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Gas Exchange, Translocation and Root Growth of Cold Desert Plants

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IBP

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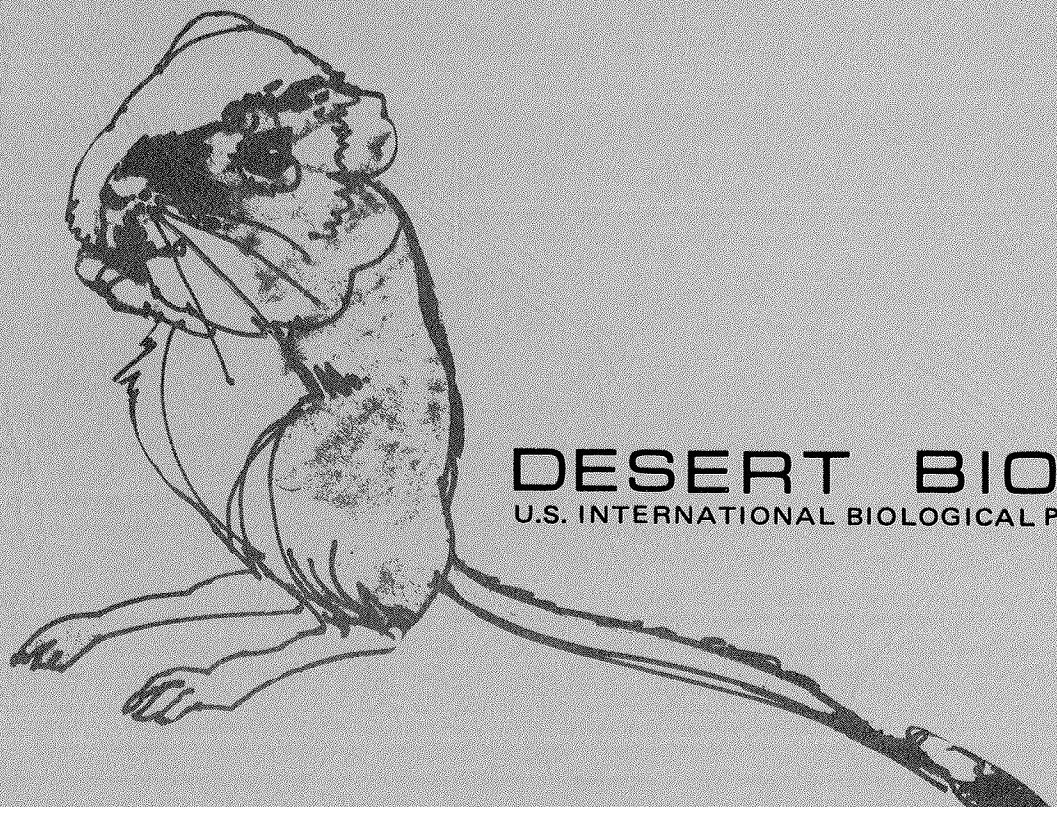

DESERT BIOME
U.S. INTERNATIONAL BIOLOGICAL PROGRAM

1972 PROGRESS REPORT

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ABSTRACT

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

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

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

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

Pulse labeling with $^{14}CO_2$ was assessed as a technique for determination of root growth rates in undisturbed field conditions. This was only moderately successful in the field for these Great Basin shrub species.

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

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

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

INTRODUCTION

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

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

OBJECTIVES

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

During 1972 our specific objectives were:

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

METHODS

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

A brief summary of these methods follows:

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

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

To obtain an atmosphere of 2.0% oxygen, bottles of compressed nitrogen, oxygen and CO_2 in nitrogen were mixed with a gas mixing pump to simulate the artificial atmosphere. Water vapor concentrations, temperature and irradiation were held constant for these comparative determinations of net photosynthetic rates in low and normal oxygen concentrations.

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

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

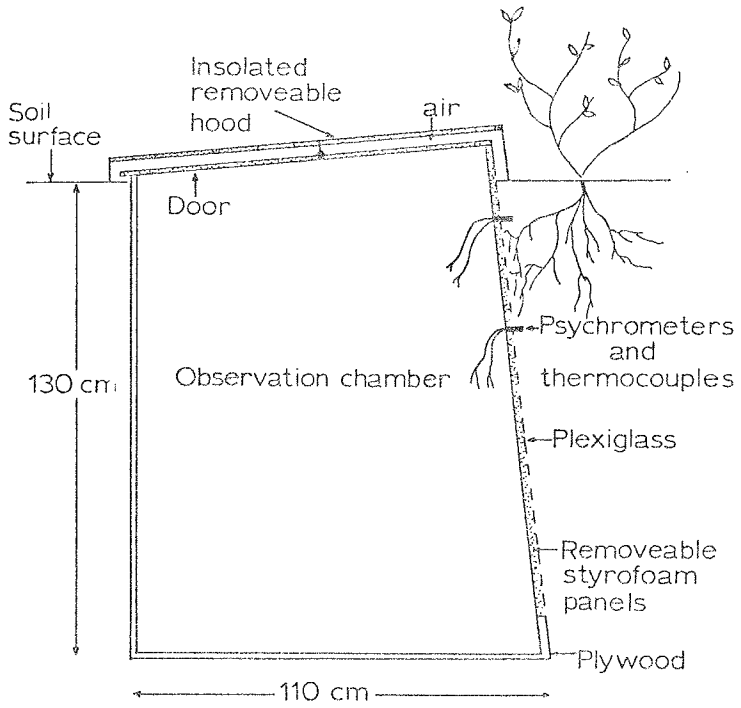


Diagram 1. Diagram of soil-root observation chambers.

