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# Plant Productivity and Nutrient Interrelationships of Perennials in the Mohave Desert

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# RESEARCH MEMORANDUM

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PLANT PRODUCTIVITY AND NUTRIENT
INTERRELATIONSHIPS OF PERENNIALS IN
THE MOHAVE DESERT

Samuel Bamberg, Project Leader
Arthur Wallace, Gale Kleinkopf
and Arthur Vollmer

# DESERT BIOME
U.S. INTERNATIONAL BIOLOGICAL PROGRAM

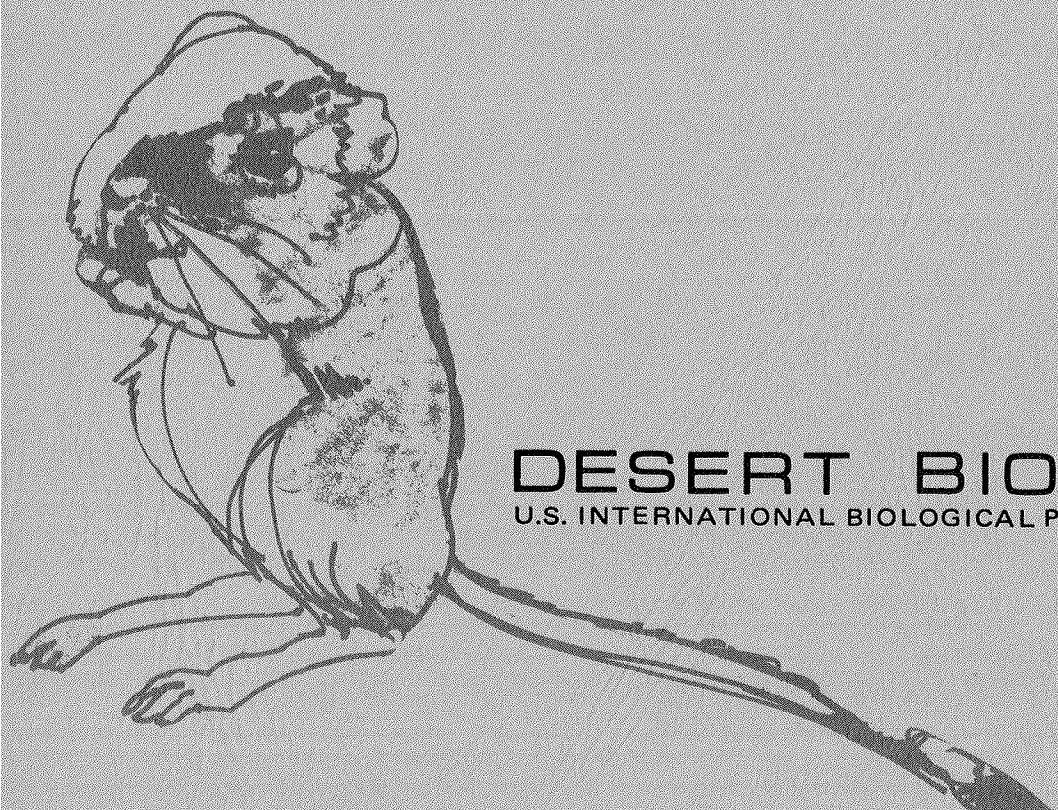1972 PROGRESS REPORT

PLANT PRODUCTIVITY AND NUTRIENT INTERRELATIONSHIPS OF PERENNIALS

IN THE MOHAVE DESERT

Samuel Bamberg, Project Leader

Arthur Wallace

Gale Kleinkopf

Arthur Vollmer

University of California, Los Angeles

MAY 1973

PART I


GAS EXCHANGE AND ASSIMILATE DISTRIBUTION
IN MOHAVE DESERT SHRUBS


2.3.1.3.-1

# ABSTRACT

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

Gas exchange rates were determined using a Siemens null-point gas exchange apparatus (Part I) and assimilate partitioning by incorporation of $^{14}CO_2$ and subsequent whole shrub excavation (see Parts II, III, IV). Tests were done on plants in Rock Valley under natural field conditions and at Mercury under natural and manipulated conditions.

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

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

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

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

# INTRODUCTION

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

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

# OBJECTIVES

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

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

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

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

2.3.1.3.-4

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

# METHODS

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

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

Gas exchange was measured using a modified null-point Siemens chamber (Koller, 1970). Use and description of this system are given in the 1971 Progress Report (Bamberg and Wallace, 1972). The system simultaneously measures $CO_2$ exchange and transpiration of enclosed plants while maintaining constant conditions of temperature, humidity and $CO_2$ concentration of circulating air in the chamber. The chamber also can be set to approximate ambient conditions. Transpiration is given in g $H_2O$/g dry wt/hr and photosynthesis and respiration in mg $CO_2$/g dry wt/hr (A3UBD01, A3UBD02).

