5-1974

The Dynamics Of Root Growth And The Partitioning Of Photosynthates In Cool Desert Shrubs

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THE DYNAMICS OF ROOT GROWTH AND THE PARTITIONING OF PHOTOSYNTHATES IN COOL DESERT SHRUBS

by

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A dissertation submitted in partial fulfillment
of the requirements for the degree

of

DOCTOR OF PHILOSOPHY

in

Range Science

Approved:

UTAH STATE UNIVERSITY
Logan, Utah

1974

ACKNOWLEDGMENTS

I wish to express my sincere appreciation to Dr. Martyn M. Caldwell for his support and guidance through my research, for his critical review of this manuscript, and the many helpful suggestions he has offered for its improvement.

I am deeply indebted to Dr. Cyrus M. McKell because his sincere advice and encouragement was a principal factor in my decision to undertake a study of this nature.

I would like to express my thanks to Dr. Neil E. West for allowing me the use of his unpublished data which is related to various aspects of my research. I also extend my sincere thanks to Mr. Lee B. Camp for his assistance and many helpful suggestions and criticisms.

In addition I would like to extend my appreciation to the "Universidad Nacional del Sur" Bahia Blanca, Argentina for the special leave they granted which allowed me to accomplish this program. Also to the Ford Foundation for their financial assistance during the duration of my studies. This project was also partially supported through the US/IBP Desert Biome Program (National Science Foundation Grant GB 32139) and the Utah Agricultural Experiment Station.

Finally, to my wife, Irma, I cannot express my gratitude for her support, encouragement and patience during these past two and a half years.

Osvaldo Alberto Fernandez

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Of Photosynthates In Cool Desert Shrubs

by

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Utah State University, 1974

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This study addresses the nature of physiological and phenological evolutionary strategies of root growth dynamics and energy allocation followed by Atriplex confertifolia, Ceratoides lanata, and Artemisia tridentata growing in their natural cool desert environment.

Root observation chambers with inclined Plexiglass windows were installed in monospecific desert communities of Atriplex confertifolia, Ceratoides lanata and Artemisia tridentata. Soil temperature and water potential measurements taken immediately adjacent to the observation windows indicated a minimal disturbance was caused by the presence of these chambers. For the three species initiation of root growth was observed before initiation of shoot activity, furthermore, active root growth extended over much longer periods during the year than shoot growth. Initial growth was observed for the three species in the upper soil layers in the spring. Later in the season most of the growth activity was measured at progressively greater depths in the soil. Measurable root growth was observed for Atriplex in August when the soil water potentials were in the range of -70 bars for 1972, and at

water potentials of -60 bars for all three species during 1973. Detectable growth for these three species was recorded as late as January in 1974. Except for the main extension roots, individual apical meristems were seldom active for more than 2 weeks.

Atriplex confertifolia and Ceratoides lanata plots were labeled during the growth season with $^{14}CO_2$ in polyethylene enclosures to study both the partitioning of photosynthates to plant parts and their total allocation of carbon at the community level. A definite seasonal pattern of partitioning of recent photoassimilates corresponding to phenological events emerged. In the spring, photoassimilates were principally directed to shoot growth, especially expanding new leaves and vegetative buds. In terms of relative energy allocated to plant parts per unit dry weight basis, it appears that Ceratoides lanata expends less energy for reproductive organs. For both species, carbon used for new stems and previous years shoot growth appears to constitute a significant sink for energy use and storage. Relative translocation of carbon to roots was minimal during the spring for both species. It increased with the progression of the season reaching a maximum in July for Atriplex and at the end of the season for Ceratoides. Energy allocation at the community level for these species showed that approximately 60 and 40 percent of the recently photoassimilated ^{14}C for the Atriplex-dominated community in July and September, respectively, appeared localized in the new shoot growth, the remaining was distributed in nearly equal amounts between previous year's shoot growth and the root system. The scheme of energy allocation in Ceratoides showed similar patterns of carbon utilization in July

and September; approximately 80 percent of the fixed carbon was allocated in approximately equal amounts to roots and new shoot growth with the remainder to the previous year's shoot growth.

In the Ceratoides-dominated community 65 percent and 36 percent of ^{14}C photoassimilated in April and July, respectively, and still remaining in the plant by September, was localized in the underground structures. Similarly, in the Atriplex community, 35 percent and 29 percent of the ^{14}C incorporated in April and July appeared in the root system. From the total ^{14}C photoassimilated in July for both communities, approximately 60 percent and 50 percent was retained in the plants by September in the Atriplex- and Ceratoides-dominated communities, respectively.

(131 pages)

CHAPTER I

INTRODUCTION

There has been considerable interest recently (Ghilarov et al., 1968; Whittington, 1969; Head, 1971) in the study of plant roots and in the assessment of their importance in the context of the plant community. In part this is due to the fact that the lack of knowledge of root function is one of the main factors limiting the interpretation of community and ecosystem level function.