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

To determine root growth rates of individual roots in an undisturbed soil environment, a pulse labeling technique was attempted. This technique was described by Wardlaw (1969) for grass roots. This technique involved the administration of $^{14}CO_2$ to leaves of the plant for two short periods of time with an intervening interval of at least several weeks between

the pulses of $^{14}CO_2$. This technique was applied to several plants in the laboratory and also in a few field trials. Labeling was carried out by evolving $^{14}CO_2$ from labeled bicarbonate and exposing shoots of the plant to approximately 0.3 mc for one hr in a plastic cuvette. The plant was then excavated after a few days or several weeks using a water stream to carefully remove the root system, keeping it as intact as possible. Autoradiography was used to determine the qualitative distribution of labeled carbon in the root system.

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

Use of radioactive carbon was tested as a medium for analyzing translocation of photoassimilates and root productivity. Labeling was carried out by exposing the plants to $^{14}CO_2$ (0.1 mc per plant) in a plexiglass chamber for approximately three hours. Seven days following this exposure to $^{14}CO_2$ a major branch of each plant was harvested and immediately chilled to arrest respiration. An 8-cm diameter orchard auger was used to extract a soil-root core in the vicinity of each plant. This core was separated into two increments, 0-30 cm and 30-60 cm.

Harvested plant samples were separated manually into branches, leaves, flowers, etc. (see Figure 18 in the Results section, Figures 19 and 20 in the Discussion and Tables 1, 2, and 3 in the Discussion for enumeration of plant parts). Roots were passed through a sieve using a water stream to remove adhering soil particles and then floated on water for separation of "living" from "dead" roots. This assessment as to living or dead was based only on color and physical appearance. "Live" roots tend to be white to cream in color and quite elastic as opposed to the brittle and dark-colored "dead" roots. This has been substantiated to a limited degree by observation of autoradiographs of labeled intact roots. Detailed separation of living from dead roots based on microtechniques or autoradiograms is not feasible on the sampling scale required for this study. Following the separation of plant parts to different segments and size classes, the plant samples were dried for 48 hr at 60 C. Plant tissues with moderate to low fiber content were ground in a mortar. A dry in-vial combustion procedure was used as a rapid, convenient method of combustion and allowing accurate determinations of $^{14}CO_2$ from the plant samples.

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

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

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

RESULTS

Morphology and phenology of *Artemisia tridentata*.

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

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

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

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

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

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

Water potential of *Artemisia tridentata*

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

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

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

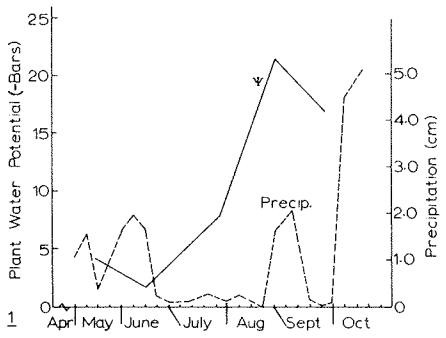


Figure 1. Seasonal pattern of precipitation and *Artemisia tridentata* plant water stress through a growing season at Green Canyon. Water stress values are means of ten to fifteen plants sampled every month.

Gas exchange of *Artemisia tridentata*

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

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

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

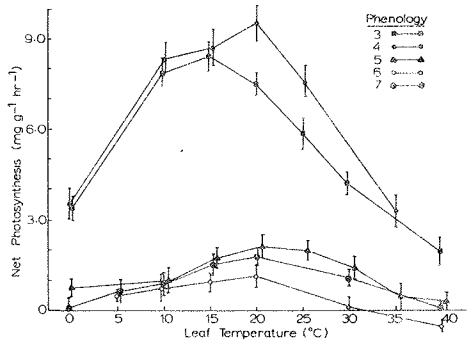


Figure 2. Net photosynthesis of *Artemisia tridentata* at five phenological stages through a growing season under conditions of constant irradiation (1150 microeinsteins m^{-2} sec^{-1}) and varying leaf temperatures. Values are means of measurements of four to six plants, shown with ± one standard deviation.

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

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

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

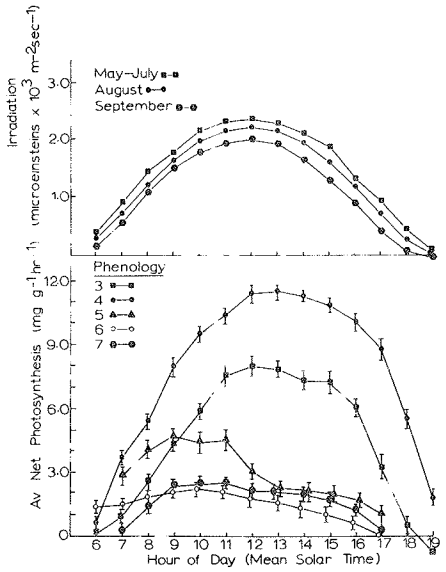


Figure 3. Net photosynthesis of *Artemisia tridentata* at five phenological stages during the course of a growing season under conditions of constant temperature (20 C) and irradiation varying through the course of a day. Gas exchange values are means of measurements of four to six plants, shown $\pm$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

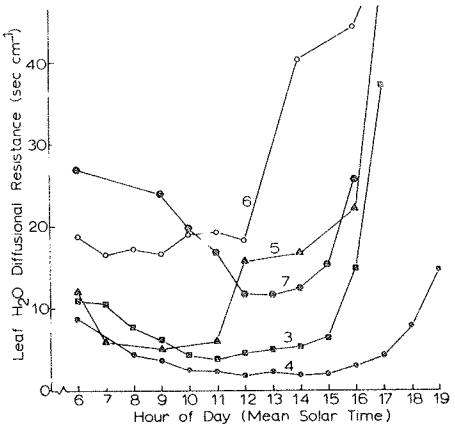


Figure 4. Leaf water vapor diffusional resistance, $r_a + r_s$, of *Artemisia tridentata* at five phenological stages during the course of a growing season under conditions of constant temperature (20 C) and varying irradiation through the course of a day.

