shedding during mid-April. The leafless state persisted throughout the remaining months of the year, except for the short-lived response to the July rains. The deciduous nature of *C. microphyllum* is also regulated by water stress, although this species is the most sensitive to water stress of the three species studied. Leaf production appears to occur whenever plant water potentials are greater than -10 to -15 bars.

Plants of *O. tesota* demonstrated the shortest deciduous state during 1975. The initiation of leaf shedding does not appear to be directly regulated by water stress, since the midsummer deciduousness occurred despite high plant water potentials. Moreover, this plant species had the highest water potentials throughout this midsummer period of deciduousness.

**Stomatal Resistance**

The annual patterns of stomatal diffusive resistances, specifically the minimum observed values for each sampling period, are presented in Figure 5. The data for January to mid-February are missing, since the diffusive porometers were not received until mid-February. Stomatal resistances of 50 sec/cm or greater were interpreted as the diffusive resistance to water vapor transfer arising from completely closed stomata.

The patterns of stomatal resistance for *A. deltoidea* and *O. tesota* appear to be inversely related to the variation of plant water potentials throughout 1975. Only preliminary information is available for *C. microphyllum*, which was deciduous throughout most of 1975. The lowest annual diffusive resistances measured for the three plant species were 1, 2 and 8 sec/cm for *A. deltoidea*, *O. tesota* and *C. microphyllum*, respectively. Throughout the interval from February to October, the stomatal resistance was consistently lower in plants of *A. deltoidea* than in plants of *O. tesota*. This relationship was reversed from October through mid-December, probably the result of a lower level of water stress in the tree species than in the shrub species. The stomatal resistances of both species increase during the
Figure 3. Top. Annual pattern of plant water potentials at the study area during 1975. The predawn water potentials are presented for *Ambrosia deltoidea* (dashed line), *Cercidium microphyllum* (solid line) and *Olneya tesota* (dotted line). Plant water potential in units of bars (A^3USZ02).

Figure 4. Bottom. Annual pattern of phenology for the three species during 1975. The phenological stages are presented for periods when the plant had leaves (horizontal bar), when the plant was deciduous (horizontal line) and when flowers and fruits were present (vertical line).

Figure 5. Annual pattern of stomatal diffusive resistance for the three species during 1975. The data of minimum observed stomatal resistances are presented for *Ambrosia deltoidea* (dashed line), *Cercidium microphyllum* (solid line) and *Olneya tesota* (dotted line). Stomatal diffusive resistance in units of seconds per centimeter (A^3USZ02).
two periods of increasing drought -- May to mid-June and August to mid-November. During the first drought period of summer, plants of *O. tesota* show a progressive increase in stomatal resistance, despite increasing plant water potentials. Such results may have been due to an effect of leaf age as the plants were progressively shedding leaves during this period and were deciduous by the end of June. During this same drought period, *A. deltoidea* also showed a progressive increase in stomatal resistance, although appearing to be less sensitive to low plant water potentials than the tree species. The shrub was capable of maintaining low diffusive resistances, 6 sec/cm, with concomitant predawn water potentials of -28 bars, and did not terminate gas exchange until water potentials had decreased to around -60 bars.

The same type of pattern occurred during the second drought period -- from August to mid-November. Minima stomatal resistances of 1 and 2 sec/cm were recorded in plants of *A. deltoidea* and *O. tesota*, while concomitant predawn water potentials were -54 and -23 bars. Plants of *O. tesota* maintained minima resistances near 10 sec/cm during periods of -30 bar water potentials. Plants of *A. deltoidea* demonstrated a progressive increase in minima resistances as long as the drought conditions persisted. Both plant species responded to the winter rains with decreasing minima diffusive resistances.

Photosynthesis

The patterns of photosynthesis rate during the interval from July to December are presented in Figure 6 (Fig. 6A for *A. deltoidea*, Fig. 6B for *O. tesota*). The measurement of photosynthesis by the short-time $^{14}$CO$_2$ method is assumed to measure the gross photosynthesis rate. Photosynthesis data for the January-to-July interval are missing, since the construction and shipment of the $^{14}$CO$_2$ porometry system was not complete until June 1975. Measurements of photosynthesis for the month of June were not reported due to a low, and very irregular, efficiency of leaf digestion using a wet-digestion technique of Shimshi (1969). Leaf material was subsequently combusted in an oxygen, in-vial system, yielding a higher efficiency of $^{14}$C recovery.

The maximum rates of $^{14}$CO$_2$ photosynthesis were higher in plants of *A. deltoidea* than in plants of *O. tesota* -- 21 and 10 mg CO$_2$·dm$^{-2}$·hr$^{-1}$, respectively. Also maximum values occurred at different times during the course of the year. The shrub species demonstrates a more marked response to rainfall, with enhanced rates of $^{14}$CO$_2$ assimilation following the July and November rains. However, higher rates of photosynthesis did not occur following the September rains when plant water potential increased to only -50 bars. The tree species demonstrates the highest

![Figure 6](image-url)
photosynthetic rate following the midsummer July rains and a small response occurred following the September rains. However, an apparent enhancement of photosynthesis rate did not occur following the winter rains of November and December, despite plant water potentials increasing during this period to approximately -20 bars.