Root studies have been neglected largely because roots are difficult to study under natural conditions.

Information on energy relationships and root productivity under field conditions for a single plant or a whole community is limited, except for some studies on the energy content of roots and aerial plant parts (Hadley and Kieckhefer, 1963).

Plants of arid regions have evolved different competitive strategies for the utilzation of underground resources as it was indicated in earlier studies by Cannon (1911) and Markle (1917). In the case of cool desert land shrubs, root studies could be singularly important if for no other reason than the high root-shoot ratio frequently observed (Rodin and Bazilevich, 1965; Federova, 1968; Shalyt and Zhivotenko, 1968; Sveshnikova, 1968; Bjerregaard, 1971).

Perennial plants of cool desert regions are subjected to environmental conditions which are beyond the physiological limits of most other species. This is the case for both aerial and

subterranean plant organs. It appears that roots and shoots have evolved to cope with environmental hardships of a different nature imposed by the subterraneal and aerial environments.

Plant shoots of cool arid lands are exposed to an environment that combines a high capacity for desiccation with drastic changes in temperature on an annual as well as a seasonal basis. The suitability of cool desert soil as a medium for root growth is characterized by the shortage of available water, low temperature and frequently high salt content. The below-ground habitat in most cases is completely occupied by roots contrary to the aerial environment where shoots frequently appear widely separated. It can be postulated that the desert community organization must greatly depend on selective pressures of the underground environment.

It is generally conceded that young roots are mainly responsible for water and nutrient uptake (Hayward and Spurr, 1943; Kramer and Wiebe, 1952; Canning and Kramer, 1958). It can be hypothesized that a cyclic mechanism of root growth and turnover exists and that the dynamics of root growth may change through the growing season according to changes in soil temperature and water potential. Root phenology may be as complex as shoot phenology because of adaptative options; survival depending critically on the timing of root growth, soil exploration, and partitioning of energy for growth.

If the below-ground root system is to maintain a dynamic turnover, a significant share of photosynthates must be available for the root system. Energy incorporated through photosynthesis

has to be selectively allocated throughout the growing season to the different plant structures according to the different strategies for survival and reproduction.

Objectives

The objectives of this study were as follows:

a) To elucidate the seasonal pattern of root growth and growth characteristics for Atriplex confertifolia (Torr and Frem) S. Wats, Ceratoides lanata, Nevski, and Artemisia tridentata Nutt subspecies wyomingensis Beetle, in the field. The hypothesis to be tested, is that the phenological events of the above-ground plant and the changes occurring in the soil physical environment (Moore and Caldwell, 1972), are correlated with the seasonal dynamics of root growth in these three species.

b) The success of a plant in its particular environment has to be related to the balance in the utilization of energy for survival and reproduction. It was with this aim that a study of the partitioning of ^{14}C-photosynthates from foliage to the roots and other plant organs was initiated.

c) The third objective of this project was to quantitatively determine allocation of ^{14}C to above- and below-ground plant structures on a community basis, in Atriplex- and Ceratoides-dominated communities. Due to the high root-shoot biomass of these species (Bjerregaard, 1971) it is assumed that a considerable amount of energy resources should be allocated on a community basis to the underground root system for maintenance and turnover. This hypothesis is here tested and interpreted through experimentation.

CHAPTER II

DESCRIPTION OF THE STUDY AREA

A site in Curlew Valley representative of the cool salt desert of the "Great Basin" was chosen for this study. The study site lies in a flat lacustrine bay occupied by Lake Bonneville during the Pleistocene. It is located in Box Elder County, Utah, at an altitude of 1350 m, about 30 km south of Snowville (approximately 113°5' W, 41°5' N).

The lake exerted a major influence on the soil composition and topography. The valley slopes downwards towards the Great Salt Lake to the South. Gates (1956) describes the soils of the area as having origin from sedimentary deposits from the nearby mountains.

The soils in the study sites are homogeneous and have the general characteristics of aridisols. In consequence they have few diagnostic features. Texture varies from silt loam to sandy loam. A description of the physical characteristics of this soil was presented by Mitchel (1965) and Mitchel et al., (1966). The pH of the soil is about 8.0

The Valley is covered by vegetation dominated by Artemisia tridentata Nutt. subspecie tridentata, with juniper (Juniperus osteosperma (Torr) Little) on the higher slopes. In the lower part of the valley, Atriplex confertifolia (Torr and Frem) S. Wats, and Ceratoides lanata, Nevski, are the dominant species. The soil

in the lower regions is of finer texture and is more heavily loaded with salts. In some places these two dominant species are mixed with Artemisia tridentata but in other places the plant communities are represented by extensive monospecific stands.

The dominant shrub species may be accompanied by other shrubs such as Atriplex falcata, Sarcobatus vermiculatus (Hook) Torr, Grayia spinosa (Hook) Moq, Kochia americana Wats, and Artemisia spinescens L. Invading annual species, such as Halogeton glomeratus (Bieb) C. A. Mayer, and Bromus tectorum L. are common.