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

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

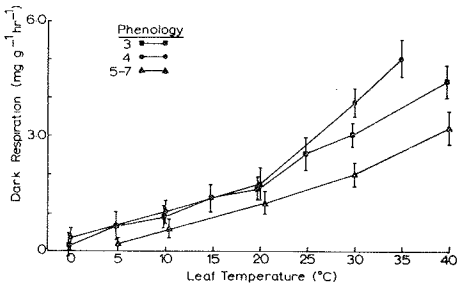


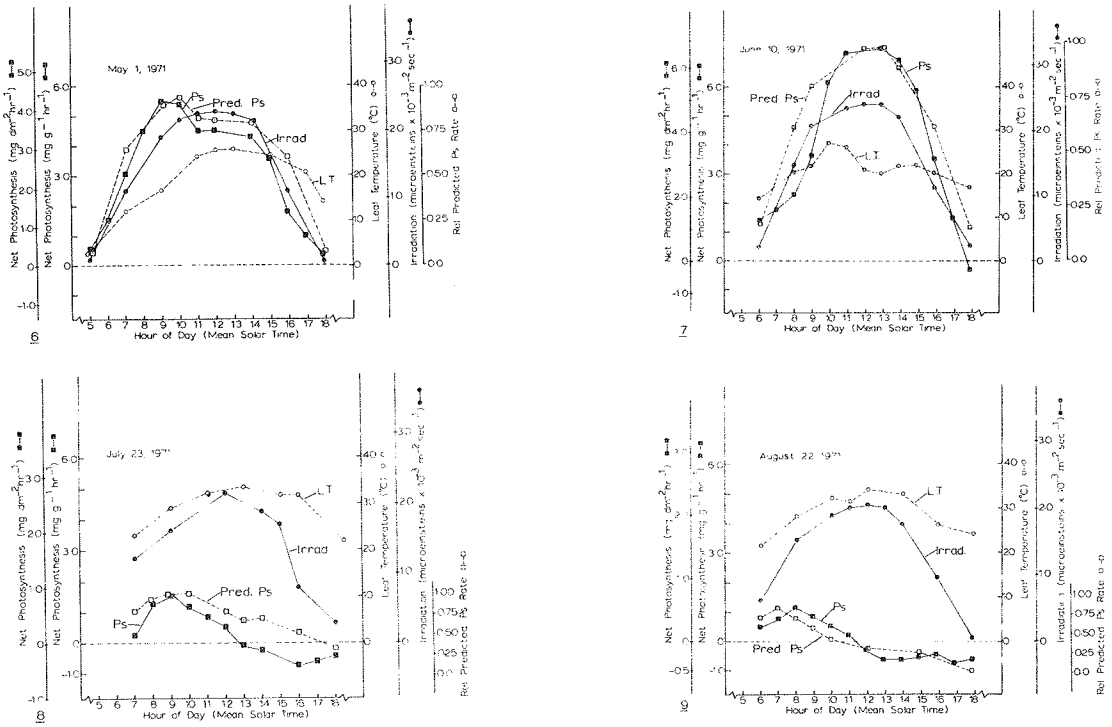
Figure 5. Dark respiration of *Artemisia tridentata* at various phenological stages through the course of a growing season under conditions of varying temperature. Values are means of measurements of four to six plants, shown with ± one standard deviation.

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

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

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

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



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

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

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

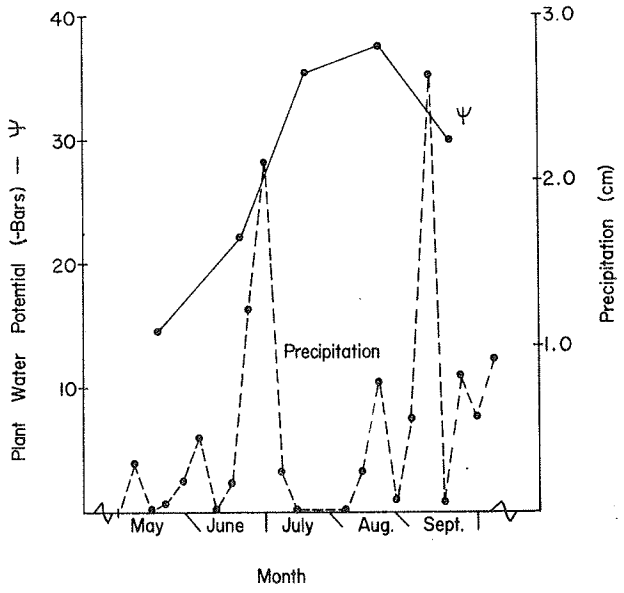


Figure 10. Precipitation and plant water potential of *Gutierrezia sarothrae* as measured by pressure bomb in 1972.

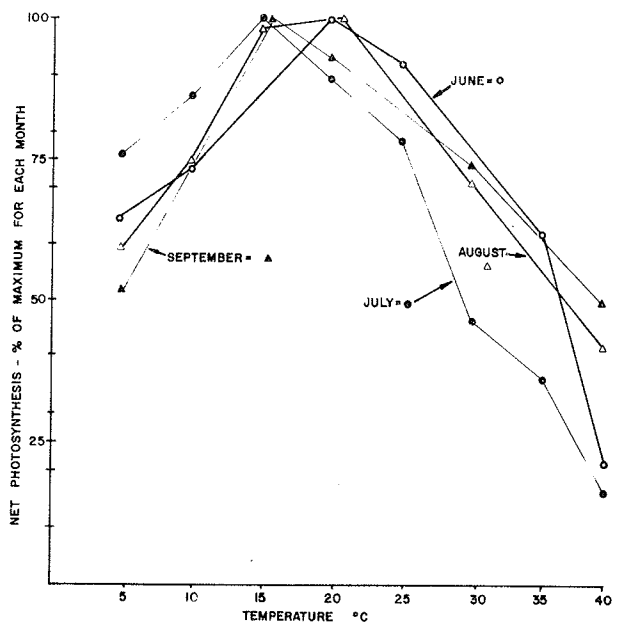


Figure 11. Net photosynthesis of *Gutierrezia sarothrae* as a function of leaf temperature and constant irradiation intensities at different times of the season in 1972.