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

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

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

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

# RESULTS AND DISCUSSION

## ROCK VALLEY (A3UTJ02, A3UTL08, A3UTJ09, A3UTJ12)

### Abiotic

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

### $CO_2$ exchange (A3UBD01, A3UBD02)

The basic pattern of diel $CO_2$ exchange of *A. dumosa* is illustrated in Figure 3 as a representative example. Uptake of $CO_2$ started at a relatively high rate and peaked between 0800 and 1200 hours. The rate of $CO_2$ uptake then tapered off until dusk. No midday depressions and subsequent late afternoon peaks, as reported by other workers (Strain, 1970; Lange et al., 1969), were observed. Respiration remained low throughout the night. The highest rates of $CO_2$ loss as respiration occurred in early evening and decreased gradually throughout the night.
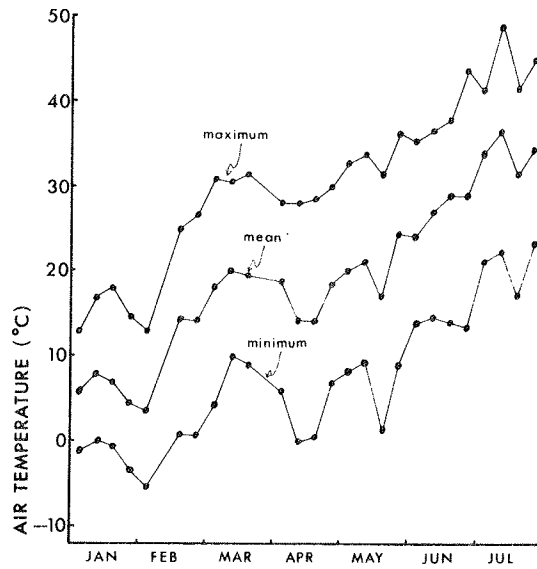
Figure 1.  Weekly maximum, minimum, and air temperature in Rock Valley for January –
           July, 1972.  Data from U.S. Weather Bureau Station in Rock Valley.
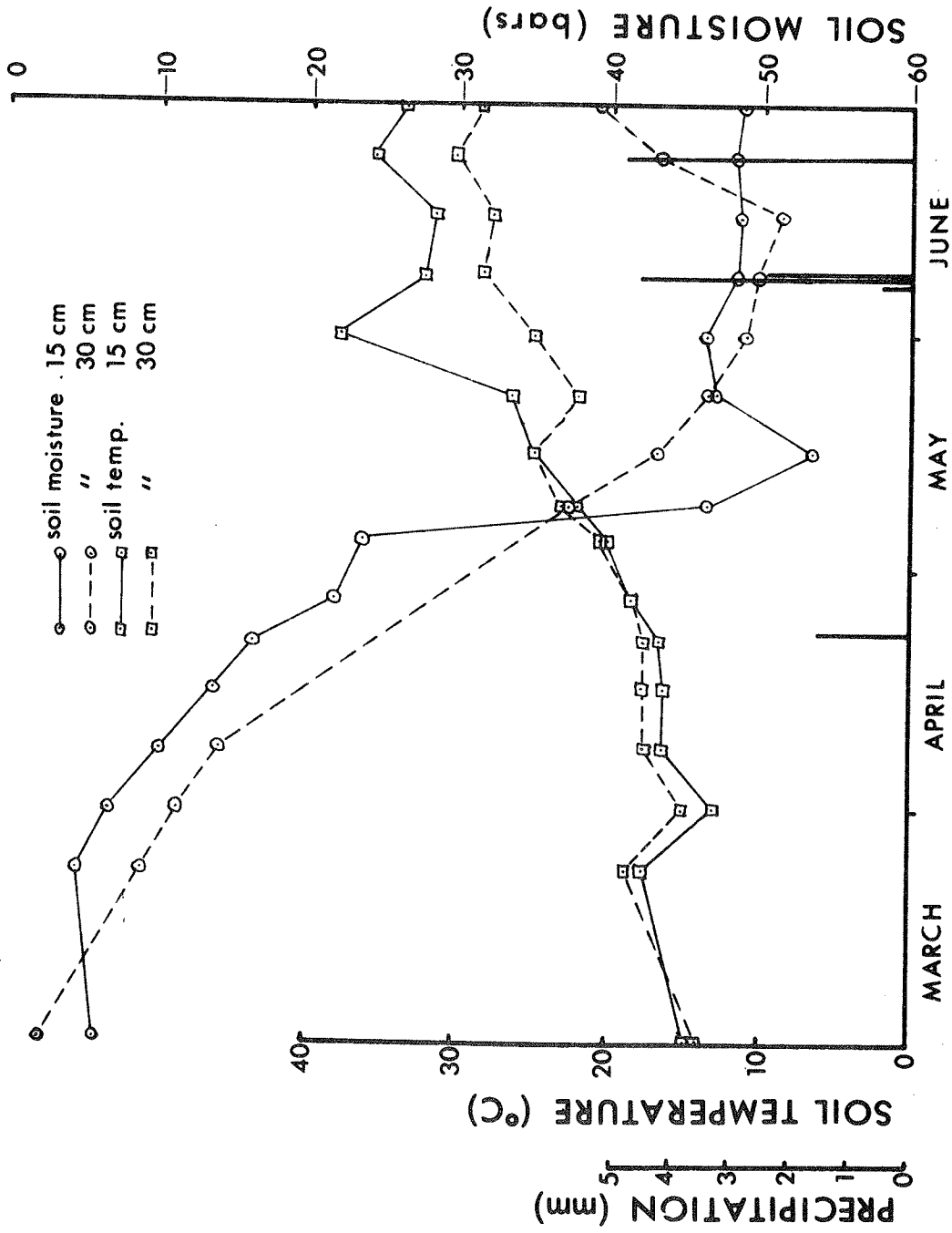
Figure 2. Precipitation and soil moistures and temperatures at 15 cm and 30 cm under-shrubs in Rock Valley. Data from Rock Valley IBP Station 1.
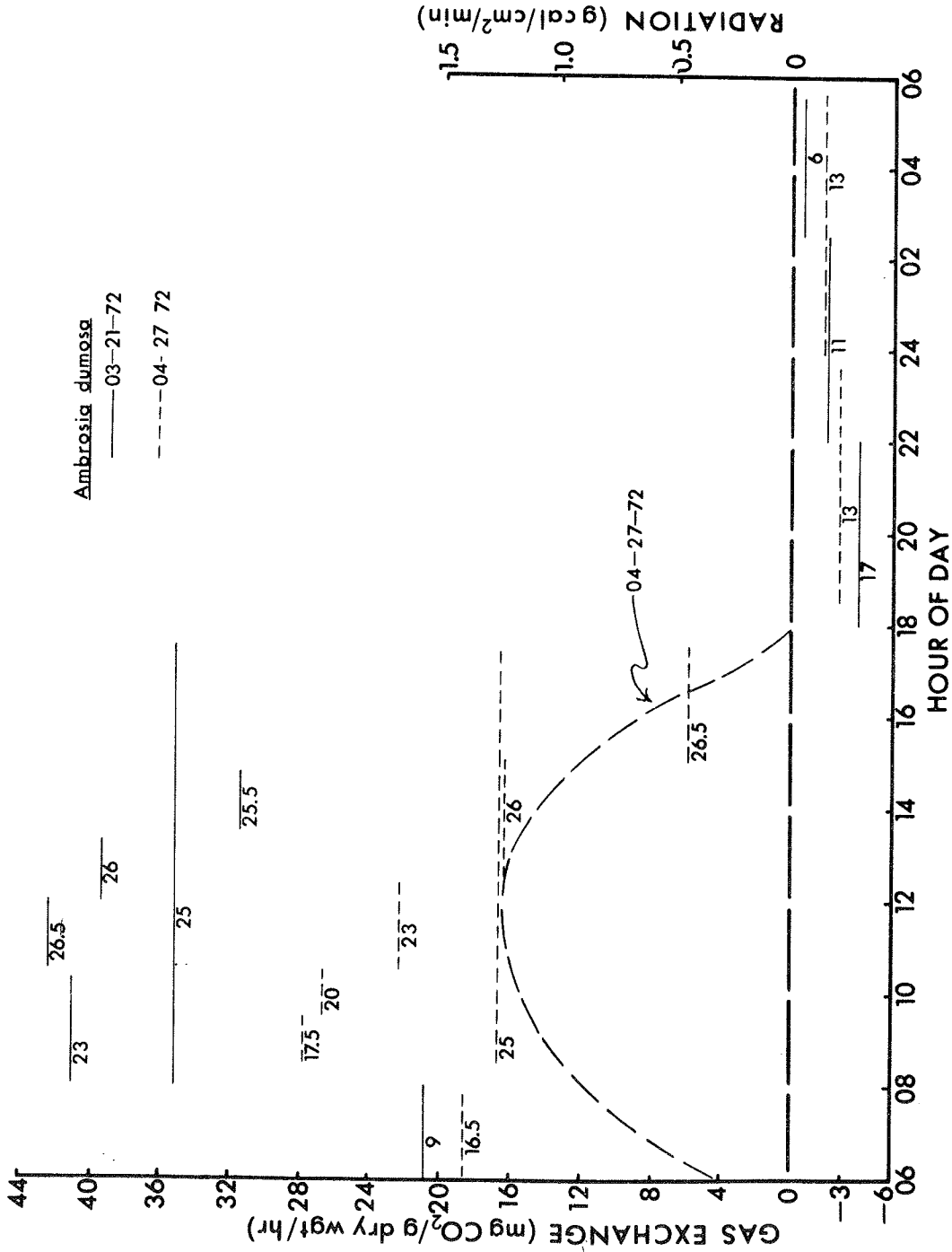
Figure 3. Daily rates of CO$_2$ exchange for *Ambrosia dumosa* in Rock Valley under ambient conditions. Horizontal lines indicate time period over which rates were determined; numbers represent mean temperature (C) during each interval. Radiation curve is indicated by a dashed line labled as 04-27-72.