The climate of the study site is characterized by annual precipitation of approximately 250 mm, with warm, dry summers and very cold winters. Annual and seasonal precipiation is quite variable (Fig. 1). Air temperature ranges from below 0°C to above 40°C during the growing season.

Nearly pure stands of Atriplex confertifolia and Ceratoides lanata are often growing side by side. Both species are able to tolerate a high salt content in the soil. Atriplex possesses the C_4 photosynthetic pathway while Ceratoides possesses the normal C_3 pathway (Welkie and Caldwell, 1970).

Artemisia tridentata is also a C_3 plant (Welkie and Caldwell, 1970). Communities dominated by this species would tend to be present at higher elevations in the valleys in less salty soils. However, frequently they can be found mixed in mosaic stands with these halophytic species.

Detailed profile descriptions of the soil for each of the communities of this study have been recently reported by Skujins and West (1973).

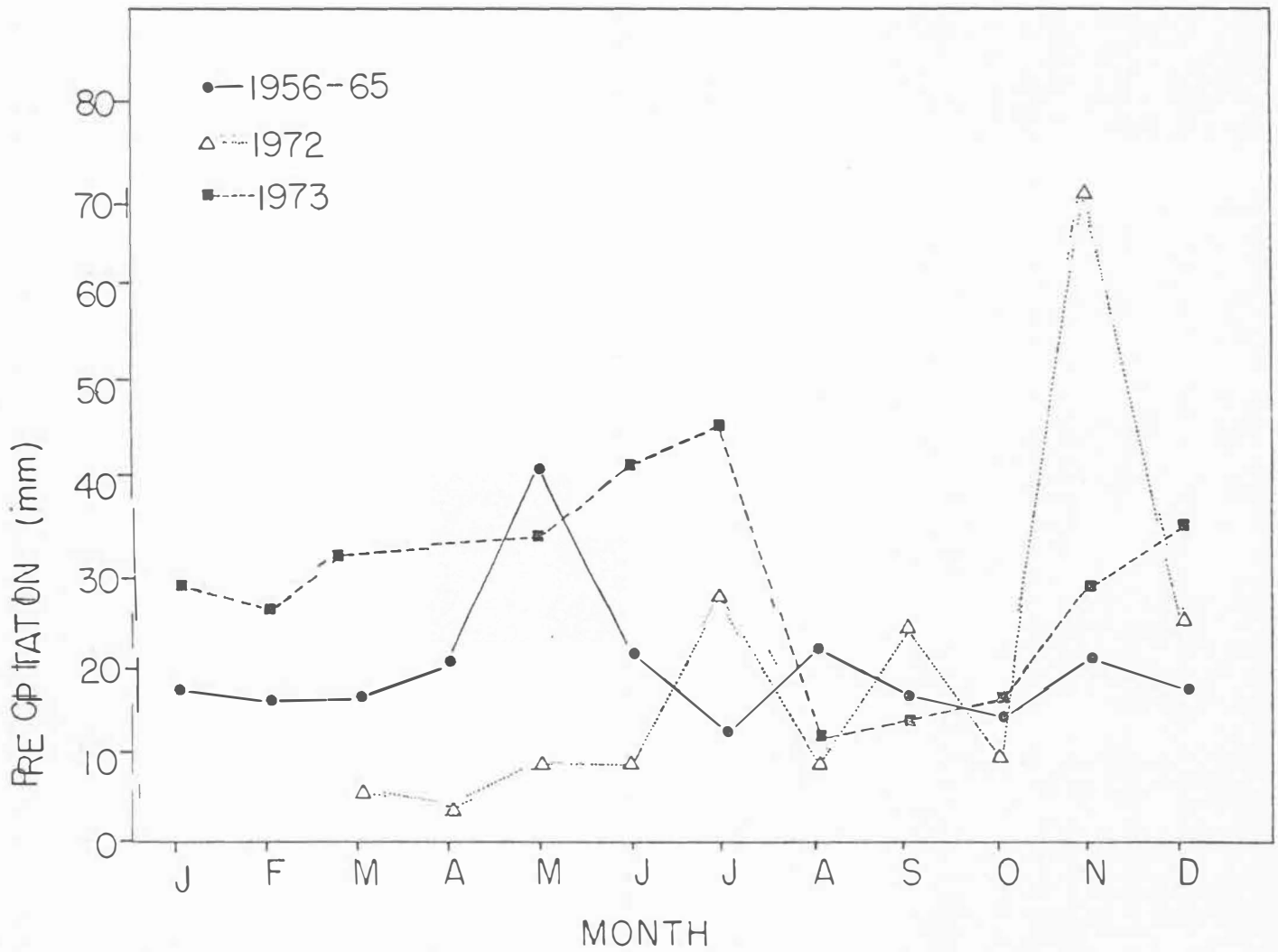


Figure 1. Monthly precipitation averages for Curlew Valley. Total yearly averages 1956-65 = 230 mm, 1972 = 220 mm, 1973 = 315 mm.