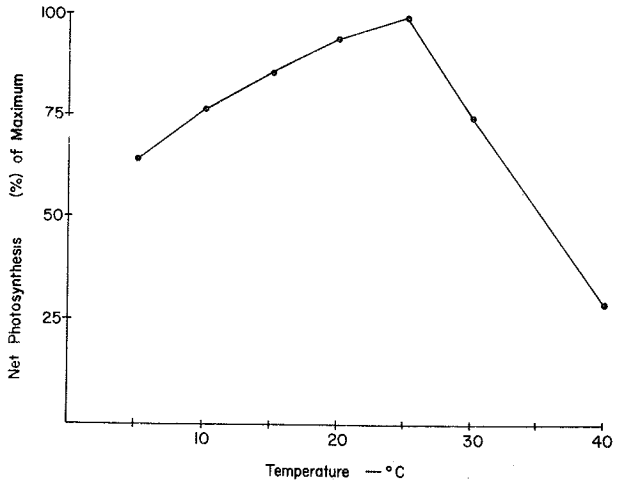


Figure 12. Net photosynthesis of *Agropyron spicatum* as a function of leaf temperature and constant irradiation intensities in June, 1972.

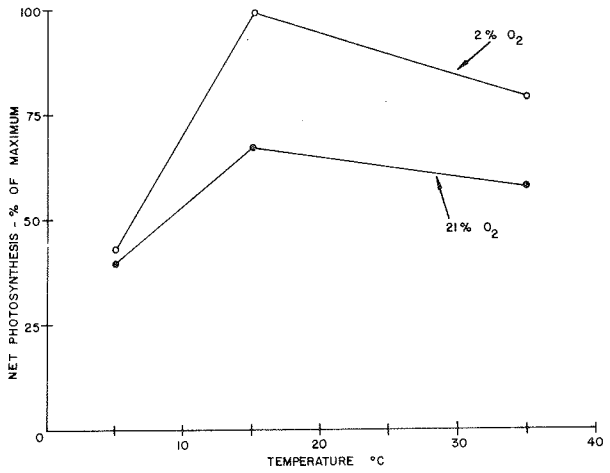


Figure 13. Net photosynthesis of *Gutierrezia sarothrae* as a function of leaf temperature at two levels of oxygen concentration. All other environmental factors were held constant.

Soil Root Observation Chambers

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

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

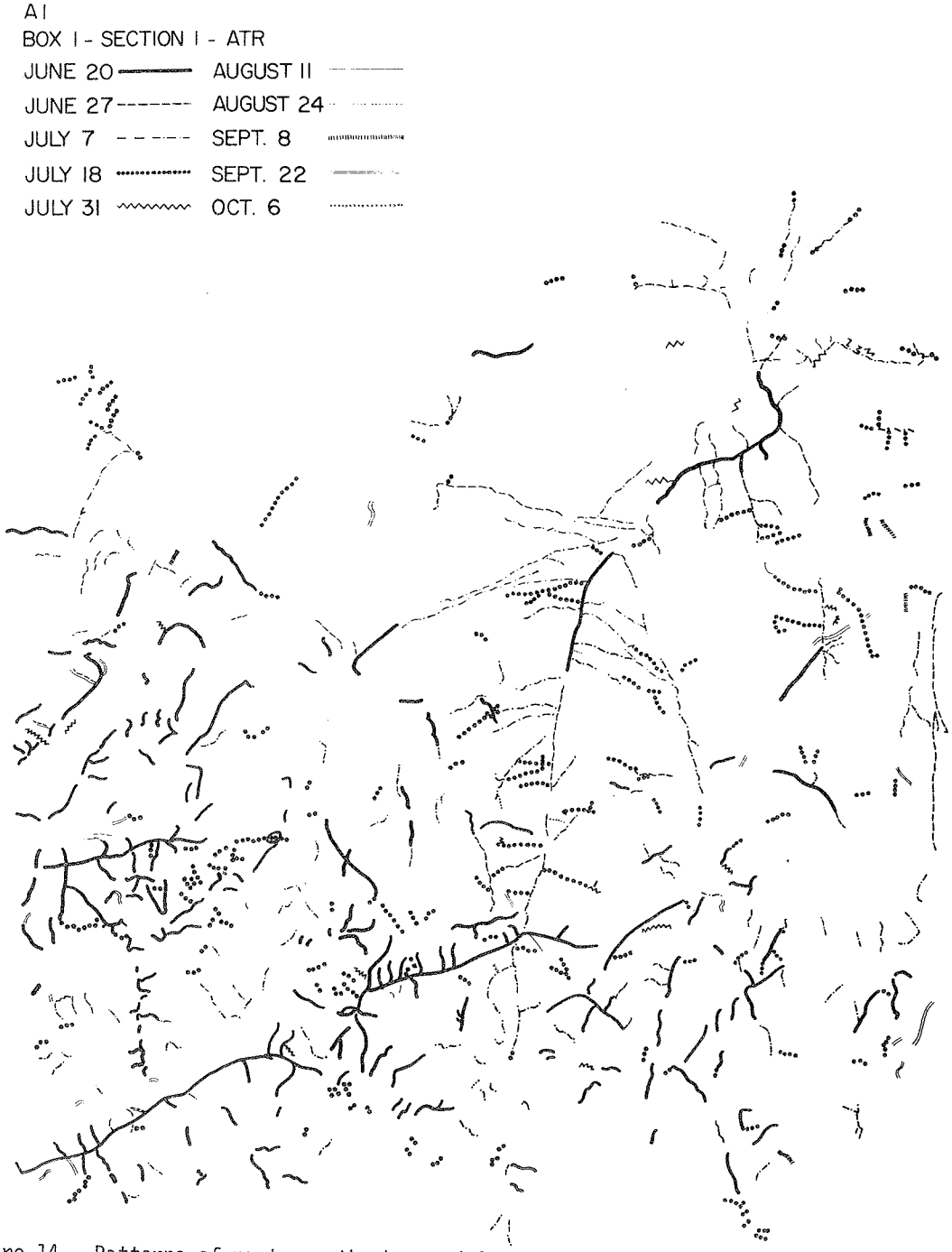


Figure 14. Patterns of root growth observed in one chamber during the 1972 season in a pure stand of *Atriplex confertifolia*.