Interspecific differences in net diurnal photosynthesis were noted within the same season (Table 1). Actual periods of time for daily $CO_2$ uptake or release are given in Table 2. Deciduous plant species (*A. dumosa*, *L. andersonii* and *L. pallidum*) had higher rates early in the season and maintained a higher rate than evergreen species until leaf abscission. Evergreen species under the field conditions of this season never attained high rates and by mid-June had only a small net photosynthesis. We assume no significant photosynthetic activity until rains in mid-August of 1972. Seasonal variation in net diurnal photosynthesis was exhibited by all species (Figures 4-8).

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

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

*mg $CO_2$/g dry wt/hr

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

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

*in mg $CO_2$/g dry wt/hr uptake or release.
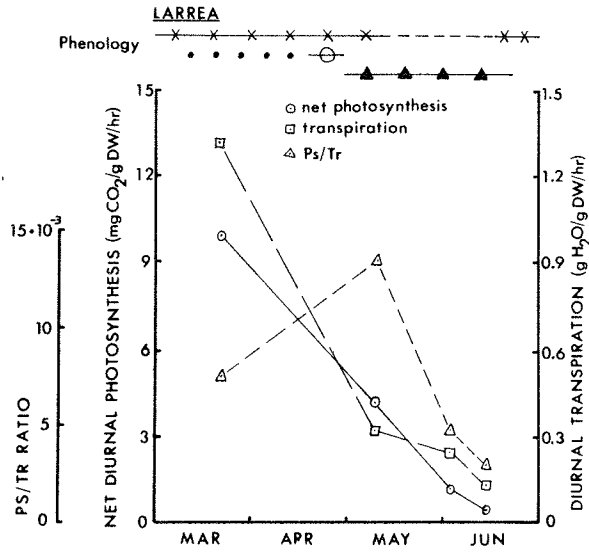
Figure 4. Seasonal changes in diurnal photosynthesis, transpiration and water efficiency use of *Larrea divaricata* in Rock Valley. Phenology symbols:
o = Bud     -O- = Flower     − − = Leaf Fall
✳ = Leaf     ▲ = Fruit     ⊣ = Dormancy
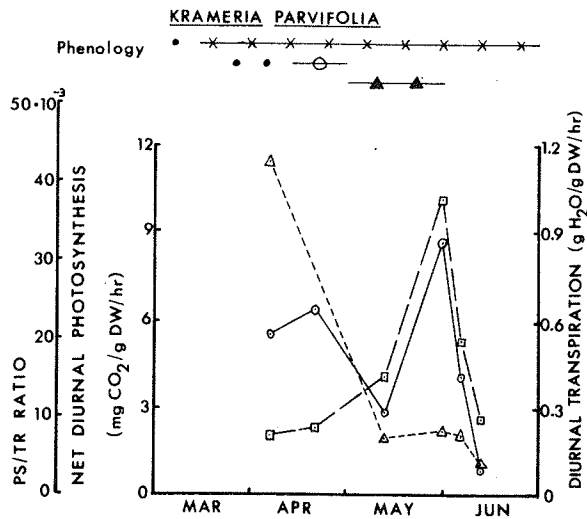


Figure 5. Seasonal changes in diurnal photosynthesis, transpiration and water use efficiency of *Krameria parvifolia* in Rock Valley. Graphic representations are as in Figure 4.
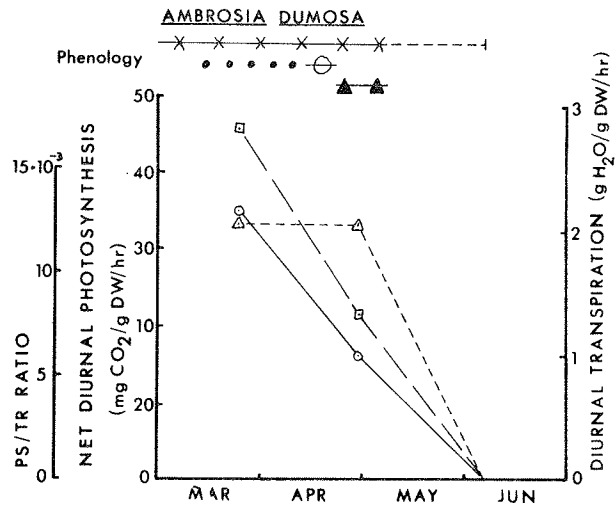
Figure 6. Seasonal changes in diurnal photosynthesis, transpiration and water use efficiency of *Ambrosia dumosa* in Rock Valley. Graphic representations are as in Figure 4.
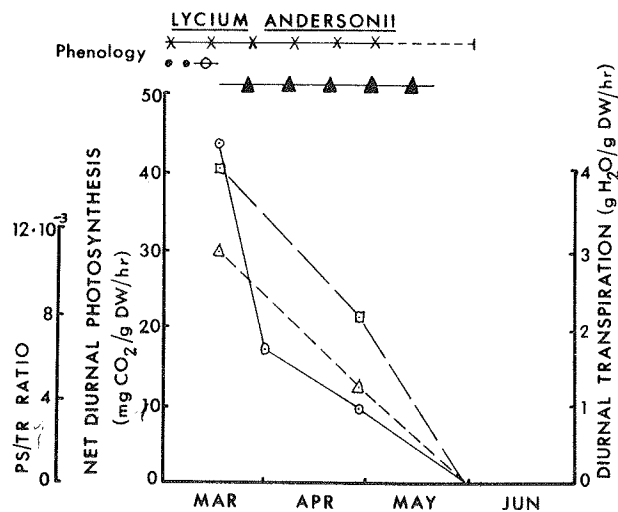


Figure 7. Seasonal changes in diurnal photosynthesis, transpiration and water use efficiency of *Lycium andersonii* in Rock Valley. Graphic representations are as in Figure 4.
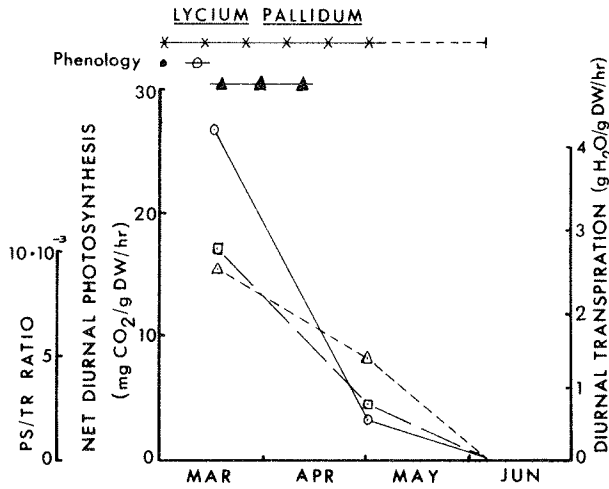
Figure 8.  Seasonal changes in diurnal photosynthesis, transpiration, and water use
efficiency of *Lycium pallidum* in Rock Valley.  Graphic representations
are as in Figure 4.

Figure 9 illustrates the effect of temperature on the $CO_2$ exchange of *L. andersonii*
at three times during the spring.  The responses of all plants subjected to temperature
manipulation at various times during the season are shown in Table 3.