The shrub and tree species differ in a second aspect of their annual pattern of photosynthesis, i.e., minimum rate values remain at 1 mg CO₂·dm⁻¹·hr⁻¹ in O. tesota while concurrent CO₂ uptake is virtually zero in A. deltoidea. This difference was most readily shown during the fall drought in the month of October. Following the reduction in plant water potential to -80 and -30 bars in A. deltoidea and O. tesota, respectively, concomitant minima diffusive resistances were 40 and 10 sec/cm. Photosynthesis in the tree species persists throughout the period of drought in response to a lower level of plant water stress.

Photosynthate Distribution

The monthly data for the distribution of ¹⁴C photosynthate in A. deltoidea, C. microphyllum and O. tesota are presented in Tables 3, 4 and 5, respectively. Seasonal photosynthesis rates of the different plant parts of each species are presented in Table 6. The terminology for the plant parts is as follows: Leaf = leaf and petiole material; Flower = all flower parts above and including the sepals; Fruit = fruit material in any stage of development; Stem 3° = distal segment of stem to which the leaf material is attached; Stem 2° = stem segment from which Stem 3° is attached; and Stem 1° = stem segment similar to Stem 2°, which was not initially exposed to ¹⁴CO₂. Throughout the course of each month, ¹⁴C photosynthate in the plant parts is depleted due to the combined action of respiration and translocation. The radioactivity appearing in segments of Stem 1° is assumed to be due to translocation only. The decrease in total radioactivity in leaf material and the concomitant increase in total radioactivity in flower, fruit and stem material during weeks 1 and 3 occur due to translocation of ¹⁴C photosynthate.

Table 3. Distribution of ¹⁴C photosynthate in plant parts in Ambrosia deltoidea¹

<table>
<thead>
<tr>
<th>Plant Part</th>
<th>APR</th>
<th>MAY</th>
<th>JUN</th>
<th>JUL</th>
<th>AUG</th>
<th>SEP</th>
<th>OCT</th>
<th>NOV</th>
<th>DEC</th>
</tr>
</thead>
<tbody>
<tr>
<td>Leaf</td>
<td>93</td>
<td>30</td>
<td>14</td>
<td>72</td>
<td>65</td>
<td>65</td>
<td>99</td>
<td>80</td>
<td>69</td>
</tr>
<tr>
<td>Flower</td>
<td>M</td>
<td>M</td>
<td>M</td>
<td>M</td>
<td>M</td>
<td>M</td>
<td>M</td>
<td>M</td>
<td>M</td>
</tr>
<tr>
<td>Fruit</td>
<td>1</td>
<td>33</td>
<td>43</td>
<td>17</td>
<td>M</td>
<td>M</td>
<td>M</td>
<td>M</td>
<td>M</td>
</tr>
<tr>
<td>Stem 3°</td>
<td>6</td>
<td>24</td>
<td>22</td>
<td>11</td>
<td>18</td>
<td>14</td>
<td>1</td>
<td>4</td>
<td>2</td>
</tr>
<tr>
<td>Stem 2°</td>
<td>T</td>
<td>10</td>
<td>16</td>
<td>T</td>
<td>11</td>
<td>11</td>
<td>T</td>
<td>4</td>
<td>8</td>
</tr>
<tr>
<td>Stem 1°</td>
<td>0</td>
<td>3</td>
<td>5</td>
<td>0</td>
<td>6</td>
<td>10</td>
<td>0</td>
<td>5</td>
<td>7</td>
</tr>
</tbody>
</table>

¹ in units of percent of total radioactivity
M = missing plant part
T = trace

Table 4. Distribution of ¹⁴C photosynthate in plant parts of Cercidium microphyllum¹

<table>
<thead>
<tr>
<th>Plant Part</th>
<th>APR</th>
<th>MAY</th>
<th>JUN</th>
<th>JUL</th>
<th>AUG</th>
<th>SEP</th>
<th>OCT</th>
<th>NOV</th>
<th>DEC</th>
</tr>
</thead>
<tbody>
<tr>
<td>Leaf</td>
<td>73</td>
<td>73</td>
<td>M</td>
<td>M</td>
<td>M</td>
<td>M</td>
<td>M</td>
<td>M</td>
<td>M</td>
</tr>
<tr>
<td>Flower</td>
<td>M</td>
<td>M</td>
<td>20</td>
<td>92</td>
<td>85</td>
<td>M</td>
<td>M</td>
<td>M</td>
<td>M</td>
</tr>
<tr>
<td>Fruit</td>
<td>M</td>
<td>M</td>
<td>47</td>
<td>92</td>
<td>80</td>
<td>52</td>
<td>43</td>
<td>47</td>
<td>M</td>
</tr>
<tr>
<td>Stem 3°</td>
<td>8</td>
<td>17</td>
<td>71</td>
<td>36</td>
<td>3</td>
<td>8</td>
<td>21</td>
<td>7</td>
<td>15</td>
</tr>
<tr>
<td>Stem 2°</td>
<td>19</td>
<td>6</td>
<td>22</td>
<td>44</td>
<td>4</td>
<td>5</td>
<td>11</td>
<td>1</td>
<td>5</td>
</tr>
<tr>
<td>Stem 1°</td>
<td>0</td>
<td>4</td>
<td>7</td>
<td>0</td>
<td>1</td>
<td>2</td>
<td>0</td>
<td>2</td>
<td>0</td>
</tr>
</tbody>
</table>

¹ in units of percent of total radioactivity
M = missing plant part
T = trace
Table 5. Distribution of \( ^{14} \text{C} \) photosynthate in plant parts of *Olneya tesota*.