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

Pattern of root development in *Artemisia tridentata*

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

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

Root growth of *Atriplex* as measured by pulse labeling

The goals of this study were to determine the applicability of the pulse labeling technique to estimates of growth of roots of desert shrubs. Preliminary applications of this technique to corn roots in the laboratory proved successful as described by Wardlaw (1969) for *Lolium*. Since radioactive carbon is permanently incorporated in cellulose of cell walls, among other compounds, the concentration of radioactive carbon will accumulate in that portion of the root where cellulose synthesis took place subsequent to incorporation of $^{14}CO_2$ in photosynthesis. On an autoradiogram this location of accumulated radioactive carbon would appear as a particularly dark band or region on the root system. The interval between these dark bands would indicate the amount of root growth which had taken place between the pulses of $^{14}CO_2$ taken up in the plant photosynthesis.

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

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

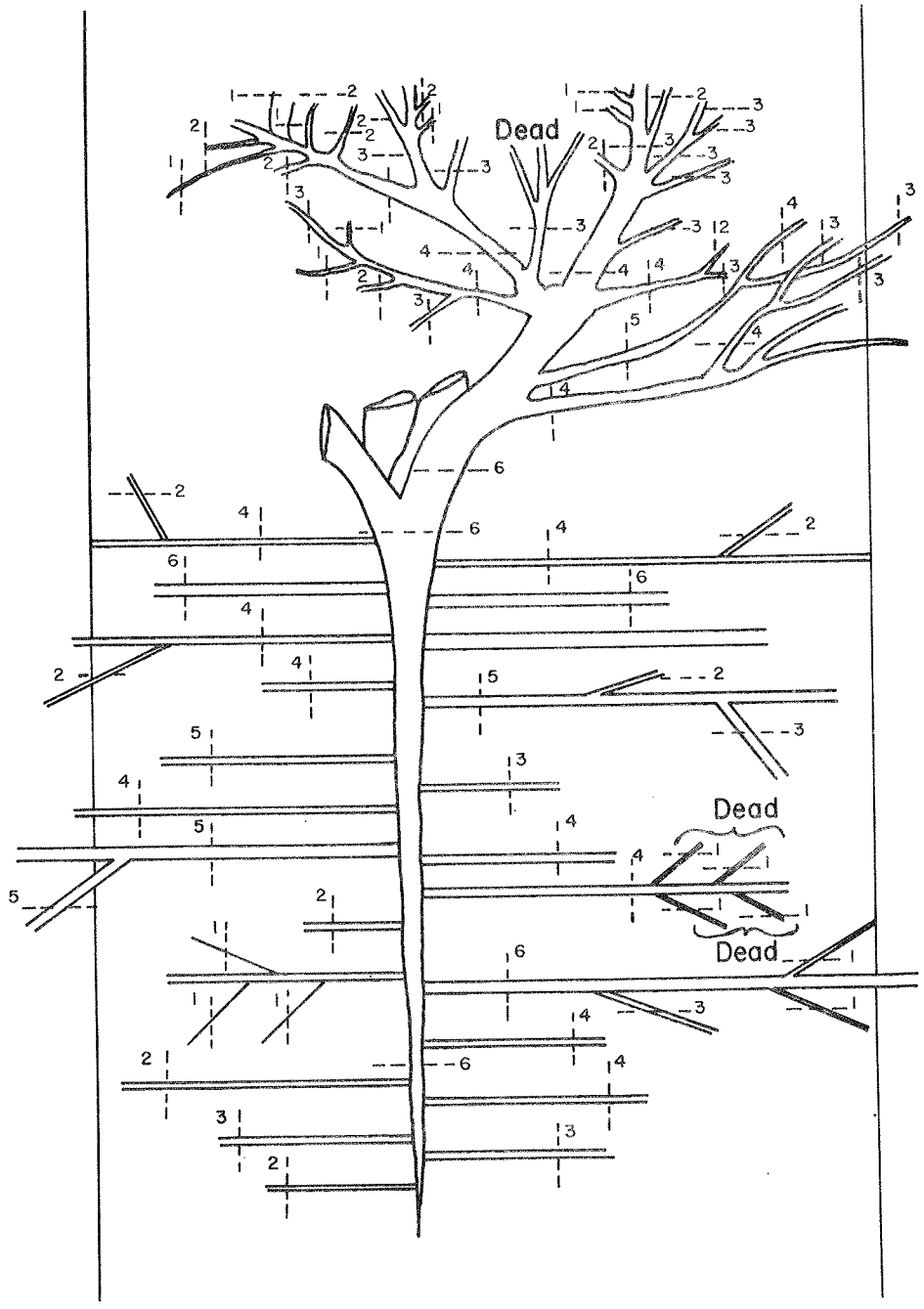


Figure 15. Diagrammatic representation of annual ring counts for the shoot and root system of a 6-year *Artemisia tridentata* plant.

easy as any soils to work with in a field situation. However, there is an immense profusion of fine roots which are difficult to extract from the soil intact even by using the most careful washing techniques. Growth apices are also extremely difficult to locate. In Figures 16, 17 and 18 are photographs of different portions of the root system with a comparable print of the autoradiograms of these roots of a single *Atriplex* plant on which this pulse labeling technique was applied. The plant was labeled with .37 mc of $^{14}CO_2$ for one hour on October 23, 1970, and again on 22 July, 1971. Roots of the plant were carefully removed from the soil by washing with a jet of water on 8 July, 1972. Almost all roots which were saved were positively traced back to the treated plant. The roots were mounted while still wet on herbarium sheets, covered with plastic film, and dried in a plant press. After drying they were attached permanently with tape to the sheets. Autoradiograms were prepared by exposing x-ray film for 65 days.