During the study period, soil moisture as well as temperature affected the net
photosynthesis of desert shrubs.  Fig. 10 illustrates the effect of these factors on
the $CO_2$ exchange of *K. parvifolia*.  It exhibits a changing temperature optimum for maxi-
mum uptake and thermal compensation and a lowered net $CO_2$ exchange as soil moisture
tensions increase in late season.
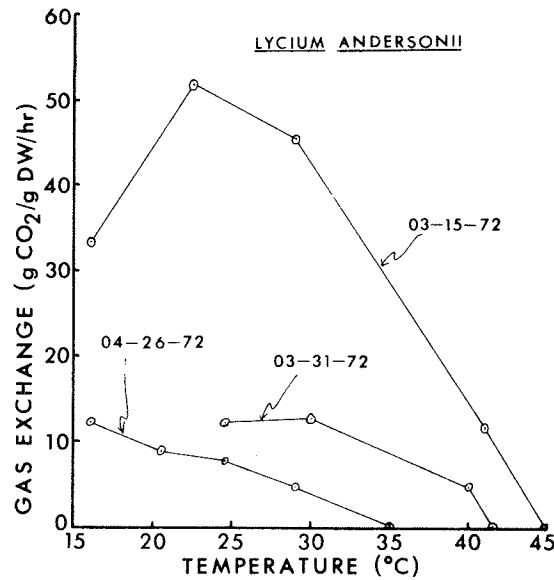
Figure 9. Effect of chamber temperature on daytime gas exchange ($CO_2$ uptake) of *Lycium andersonii* at different seasons in Rock Valley.

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

| Temperature ( C) | | 15 | 20 | 25 | 30 | 35 | 40 | 45 |
|---|---|---|---|---|---|---|---|---|
| Species | Date | | | mg $CO_2$/g dry wt/hr | | | | |
| *Larrea* | 3-21 | -- | 11.0 | 10.8 | 10.5 | -- | 3.3 | 0.0 |
| *divaricata* | 5-10 | 7.7 | 7.0 | 5.0 | 2.6 | -- | 0.0 | -- |
| | 6-02 | -- | -- | 1.9 | 1.2 | 0.6 | 0.0 | -1.0 |
| *Ambrosia* | 3-23 | 32.3 | -- | 38.8 | 33.1 | -- | 8.4 | -- |
| *dumosa* | 4-28 | 19.2 | -- | 20.6 | 15.8 | 5.4 | 0.5 | -- |
| *Krameria* | 5-12 | -- | 10.0 | 5.1 | 2.7 | 0.0 | -4.5 | -- |
| *parvifolia* | 5-31 | -- | -- | -- | 8.9 | 4.0 | 0.9 | -3.2 |
| | 6-06 | -- | 3.0 | 3.1 | 3.7 | 3.1 | 1.8 | 0.0 |
| | 6-15 | -- | 3.6 | 3.6 | 2.2 | 2.0 | 0.0 | -- |
| *Lycium* | 3-15 | 34.0 | 53.2 | 40.5 | 39.4 | -- | 10.7 | 0.0 |
| *andersonii* | 3-31 | -- | -- | 11.5 | 11.5 | -- | 4.5 | -12.2 |
| | 4-26 | 12.2 | 9.3 | 7.9 | 4.3 | 0.0 | 0.0 | -- |
| *Lycium* | 3-17 | 34.8 | 33.5 | 32.8 | 30.2 | -- | 12.0 | -- |
| *pallidum* | 5-03 | -- | -- | 10.3 | 3.9 | -- | 0.0 | -- |
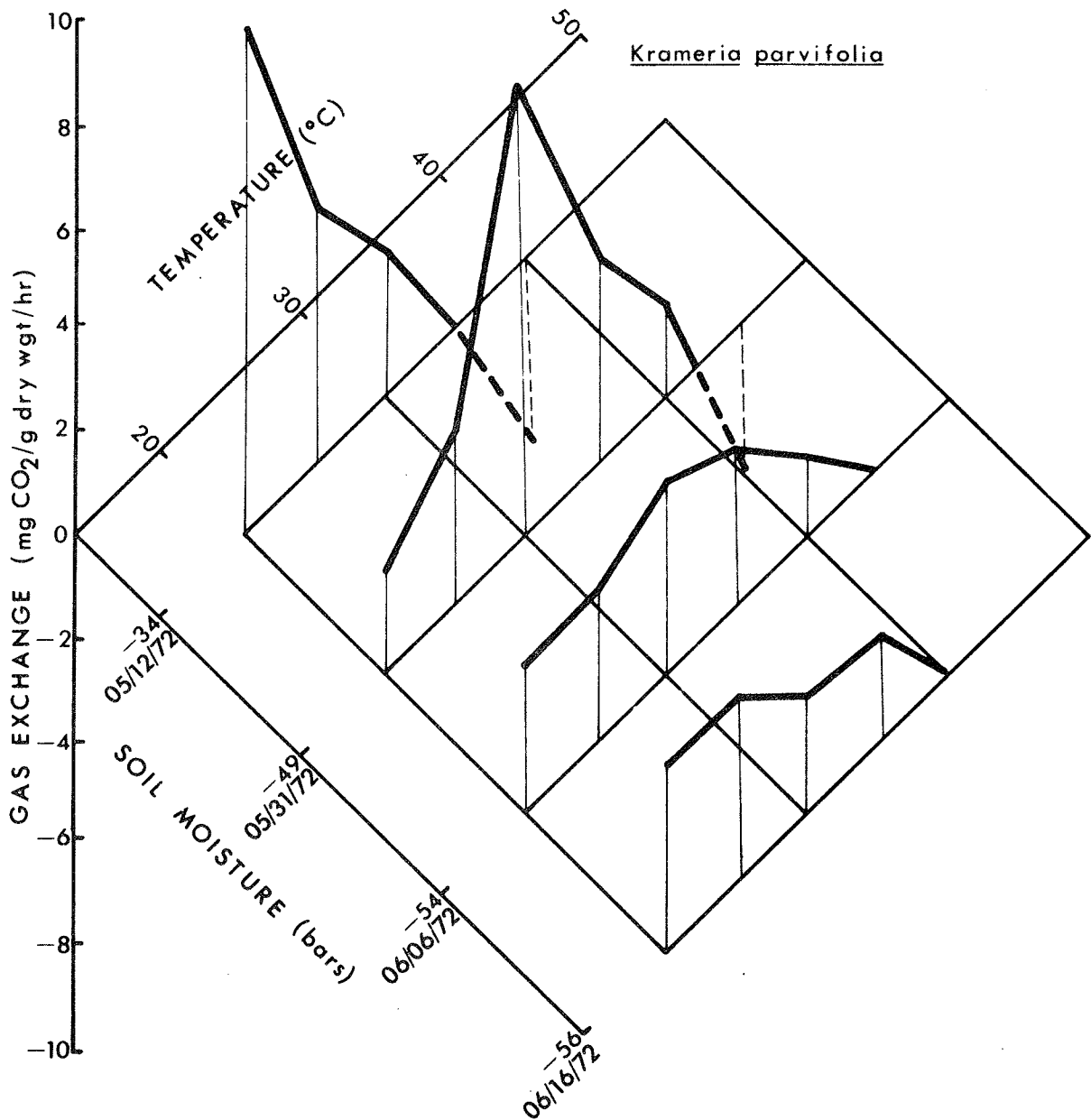
Figure 10. Gas exchange of *Krameria parvifolia* as related to soil moisture and chamber temperature. *Krameria* exhibits a definite shift in optimum $CO_2$ uptake toward a higher temperature in late spring as long as soil moisture is adequate (less than -50 bars). At higher soil moisture tensions the optimum net $CO_2$ uptake again shifts to below 25 C.