Figure 2. A general view of the Atriplex confertifolia study area.

Figure 3. A general view of the Ceratoides lanata study area.

Figure 4. A general view of the Artemisia tridentata study area.

CHAPTER III

ROOT GROWTH STUDIES

Various techniques have been employed in the study of root systems. Most determinations of rooting behavior was obtained by excavating roots from the soil (Cannon, 1911; Markle, 1917; Weaver, 1919; Jeffrey and Torrey, 1921; Rogers, 1932, Rogers and Vivian, 1934; Stukey, 1941; Hellmers et al., 1955; Coker, 1958; Dittmer 1959, 1969; Doll, 1961; McMinn 1963; Cockroft and Wallbrink, 1966; Kreutzer, 1968; Nechaeva, 1968; Samailova, 1968; Zapryagaeva, 1968; Williams, 1969). One of the most extensive studies on the rooting habits of desert plants was conducted by Cannon (1911) in Arizona. The labor and expense required to extract roots from the soil undoubtedly discouraged many other studies. In addition, the measurement is destructive and unless extreme care is taken most of the thin rootlets remain in the soil.

The extraction of soil monoliths has been preferred by many researchers for the study not only of root morphology and distribution but also for root biomass calculations (Pavlichenko, 1937; Ignatenko et al., 1968; Karazumi, 1968; Keresztesi, 1968; Rakhteenko and Yakushev, 1968; Shalit and Zhivotenko, 1968; Fryrear and McCully, 1972; Weaver and Voigt, 1950; Eavis and Payne, 1969). In this method soil block samples were excavated down to the base of the root penetration zone and roots are most frequently removed from the soil by washing. A modification of this method is the pin-board

technique described first by Weaver (1926) and more recently by Wiersum (1967) and Schuurman and Goedewaagen (1971). Roots included in the soil monolith kept their original pattern of distribution in the soil during washing. With slight modifications the same principle has recently been used by several workers (Schuster, 1964; Gooderham, 1969; Nelson and Allmores, 1969; DeRoo, 1969).

Another technique sometimes used to study depth and distribution of tree roots in different soil profiles consists of digging either a radial or tangential trench some distance from the tree and then counting or mapping the cut root elements in their position in the soil (Weaver, 1919; Havis, 1938; Nechaeva, 1968; Kochenderfer, 1972).

A more rapid method of root studies usually involves core soil sampling. Representative data can be obtained by this method if enough replicates are taken. It is the procedure preferred by many authors for calculations of root biomass or assessing root growth and penetration (Fehrenbarcher and Snider, 1954; Ovington et al., 1963; Dahlman and Kucera, 1965; Fiala et al., 1968; Russell and Ellis, 1968; Welbank and Williams, 1968; Chapman, 1970; Bjerregaard, 1971; Swift and French, 1972; Singh and Coleman, 1973; Bartos and Sims, 1974). The advent of mechanically and hydraulically operated coring machines (Swanson, 1950; Fehrenbarcher and Alexander, 1955; Jensen et al., 1960; Boehle et al., 1963; Dahlman and Kucera, 1965; Tackett et al., 1965; Kawatake, 1968; Russell and Ellis, 1968; Welbank and Williams, 1968; Bartos and Sims, 1974) has made it possible to extract a large number of uniform soil samples at a considerable depth in a short time in some studies.

With most techniques, studying roots directly without disturbing them is impossible. Methods that require excavation of the total root system or part thereof do not allow subsequent observations of the same root system.

One technique which permits root growing in the soil to be observed and measured nondestructively consists of root observation chambers. With this method the phenology of root growth, behavior, thickening, and sometimes decay can be conveniently recorded. Roots can be photographed and microscopically observed. The principle of the transparent-faced observation chambers is certainly not new. In 1888, Comstock utilized glass-faced cages for the study of soil-borne insect pests on root plants.

Many investigators have molded the idea to their own requirements for use in the field (McDougall, 1916; Crider, 1928; Collison, 1935; Lavin, 1961; Rogers and Head, 1962: Lyr and Hoffman, 1968; Pearson and Lund, 1968; Bhar et al., 1970; Mason et al., 1970; Taylor et al., 1970; Khatamian and Hilton, 1971) or in the laboratory (Freisner, 1920; Dean, 1929; Sideris, 1929; Muzik and Cruzado, 1953; Muzik and Whitworth, 1962; Walker and Barber, 1962). Though only a small part of the root system can be observed and the growth of the roots is restricted to one plane, growth appears to be normal, and useful information can be gathered on many features of root growth and root characteristics.