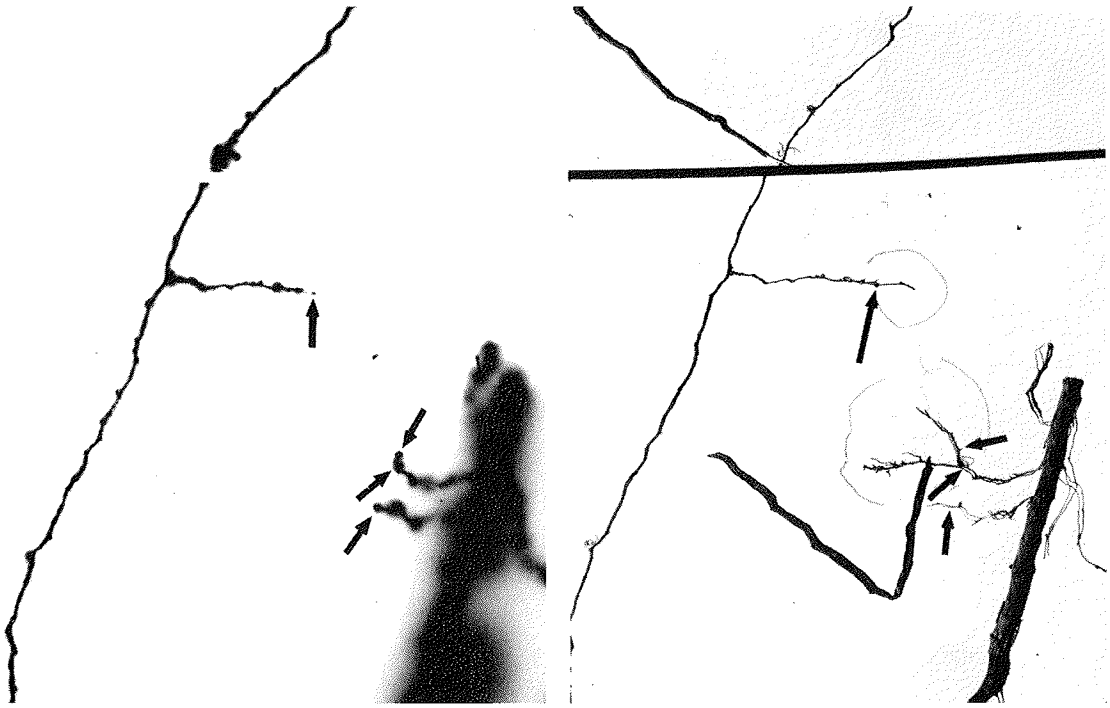


Figure 16. Photograph (left) and autoradiogram (right) of the main root and a long lateral root, each with branch roots, pulse-labeled with 14-carbon. The arrows point to the terminus of radioactivity on the photograph. Apparently, the portion of the root extending beyond this abrupt termination of radioactivity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

Figure 17. Photograph (left) and autoradiogram (right) of 14-carbon pulse-labeled long lateral roots with terminal rootlets. Some of the small terminal rootlets designated by the letter "a" are more heavily labeled than the long lateral root and are thought to have developed shortly after the exposure of the shoot of the plant to $^{14}CO_2$. Some terminal roots appear only as dots designated by the letter "c" on the autoradiogram.

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

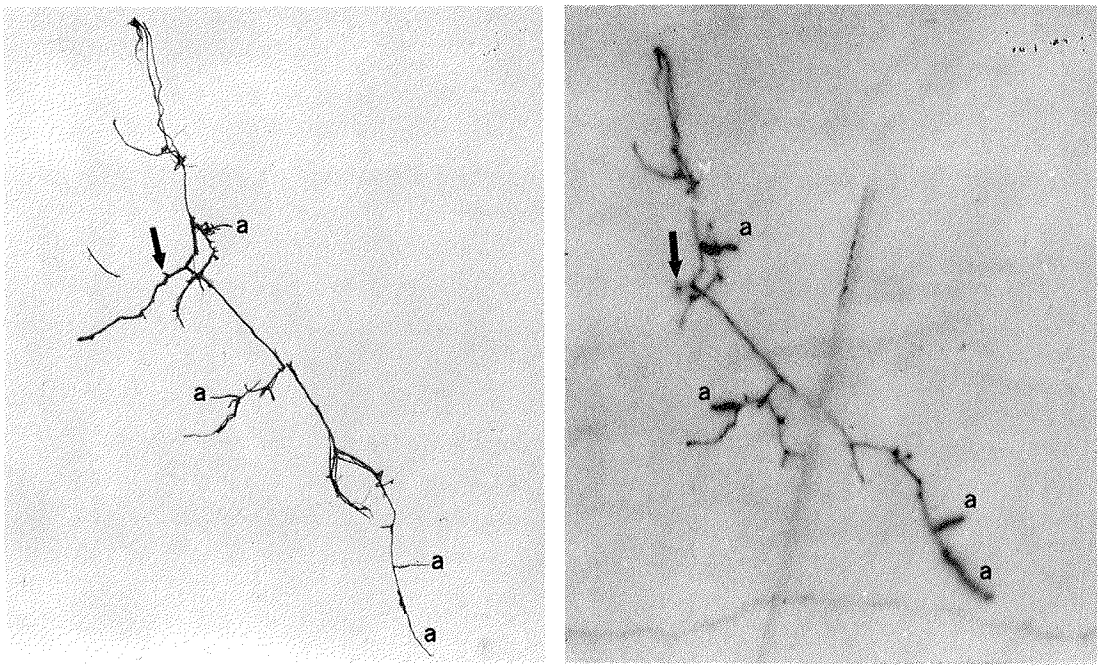


Figure 18. Photograph (left) and autoradiogram (right) of 14-carbon pulse-labeled terminal root system. The arrow indicates a lateral root which was apparently dead beyond this point at the time of plant exposure to $^{14}CO_2$. The short terminal rootlets designated by the letter "a" apparently developed concurrently or shortly following the exposure to $^{14}CO_2$.