<table>
<thead>
<tr>
<th>Plant Part</th>
<th>APR</th>
<th>MAY</th>
<th>JUN</th>
<th>JUL</th>
<th>AUG</th>
<th>SEP</th>
<th>OCT</th>
<th>NOV</th>
<th>DEC</th>
</tr>
</thead>
<tbody>
<tr>
<td>Leaf</td>
<td>99</td>
<td>99</td>
<td>93</td>
<td>95</td>
<td>97</td>
<td>94</td>
<td>87</td>
<td>97</td>
<td>75</td>
</tr>
<tr>
<td>Flower</td>
<td>M</td>
<td>M</td>
<td>M</td>
<td>M</td>
<td>M</td>
<td>M</td>
<td>M</td>
<td>M</td>
<td>M</td>
</tr>
<tr>
<td>Fruit</td>
<td>M</td>
<td>M</td>
<td>M</td>
<td>M</td>
<td>M</td>
<td>M</td>
<td>M</td>
<td>M</td>
<td>M</td>
</tr>
<tr>
<td>Stem 3°</td>
<td>1</td>
<td>2</td>
<td>3</td>
<td>2</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>Stem 2°</td>
<td>T</td>
<td>2</td>
<td>3</td>
<td>2</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Stem 1°</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

1 in units of percent of total radioactivity

\( \text{M} = \) missing plant part

\( \text{T} = \) trace

\( \text{a} = \) missing data

Table 6. Photosynthesis rates of the different plant parts.

<table>
<thead>
<tr>
<th>Species</th>
<th>Plant Part</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Ambrosia deltoidea</em></td>
<td>Leaf: 917, Flower: 497, Fruit: 43, Stem 3°: 1</td>
</tr>
<tr>
<td><em>Cercidium microphyllum</em></td>
<td>Leaf: 505, Flower: 190, Fruit: 139, Stem 3°: 114</td>
</tr>
<tr>
<td><em>Olneya tesota</em></td>
<td>Leaf: 695, Flower: 153, Fruit: 131, Stem 2°: 3</td>
</tr>
</tbody>
</table>

1 Mean week 0 photosynthesis rate from April through December 1975.

Photosynthesis rate expressed as nanocuries \( ^{14} \text{C} / \) g dry weight.

Leaf material of *C. microphyllum* is the main photosynthetic plant part, although the rate of stem \( ^{14} \text{CO}_2 \) assimilation is 50% of the magnitude of leaf photosynthesis (see Tables 4 and 6). Unlike the results with *A. deltoidea*, week 0 photosynthesis in Stem 2° material occurs from April to December and exceeds photosynthesis in Stem 3° material during April and May. The latter pattern is reversed throughout the remainder of the year, and photosynthesis of Stem 3° material exceeds the magnitude of photosynthesis in Stem 2° material. The floral bracts of *C. microphyllum* show significant week 0 photosynthesis during May and June, and are important sinks for photosynthate prior to and during fruit development. Fruit material is photosynthetically active during maturation occurring in June, and the magnitude of week 0 photosynthesis is 38% of the rate of leaf photosynthesis. Moreover, the time during which fruit material is present on plants of *C. microphyllum* is the longest of the three species, and may be due to the high rate of fruit photosynthesis in this species. Translocation of \( ^{14} \text{C} \) photosynthate into fruit material is the highest during June, when translocation of \( ^{14} \text{C} \) photosynthate into Stem 1° material is the lowest of the entire year. The translocation of photosynthate from Stem 3° material is reduced during the deciduous period from August to December, and is the lowest during October when plant water potentials were less than —30 bars.

Leaf material of *O. tesota* is the main photosynthetic plant part (see Tables 5 and 6), and thus is similar to the results with *A. deltoidea*. Total stem photosynthesis during week 0 is less than the rate measured in *C. microphyllum*, although the rate is 19% of the photosynthesis rate of *O. tesota* leaf material. Significant translocation of leaf \( ^{14} \text{C} \) photosynthate occurs during April and December, and is reduced during the summer and fall months. The magnitude of translocation into stem material is the lowest during June, concurrent with flowering and preceding both leaf shedding and fruit initiation. Floral bracts subtending the petals show a low level of photosynthesis, while fruit material is photosynthetically active. The magnitude of fruit photosynthesis is comparable to the rate of stem photosynthesis, and is 22% of the rate of leaf material photosynthesis.
LITERATURE CITED