Water use (A3UBD01, A3UBD02)

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

Of the plants tested, the three deciduous species had linear relationship between temperature and transpiration rate when moisture was adequate. Transpiration increased as temperatures of the chamber were increased to the point where $CO_2$ uptake ceased. However, both *L. divaricata* and *K. parvifolia* (Table 4) restricted transpiration between 35 C and 45 C and transpired at slower rates than below 30 C or above 45 C. This is an evident adaptation to efficient gas exchange and water use at high summer temperatures.

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

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

| Temperature | ( C ) | 15 | 20 | 25 | 30 | 35 | 40 | 45 |
|---|---|---|---|---|---|---|---|---|
| Species | Date | | | g $H_2O$/g dry wt/hr | | | | |
| *Larrea* | 3-21 | 0.0 | -- | 1.4 | 2.5 | -- | 3.1 | 2.8 |
| *divaricata* | 5-10 | 0.0 | 0.5 | 0.6 | 0.6 | -- | 1.0 | -- |
| | 6-02 | -- | -- | 0.2 | 0.3 | 0.3 | 0.3 | 0.3 |
| *Krameria* | 5-12 | -- | 0.1 | 1.1 | 1.5 | 1.6 | 1.5 | -- |
| *parvifolia* | 5-31 | -- | -- | -- | 1.1 | 1.0 | 0.7 | 0.5 |
| | 6-06 | -- | 0.0 | 0.3 | 0.8 | 1.3 | 1.0 | 0.8 |
| | 6-15 | -- | 0.0 | 0.4 | 0.8 | 0.8 | 0.7 | -- |
| *Lycium* | 3-15 | 0.2 | 5.3 | 3.7 | 4.8 | -- | 8.3 | 9.4 |
| *andersonii* | 4-26 | -- | -- | 3.5 | 2.4 | 2.7 | 1.7 | -- |
| *Lycium* | 3-17 | -- | 2.2 | 4.0 | 5.2 | -- | 6.8 | -- |
| *pallidum* | 5-03 | -- | -- | 1.1 | 1.2 | -- | 1.8 | -- |

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

| Site/Date | Krameria parvifolia | Ambrosia dumosa | Larrea divaricata | Lycium andersonii | Lycium pallidum |
|---|---|---|---|---|---|
| Rock Valley | | | negative bars | | |
| 5-01-72 | 48 | 39 | 51 | 41 | 44 |
| 5-09-72 | 51 | 40 | 54 | 47 | 44 |
| 5-31-72 | 63 | | 56 | | |
| 6-01-72 | 62 | 47 | 63 | 52 | 51 |
| 6-06-72 | 65 | | | dormant | dormant |
| 6-12-72 | 66 | dormant | 63 | dormant | dormant |
| 6-19-72 | 72 | dormant | 65 | dormant | dormant |

Mercury

| Site/Date | Ambrosia dumosa $w^{1*}$ | Ambrosia dumosa $unw^2$ | Larrea divaricata w | Larrea divaricata unw |
|---|---|---|---|---|
| 7-14-72 | | | | 48 |
| 7-18-72 | | | 42 | |
| 7-19-72 | | | | 43 |
| 7-20-72 | | 35 | | |
| 7-24-72 | 27 | | | |
| 7-25-72 | | 43 | | |
| 7-26-72 | 43 | | | |
| 8-02-72 | | 43 | | |
| 8-04-72 | | | | 57 |
| 8-21-72 | | | 35 | |

* 1 = watered, 2 = unwatered

## MERCURY (A3UBD01)

### Abiotic

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

### $CO_2$ exchange

Diel $CO_2$ exchange for watered and unwatered L. divaricata and A. dumosa plants was determined (Figs. 13 - 14), and daily $CO_2$ uptake patterns were similar to those found in Rock Valley.

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

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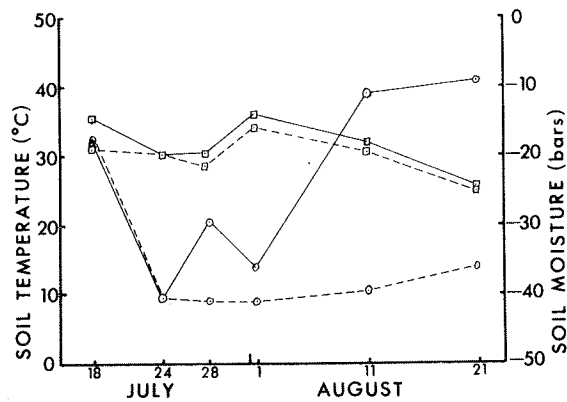


Figure 11. Soil temperature and moisture at 15 cm and 30 cm under shrubs in artificial
watered plots in Mercury for July and August, 1972. Graphic representations
as in Figure 2.
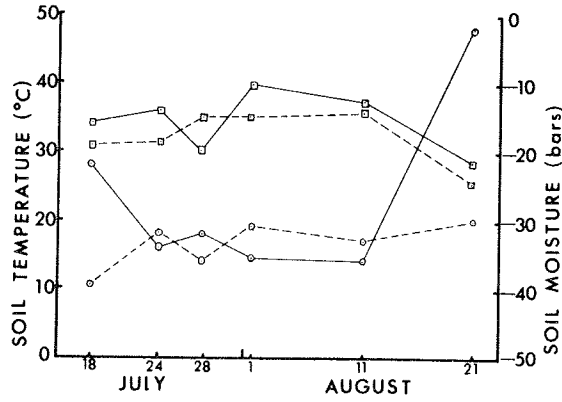
Figure 12.   Soil temperature and moisture at 15 cm and 30 cm under shrubs in naturally watered plots in Mercury for July and August, 1972.   Graphic representations as in Figure 2.
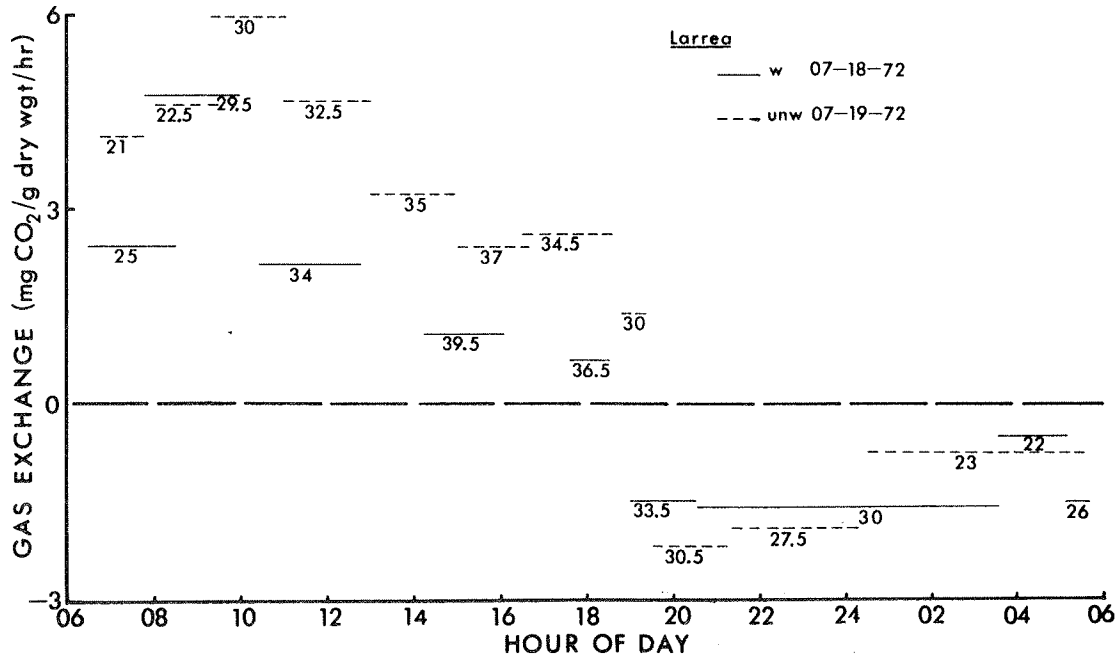