The autoradiograms indicated substantial variation in the amount of radioactive carbon accumulated in major roots. Presumably the degree of anatomical linkage with the particular shoot branch being exposed to $^{14}CO_2$ accounts for at least part of this variability in amount of radioactive carbon in these major roots. The exact location of the labeled carbon within the major root tissue was not studied but it was presumably fairly near the surface because self absorption of the weak beta radiation emitted by C^{14} would not penetrate to the film from internal root tissues. In these long-term studies, most of the labeled carbon was probably in the form of cellulose in secondary xylem and phloem tissue formed soon after photosynthetic uptake of $^{14}CO_2$. The smaller roots tended to show a fairly uniform accumulation of radioactive carbon throughout. There was no evidence of "banding" or small areas of radioactive carbon accumulation as should be expected with this pulse labeling technique (Wardlaw, 1969). Most likely the label is in secondary growth tissues of these small roots.

The smallest branch rootlets were often very radioactive. These are interpreted as rootlets formed immediatley after photosynthetic uptake of $^{14}CO_2$ by the plant, although they may have been formed at a later time as well. On some of the longer small rootlets there were areas of intense radioactivity. These may have been lateral roots or perhaps even very short lateral rootlets. They may also have been the remaining living stumps of lateral roots which had died. In a few situations on lateral roots, radioactivity was found only on a part of the root,often ending very abruptly or even with an intensified area of radioactivity. These are interpreted as being rootlets which have died in part prior to the date of $^{14}CO_2$ fixation. The radioactivity actually identified in this case the portion of the root which was still living. The somewhat intensified area of radioactivity found at the termini of the radioactive portion of the root could be due to callus formation or pathogenic activity.

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

Root Productivity -- Root Regrowth into Soil Cores

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

Root Productivity and Translocation -- Radioactive Carbon Studies

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

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

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

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

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

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

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

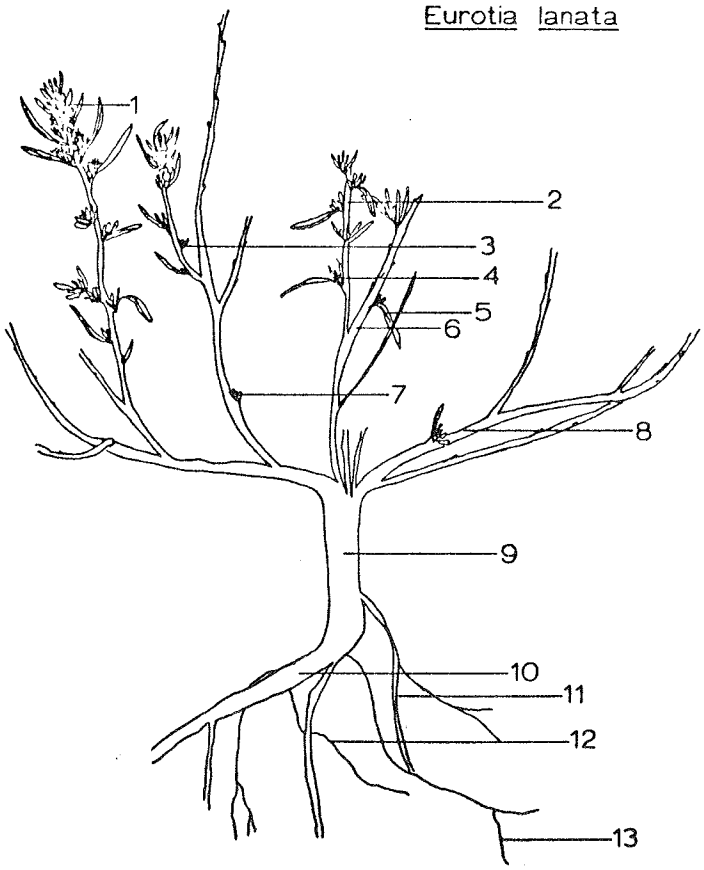


Figure 19. Diagrammatic representation of plant parts sampled for C^{14} for *Eurotia lanata*: 1. Flowers and fruits of current year's growth; 2. Current years branches; 3. New buds; 4. New unexpanded leaves; 5. Fully expanded leaves; 6. Secondary branches of previous year's growth; 7. Buds on previous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