More recently root observation laboratories have been built for root studies. They consist of a tunnel in the ground fitted on either side with transparent windows (Roger and Head, 1962; Glover, 1967; Hilton, 1969; Taylor, 1969; Lyr and Hoffmann, 1968).

They are often equipped to additionally measure oxygen, carbon dioxide, temperature and moisture of the soil. Most of these laboratories have been established in agricultural research ventures.

In recent years phosphorus-32 tracer techniques have been developed for measuring distribution and development of root systems under natural conditions (Hall et al., 1953; Burton et al., 1954; Lipps et al., 1957; Murdock and Englebert, 1958; Boggie and Knight, 1962; Kafkafi, 1962; McLure and Harvey, 1962; Hammes and Bartz, 1963; D'Aoust and Tayler, 1965; Mathis et al., 1965; Evans, 1967; Bray et al., 1969; Bassett et al., 1970; Jacobs et al., 1970). This method has been used almost exclusively for cultivated plants and consists of placing the ^{32}P at several places in the soil with subsequent detection in the shoots. An alternative approach used by Racz et al. (1964) consists of the introduction of the radioactive tracer into the plant shoots and determining the distribution of the living roots from measurements of radioactivity in the soil. Olson (1968) estimated root distribution in Liriodendron by tagging the trees with Cesium-137. A ^{14}C pulse-labelling technique was used by Wardlow (1969) to determine root growth in grasses.

Most of the studies on root development have been mainly concerned with root distribution or total amount of root biomass in the soil. In contrast with the abundant literature on seasonal phenology of shoots, a very limited amount of information is available on the seasonal dynamics of root development, rate of root extension, or root initiation and decay in perennial plant roots. Early observations of root activity through the plant growth cycle were reported

by Collison (1935) in fruit trees and by McDougall (1916) and Turner (1936) in forest trees. More recently the periodicity of root growth for fruit and forest trees has been reported by various investigators (Rogers and Head, 1969; Bahr et al., 1970; Lyr and Hoffman, 1968; Modaran, 1965; Hirobi and Watanabe, 1964).

Although many cool desert land species have a high root/shoot biomass ratio (Rodin and Bazilevich, 1965; Federova, 1968; Shaylt and Zhivotenko, 1968; Sveshnikova, 1968; Bjerregaard, 1971) and plant survival depends critically on the dynamics and extent of the root system, there is a paucity of studies to determine the seasonal dynamics of the root system of such plants in the field.

Materials and Methods

During the first week of May, 1972 two root observation chambers were installed in Curlew Valley approximately 10 to 20 cm from small groups of Atriplex confertifolia, Ceratoides lanata, and Artemisia tridentata, in communities dominated by each of these species.

Each chamber consisted of a rectangular compartment (110 x 120 x 130 cm) provided with an inclined 110 x 100 cm, 9 mm thick 'Plexiglass' thermoplastic observation window (Figure 5). The interior of the chamber was painted black and insulative black plastic sheets covered the windows when not in use. An insulative white hood covered each chamber.

Excavation of the observation chambers caused minimal disturbance for the existing root-soil system. The soil profile was cut so that only 1 to 5 mm of soil was needed to fill the gap between the