Figure 12.   Daily rates of $CO_2$ exchange for *Larrea divaricata* in Mercury under ambient conditions of light and temperature.   Graphic representations are as in Figure 3; w = watered, unw = unwatered.
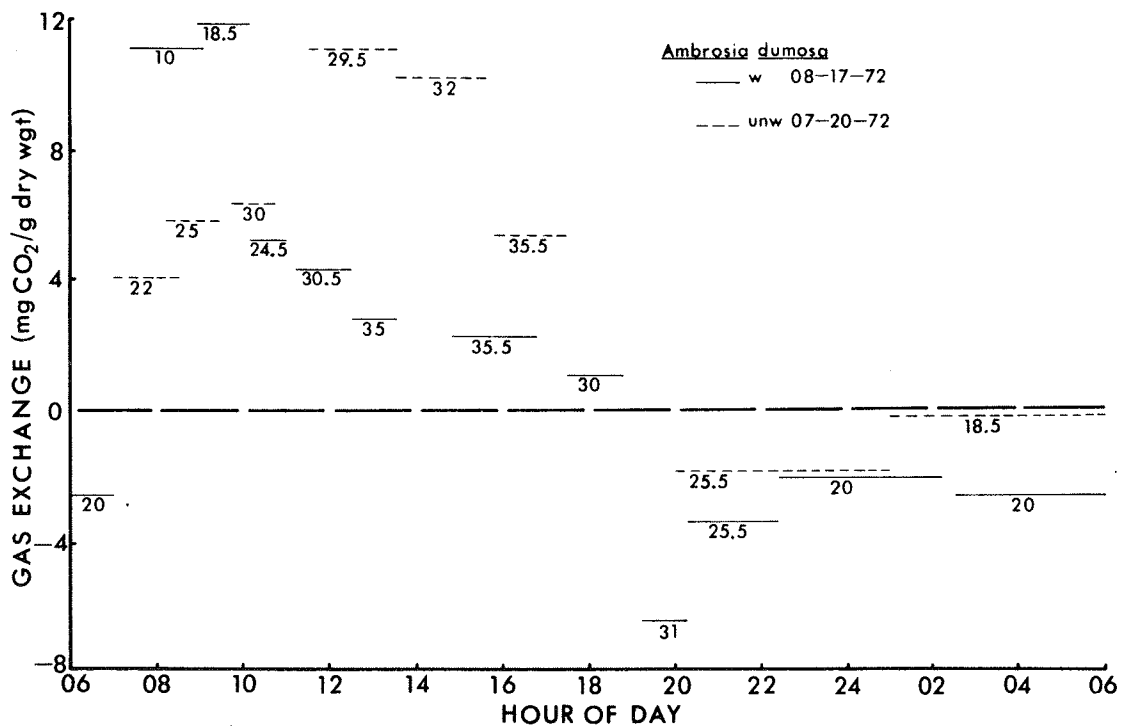
Figure 14. Daily rates of $CO_2$ exchange for *Ambrosia dumosa* in Mercury under ambient conditions of light and temperature. Graphic representations are as in Figures 3 and 13.

Table 6. Photosynthesis, transpiration and Ps/Tr ratios for *Larrea* and *Ambrosia* from watered and unwatered plots in Mercury, 1972    DSCODE——A3UBDO1

| Species/Date | Photosynthesis mg $CO_2$/g dry wt/hr | | Transpiration g $H_2O$/g dry wt/hr | | Ps/Tr | |
|---|---|---|---|---|---|---|
| Water status | w[1]* | unw[2] | w | unw | w | unw |
| *Larrea divaricata* | | | | | | |
| 7-17-72 | 2.0 | | 1.5 | | 1.3 | |
| 7-18-72 | 2.3 | | 1.5 | | 1.5 | |
| 7-19-72 | | 3.9 | | 1.9 | | 2.1 |
| 7-25-72 | | 5.0 | | 1.9 | | 2.6 |
| 7-27-72 | 4.6 | | 1.2 | | 3.8 | |
| 8-04-72 | | 1.5 | | 0.7 | | 2.2 |
| 8-08-72 | | 5.8 | | 1.5 | | 3.9 |
| 8-16-72 | 4.9 | | 3.0 | | 1.6 | |
| 8-21-72 | 6.7 | | 2.9 | | 2.3 | |
| 8-22-72 | 7.6 | | 4.4 | | 1.7 | |
| *Ambrosia dumosa* | | | | | | |
| 7-20-72 | | 9.6 | | 4.2 | | 2.3 |
| 7-24-72 | 11.2 | | 5.8 | | 1.9 | |
| 8-03-72 | | 2.3 | | 0.8 | | 2.8 |
| 8-09-72 | | 8.0 | | 6.9 | | 1.2 |
| 8-17-72 | 4.3 | | 3.7 | | 1.2 | |
| 8-23-72 | 4.6 | | 4.0 | | 1.1 | |

*1 = watered, 2 = unwatered

Water use

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

*A. dumosa* and *L. divaricata* in the plots at Mercury again showed the difference in transpiration between a drought-deciduous and an evergreen species when both are not under water stress at high summer temperatures (Fig. 15). *L. divaricata* had the same transpiration depression in the temperature range of 35 C to 45 C whereas *A. dumosa* had a linear relationship and rates of 4 to 11 g $H_2O$/g dry wt/hr transpired compared to 2 to 3 g $H_2O$ for *L. divaricata* at temperatures above 45 C.