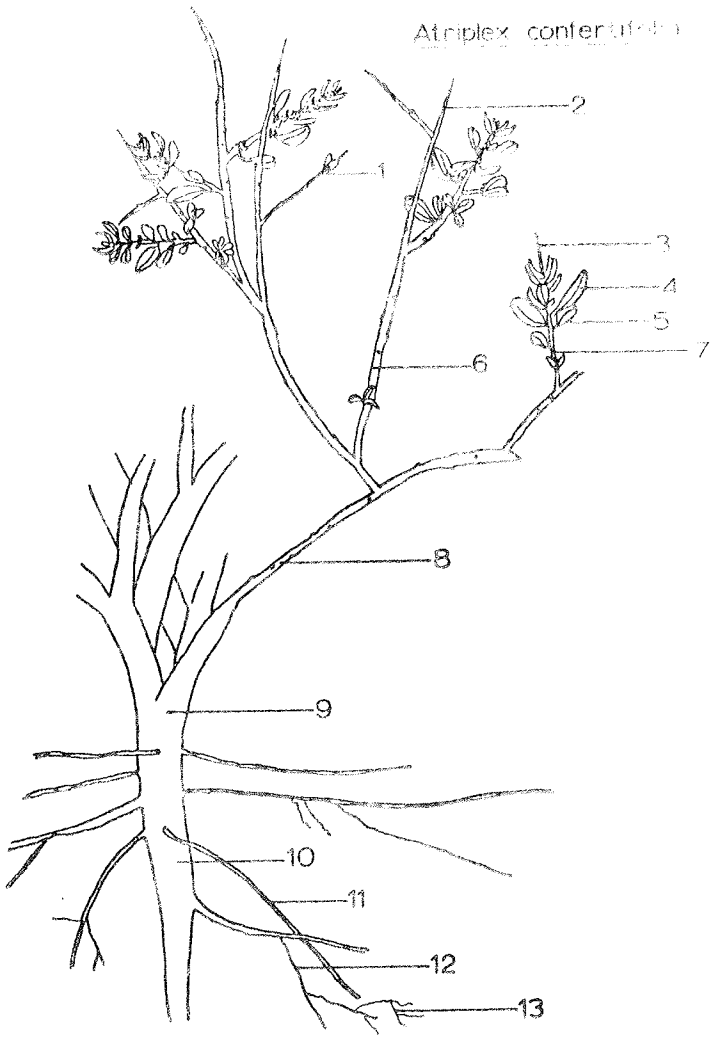


Figure 20. Diagrammatic representation of plant parts harvested for radioactivity determinations in *Atriplex confertifolia*: 1. Fruits and flowers of the current year's growth; 2. Determinate spines of the previous year's growth; 3. Spines of the current year's growth; 4. Large leaves formed in the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

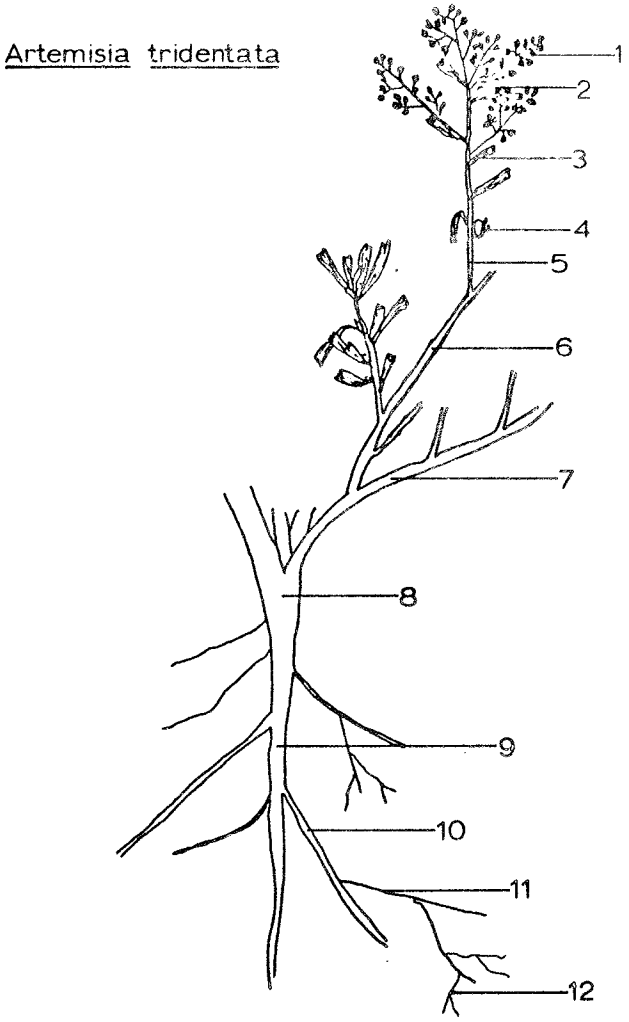


Figure 21. Diagrammatic representation of plant parts of *Artemisia tridentata* harvested for radioactivity determinations: 1. Fruit and flowers of current year's growth; 2. Reproductive shoot of current year's growth; 3. Fully expanded leaves of current year's growth; 4. Insect galls; 5. Branches of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

DISCUSSION

Gas exchange studies

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

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

where: RP = relative photosynthesis

I = irradiation % of maximum for growing season

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

Root growth and translocation

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

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

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

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

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

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

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

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

Results of the preliminary experimentation using radioactive carbon in these three species indicated substantial differences in allocation of carbon to various plant parts (see Tables 1, 2 and 3). One week following the application of $^{14}CO_2$ most of the radioactive carbon was still concentrated in the leaves. In *Eurotia lanata* most of the activity was not in the larger leaves but instead in the very small leaves which had not yet expanded. All three species had a moderate amount of activity in branches of the current year's growth. Activity in previous years' growth was usually low, although in June in *Artemisia tridentata* there was approximately 10 percent of the total radioactive carbon in the above-ground portion of the plant concentrated in primary and secondary branches of previous years' growth.

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

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

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

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

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

EXPECTATIONS

The pulse labeling technique will be attempted again in 1973 with shorter intervals between the pulse labels. Pulse labeling is designed to identify primary growth and root elongation and is ideally suited for roots without secondary growth. Such secondary diameter growth occurs along almost the entire length of the root and tends to obscure primary pulse labels. Therefore, much shorter intervals between pulses and harvesting the roots within one to two weeks following the second pulse label will be employed in the field. It is anticipated that this technique still may be of some value in confirming root growth observations in the soil-root observation chambers. Also in 1973 the soil cores installed in 1972 will be excavated and root invasion into these cylinders will be determined as an index of root productivity. A major effort will be directed towards further studies of translocation and root growth using the radioactive carbon labeling techniques in the field. Root observation chambers will be monitored at regular intervals from early spring until late fall to further elucidate the nature of timing of root growth activity in these shrubs. Preliminary studies of associated fungal hyphae will be carried out. Soil respiration studies will be initiated in the field in 1973. Finally, in the laboratory a detailed study will be centered on the complete carbon balance of individual desert shrubs bringing into account carbon dioxide exchange of roots and shoots independently and using a concomitant $^{14}C_2$ labeling to quantitatively assess translocation to various parts of the plant. Much of the 1973 effort is then to be directed to the elucidation of the relationship between plant productivity and gas exchange.

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

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