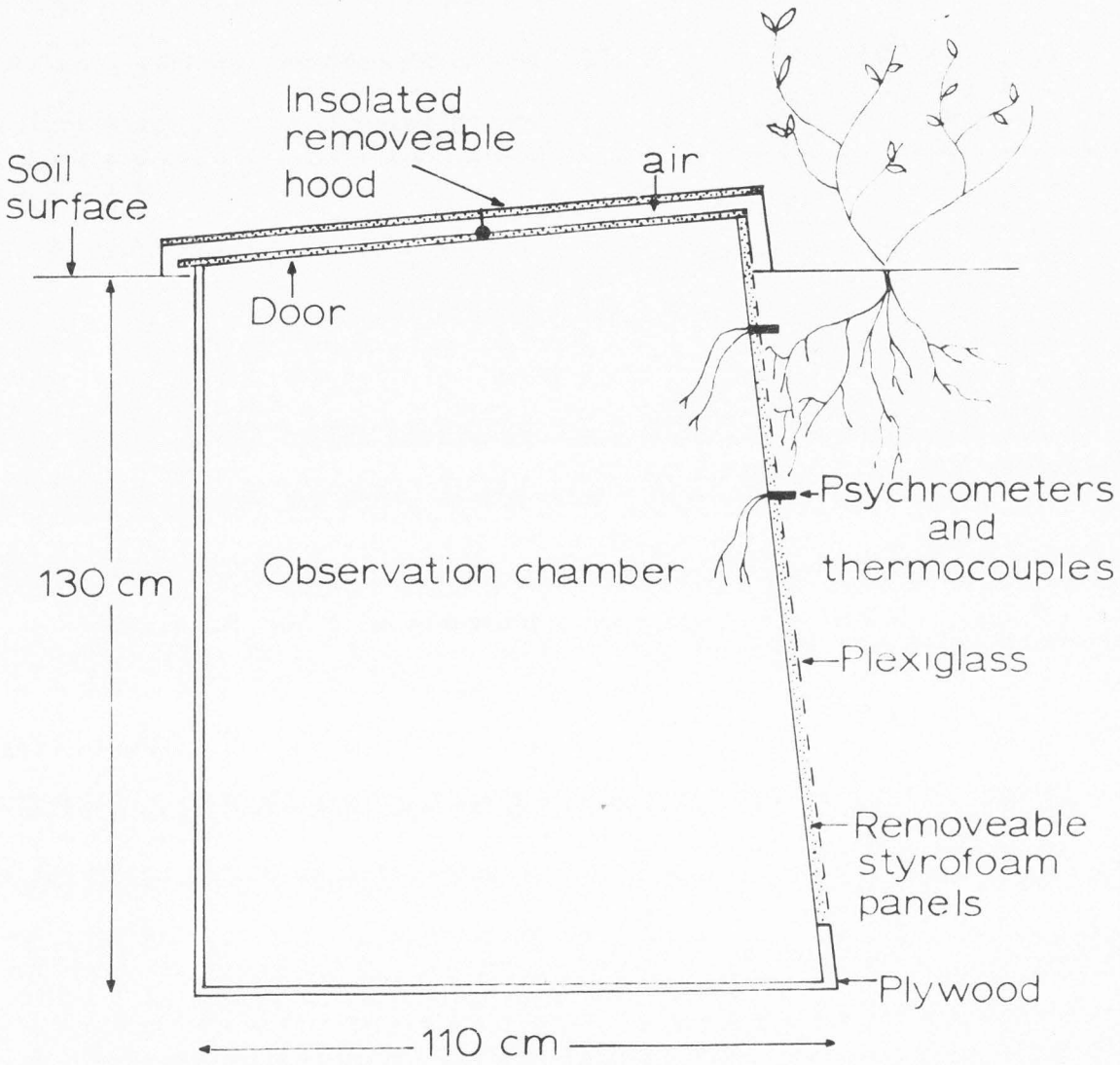


Figure 5. Diagram of the soil-root observation chambers.

outer surface of the 'Plexiglass' window and the undisturbed soil-root profile. Once the chambers were in place (Figure 6) the temperature of the underground compartment came into equilibrium with that of the surrounding soil.

In the first week of August, 1972, copper-constantan theromcouples for soil temperature measurement and Spanner type thermocouple psychrometers for soil water potential (Ψ_s) measurement (Rawlins and Dalton, 1967; Brown, 1970; Wiebe et al., 1971) were installed at 20 and 40 cm depths next to the observation pane and also at 1 m distant in the undisturbed soil profile. Thermocouples and psychrometers were removed from the soil in October, 1972. The psychrometers were recalibrated or new ones were constructed, and both types of probes were installed again in the field in the same situations in April, 1973.

Temperature and Ψ_s measurements were made periodically starting in August, 1972 for the 1972 growing season and in April for the 1973 season.

Number, length and rate of growth for roots appearing in the observation window were recorded at 10 to 15-day intervals by mapping new root growth on transparent acetate sheets placed over the window. As an aid in recording this information a 10-cm line grid was drawn on the inside of the 'Plexiglass' face.

The time required for each observation was about 10 to 30 minutes per chamber, depending on the amount of new root growth. Supplementary light was never needed, as the indirect light coming through the open door (Figure 7) was sufficient. The effect of this short

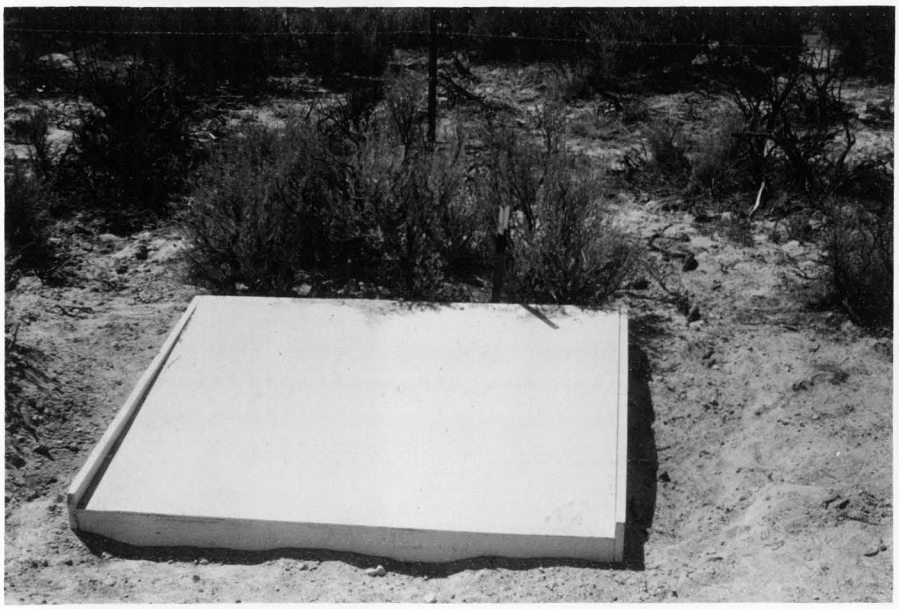


Figure 6. View of the root-observation chamber installed in the field.