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

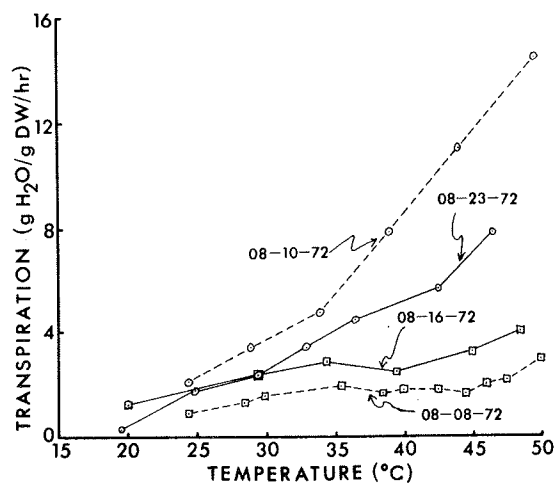| Temperature ( C ) | | 10 | 20 | 25 | 30 | 35 | 40 | 45 | 50 |
|---|---|---|---|---|---|---|---|---|---|
| Species/ water status | Date | | | mg $CO_2$/g dry wt/hr | | | | | |
| *Larrea divaricata* | | | | | | | | | |
| watered | 7-18 | -- | -- | -- | 5.0 | 2.3 | 1.1 | -- | -- |
| | 8-16 | 6.8 | 6.1 | -- | 5.1 | 4.7 | 2.2 | 0.0 | -1.7 |
| | 8-22 | -- | 10.5 | 10.6 | 9.1 | 5.1 | 2.8 | 0.3 | -- |
| unwatered | 7-25 | -- | -- | 8.1 | 7.0 | 3.2 | 0.4 | -0.7 | -- |
| | 8-04 | -- | -- | 2.9 | 2.0 | 1.3 | 0.5 | 0.1 | -- |
| | 8-08 | -- | -- | 6.0 | 6.0 | 5.1 | 4.2 | 3.3 | 2.4 |
| *Ambrosia dumosa* | | | | | | | | | |
| watered | 7-24 | -- | -- | -- | 13.0 | 9.7 | 9.4 | -- | -- |
| | 8-17 | 11.8 | 12.5 | 5.6 | 4.6 | 3.0 | 0.1 | -- | -- |
| | 8-23 | -- | 6.4 | 6.0 | 6.0 | 6.2 | 4.0 | 1.8 | -- |
| unwatered | 7-21 | -- | 4.3 | 6.2 | 6.7 | 4.6 | 1.9 | 0.0 | -- |
| | 8-03 | -- | 3.0 | 2.7 | 2.0 | -1.3 | -- | -- | -- |
| | 8-10 | -- | -- | 7.7 | 7.9 | 8.0 | 7.2 | 6.7 | -- |



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

2.3.1.3.-22

## Photosynthesis

*Seasonal:* Photosynthetic rates for the five shrub species exhibit seasonal differences which are characteristic for each species. The deciduous species, *A. dumosa*, *L. andersonii* and *L. pallidum*, which shed leaves in response to summer drought and winter cold, have high rates of net photosynthesis of up to 52 mg $CO_2$ fixed per g dry weight per hr in the morning, and a daily average of 40 mg $CO_2$/g dry wt/hr in early spring and decreasing until leaves are shed later in the season. *K. parvifolia* begins at a low rate in early spring and reaches its maximum rate in late spring or early summer. Since leaves are retained on *K. parvifolia* throughout the summer, presumably this species responds to moisture at any time from late spring until leaf fall in late October (Ackerman and Bamberg, 1972). *L. divaricata* and *K. parvifolia* had lower overall $CO_2$ uptake rates (only 10.1 mg $CO_2$/g dry wt/hr for *L. divaricata* and 8.9 mg $CO_2$ measured for *K. parvifolia*) than the three drought-deciduous species, but retained the ability to fix $CO_2$ longer at much higher soil moisture tensions through the early summer. These lower rates for leaf-retaining species may be anatomically related to their drought resistance in terms of diffusive resistance (El-Sharkawy and Hesketh, 1964).

In the watered plots at Mercury, *A. dumosa* retained leaves and both *A. dumosa* and *L. divaricata* photosynthesized throughout the whole summer. A comparison of *A. dumosa* and *L. divaricata* in the watered and unwatered plots at Mercury shows that under high temperatures of mid to late summer both species had low rates of up to 11.2 and 5.8 mg $CO_2$ fixed per hr, respectively, although earlier in the year at Rock Valley *A. dumosa* had rates of almost four times that of *L. divaricata*. *L. divaricata* had similar rates in the spring at Rock Valley and in the summer at Mercury.

*Daily cycle of gas exchange:* Gas exchange rates in all species climb during the early morning to high values between 8:00 and 9:00 and reach a maximum between 10:00 and 12:00. The rates then slowly decrease during the afternoon. These rates early in the season approximate the curve of incoming radiation over the day and net positive $CO_2$ uptake is dependent on direct sunlight, i.e., starting as soon as the sunlight hits the leaves and ceasing when the sun sets (Cunningham and Strain, 1969). At no time was a midday depression measured in either of the series tested at Rock Valley or Mercury. In Rock Valley, *L. divaricata* and *K. parvifolia* had, by mid-June, positive $CO_2$ uptake in the morning, decreasing to near zero in early afternoon as air temperature rose, but no second period of uptake in the late afternoon.

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

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

The other two species, *K. parvifolia* and *L. divaricata*, retain their leaves throughout the summer and also have net photosynthesis at higher plant tissue potentials.  In 1972 *K. parvifolia* had a small positive $CO_2$ uptake at -72 bars and *L. divaricata*  at -65 bars, under field conditions.  At soil moisture potentials above -40 bars, *L. divaricata* and *K. parvifolia* maintain a tissue water potential -10 to -15 bars higher than the other three species.  In Mercury, even on the plots with adequate soil moisture of less than -10 bars, *L. divaricata* had plant tissue potentials of not less than -35 bars.  Again, these high tissue potentials, even when soil moisture is high, are probably an adaptive response to high temperature; many such adaptive features of arid plants have been described or inferred in the literature (Bjorkman et al., 1972; Cunningham and Strain, 1969; Harrison et al., 1971; Wallace and Romney, 1972).

Effects of temperature on  photosynthesis under natural conditions are more difficult to assess.  In 1972 by mid-March, temperatures of 10 C to 30 C were favorable for $CO_2$ uptake.  Plants responded to the combined effects of temperature and moisture as the season progressed.  In 1972 a drying cycle and gradually increasing temperatures stopped plant activity in Rock Valley by mid-June, when maximum temperatures were around 35 C and soil moisture tensions exceeded -65 bars.  In contrast, during May and June, 1971, with temperatures not exceeding 32 C and soil moisture of around -30 bars, plants continued active $CO_2$ uptake until early July.

With adequate moisture both *L. divaricata* and *A. dumosa* continued active $CO_2$ uptake with air temperatures approaching 49 C in July 1972.  In the manipulated moisture plots at Mercury, as previously mentioned, the attempts to develop moisture stress in plants in the unwatered plot were interrupted by an early June rain of 2.1 cm.  This rain provided adequate moisture for both *L. divaricata* and *A. dumosa* throughout the period of June, July and early August, so that tissue water potentials were increasing but there was no measurable effect on gas exchange.  These results indicate that for moisture stress to affect gas exchange in these two plant species in the summer, a longer period of drought is needed.

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

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

In contrast to the temperature optima, upper thermal compensation points showed two trends related to moisture.  If moisture was adequate, i.e., less than -40 bars, plants continued to acclimatize to higher temperatures with the upper limit depending on the species and the previous temperature regime.  *L. divaricata* still showed a small net $CO_2$ uptake at 50 C (the limit of our control) when maximum temperatures the previous two weeks were 40 C to 50 C.  If moisture tensions increase, then all species except *K. parvifolia* show decreasing upper thermal compensation points.  *K. parvifolia* was able to acclimatize to higher temperatures even though plant tissue potentials were increasing.  The three drought-deciduous species lose their leaves as previously discussed, but also have been observed to abscise some leaves in hot, dry winds even if soil moisture is adequate (Wallace and Romney, 1972).  Lower thermal compensation could not be determined in summer since the heat loads prevented taking the chamber temperature below 10 C.  Relatively high rates of $CO_2$ uptake were observed at low temperatures (10 C) even in late summer (Table 7).  Plants are rarely subjected to daytime temperatures below 15 C from April through October.  Further tests earlier in the season will help determine if lower thermal compensation points are seasonally different.

## Water use

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

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

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

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

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

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

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

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

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

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

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

## Modelling

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

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

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

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

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

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

2.3.1.3.-28

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

PART II

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

2.3.1.3.-29

2.3.1.3.-30

# ABSTRACT

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

# INTRODUCTION

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

# OBJECTIVES

(See Part I, page  2.3.1.3.-3)

# METHODS

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

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

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

# RESULTS AND DISCUSSION

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

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

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

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

*Nonsignificance means that a normal curve may be followed
**Weighed mean or mean of the total root and total stem for all samples by species.  LSD values for this column were 7.0 (.05), 9.2 (.01)
+Corrected root/root + stem assuming that 15% of roots not recovered
++The 1.15 factor corrects for roots not recovered

# PART III

# USE OF $^{14}CO_2$ TO ESTIMATE ASSIMILATE TRANSPORT AND BELOW GROUND PRIMARY REPRODUCTIVITY AMONG EIGHT SPECIES OF PERENNIAL MOHAVE DESERT PLANTS

2.3.1.3.-34

# ABSTRACT

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

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

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

# INTRODUCTION

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

# OBJECTIVES

(See Part I, page  2.3.1.3.-3)

# METHODS

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

On June 11, 1971, about 900 hr, four *A. dumosa* plants in the northern Mohave Desert were covered with plastic bags and 125 µc $^{14}CO_2$ were released into each bag. Two hr later the bags were removed and leaf and stem samples were taken from each for determination, by Q-gas counting, the amount of $^{14}C$ fixed. The number of leaves on the samples collected was counted as well as those remaining on the plant, so that a reasonably accurate assessment of the total $^{14}C$ fixed by the plants could be made. Plants were excavated after 1 week, 2 months, and 5 months. Total $^{14}C$ present in small roots, large roots, small stems, large stems, and leaves was determined.

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

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

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

# RESULTS AND DISCUSSION

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

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

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

In the 5-month sample, 56% of the estimated $^{14}CO_2$ fixed was still present in the plant. In addition to respiration loss and loss from abscised leaves, there are losses due to flowering and fruiting and possibly also to herbivores. A portion of the 56% was present in new leaves which had grown in response to a late summer rain. At this

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

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

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

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

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

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

*Calculated by using the smallest plant as the base.
**±standard error of mean
†C.V. is coefficient of variation of $\dfrac{root}{root + stem}$ .
††Ref (Part II)

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

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

± is a standard deviation.
*cpm fixed at 50 mg counting wt.
**Original leaves had abscised and a new flush of leaves had grown in response to late summer rain, but some of these leaves had abscised also.

Table 11. Distribution of $^{14}C$ label of photosynthate in parts of field-grown plants, 1972    DSCODE—A3UBD03

| | A. dumosa | A. confertifolia | L. pallidum | L. andersonii | L. divaricata | A. canescens | E. lanata | E. nevadensis |
|---|---|---|---|---|---|---|---|---|
| n. | 4 | 4 | 4 | 2 | 2 | 2 | 3 | 3 |
| $^{14}C$ fixed in 2 hr $10^6$ cpm/plant | 3.637 | 4.411 | 4.127 | 3.297 | 1.046 | 4.558 | 4.488 | 1.643 |
| % remaining at sampling | 63.5 | 86.6 | 66.2 | 66.5 | 77.6 | 78.5 | 78.3 | 90.4 |
| **g dry wt/plant at sampling time** | | | | | | | | |
| Leaves | 10.9 | 30.1 | 1.6 | 0.0 | 6.4 | 39.4 | 13.4 | – |
| Large stems | 48.5 | 15.8 | 18.7 | 22.3 | 3.2 | 39.7 | 11.8 | – |
| Small stems | 59.8 | 16.4 | 16.1 | 31.5 | 3.0 | 38.7 | 22.9 | – |
| Roots | 118.4 | 14.7 | 62.2 | 25.0 | 4.2 | 29.5 | 9.7 | 82.4 |
| **$C_{14}$ in plant parts at sampling ($10^6$ cpm/plant)** | | | | | | | | |
| Leaves | 0.50 | 2.41 | 0.11 | 0.0 | 0.36 | 1.79 | 0.79 | – |
| Stems | 1.24 | 1.24 | 1.70 | 1.76 | 0.34 | 1.39 | 2.48 | 1.24 |
| Roots | 0.56 | 0.173 | 0.92 | 0.43 | 0.11 | 0.40 | 0.24 | 0.25 |
| **Final distribution of $^{14}C$ in stems and roots (%)** | | | | | | | | |
| Large stem | 20.3 | 19.7 | 23.3 | 17.4 | 26.5 | 38.9 | 15.3 | 16.2 |
| Small stem | 48.7 | 68.0 | 41.6 | 63.0 | 48.7 | 38.8 | 75.9 | 67.1 |
| Large root | 19.7 | 7.2 | 23.3 | 11.0 | 12.2 | 13.4 | 4.8 | 7.7 |
| Small root | 11.3 | 5.1 | 11.8 | 8.6 | 12.6 | 8.9 | 4.0 | 9.0 |
| Total | 100.0 | 100.0 | 100.0 | 100.0 | 100.0 | 100.0 | 100.0 | 100.0 |
| $^{14}C$ stem/root (ratio) | 2.23 | 7.13 | 1.84 | 4.10 | 3.03 | 3.48 | 10.36 | 4.99 |
| **Percentage of original fixed $C_{14}$ in roots on stem*** | | | | | | | | |
| Stem | 34.2 | 28.1 | 41.2 | 53.4 | 32.5 | 30.5 | 55.3 | 75.5 |
| Roots | 15.4 | 3.9 | 22.3 | 13.0 | 10.5 | 8.8 | 5.3 | 15.2 |

*Correlation coefficient $^{14}C$ in roots X $\frac{root}{root + stem}$ in field = +0.84.

PART IV

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

2.3.1.3.-42

# ABSTRACT

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

# INTRODUCTION

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

# OBJECTIVES
(See Part I, Page    )

# METHODS

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

The excavations were made by hand shovel, and roots were separated by 10 cm depth increments. Individual roots were followed as far as possible and often 1 to 2 $m^3$ of soil was removed in the excavation of a single root system. Roots were separated into those larger or smaller than 2 mm diameter. All roots were washed and dry weights determined.

# RESULTS AND DISCUSSION

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

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

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

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

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

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

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

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

Table 12. (Continued)

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

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

# EXPECTATIONS

2.3.1.3.-48

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

## Gas exchange

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

## Assimilate distribution

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

## Diffusive resistance

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

## Plant water status

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

## Nutrient distribution

Data available will be processed to show distribution among plant parts and relation-ships to phenological events.

## Respiration

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

# ACKNOWLEDGEMENTS

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