Figure 7. View of the root observation chamber open for root growth recording.

exposure to indirect light at approximately two-week intervals is not considered to have any prejudicial effect on root growth (Rogers, 1939a).

Microscopic observations and micrometer measurements of root diameter were also made. Photographs were taken with a camera attached to a dissecting microscope using an electronic flash.

Results

Soil and water potential

Soil temperature and Ψ_s measurements taken immediately next to the root observation window indicate the presence of the observation pane caused a minimal soil environment disturbance. At comparable depths, soil temperature near the window was within 2°C of temperatures in the undisturbed community and Ψ_s seldomly varied more than ± 5 atm from the soil in the undisturbed community except at the lower ranges of Ψ_s when differences nearer 10 atm were occasionally noted. There was apparently no systematic trend to these differences.

During 1973, additional thermcouples were attached to the inner side of the window. These always registered the same temperature as the soil on the other side.

Soil Ψ_s began decreasing about mid-May, increased in the middle of June and again rapidly decreased and continued descending until mid-August when after that date changes were small (Figures 8, 9 and 10). The lowest Ψ_s registered was in the order of -60 atm during 1973 and only once dropping to -65 atm. During 1972, values to -80 atm were registered.

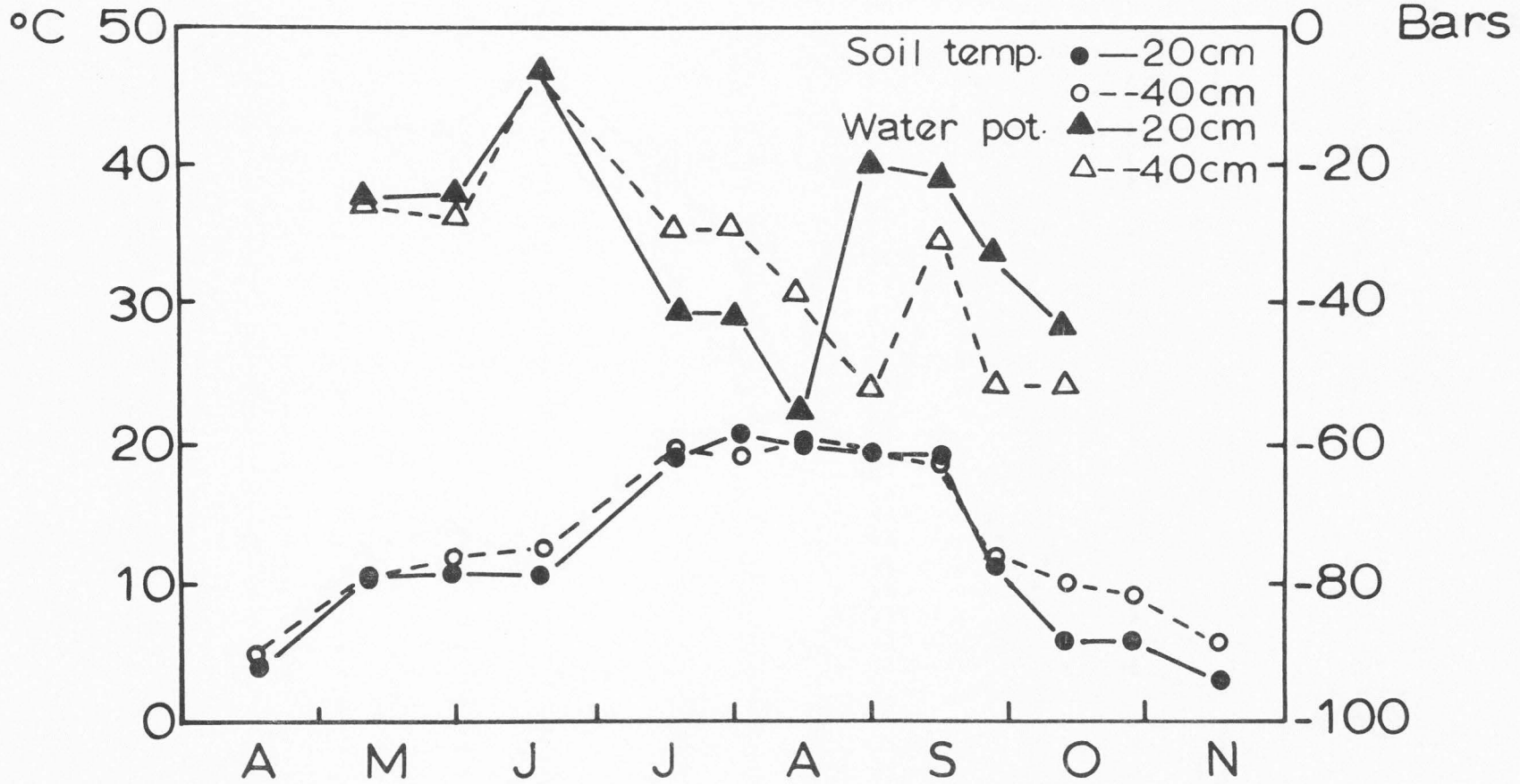


Figure 8. Soil temperature and water potential at 20 and 40 cm depths next to the observation window in the Atriplex confertifolia-dominated community.

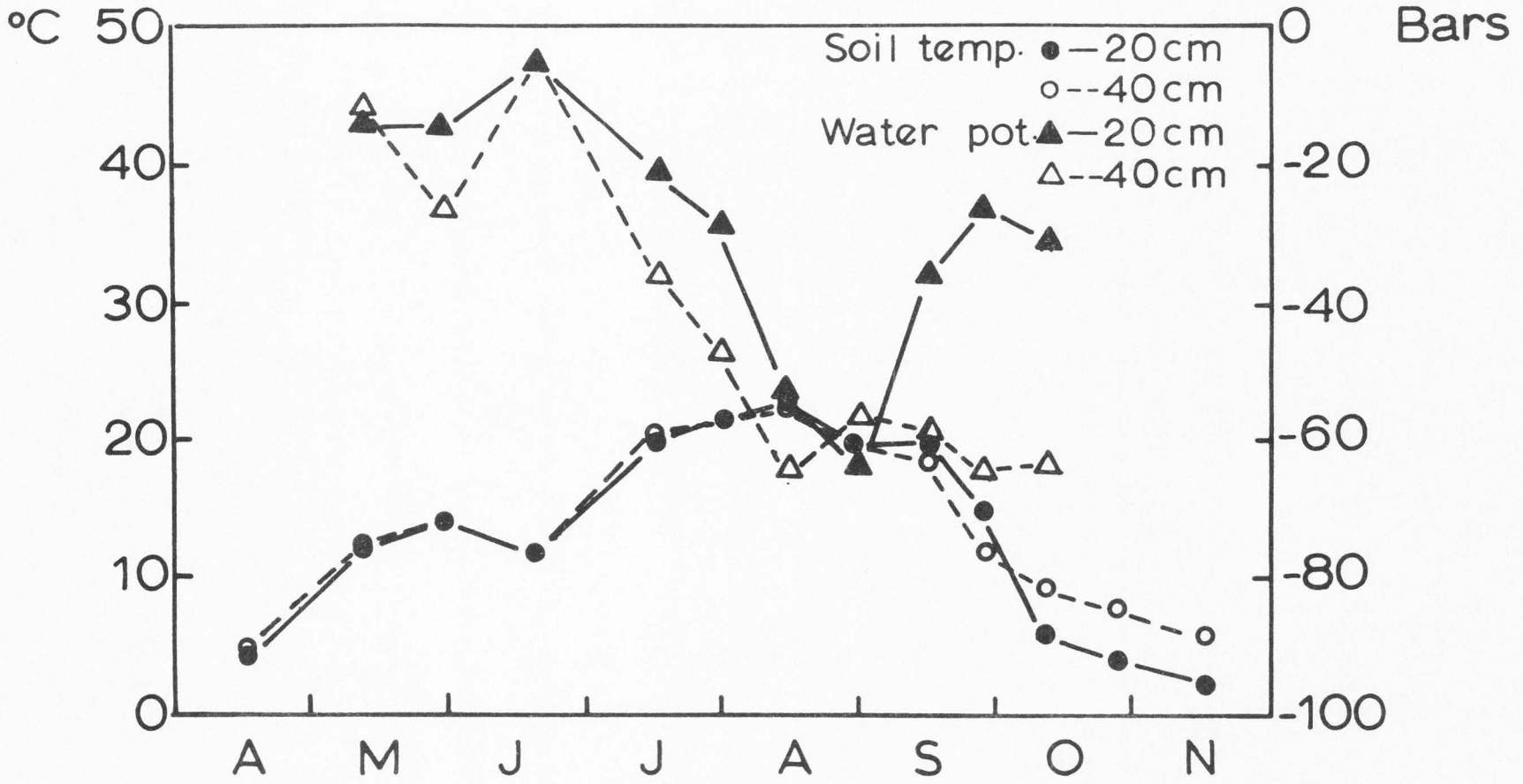


Figure 9. Soil temperature and water potential at 20 and 40 cm depths next to the observation window in the Ceratoides lanata-dominated community.

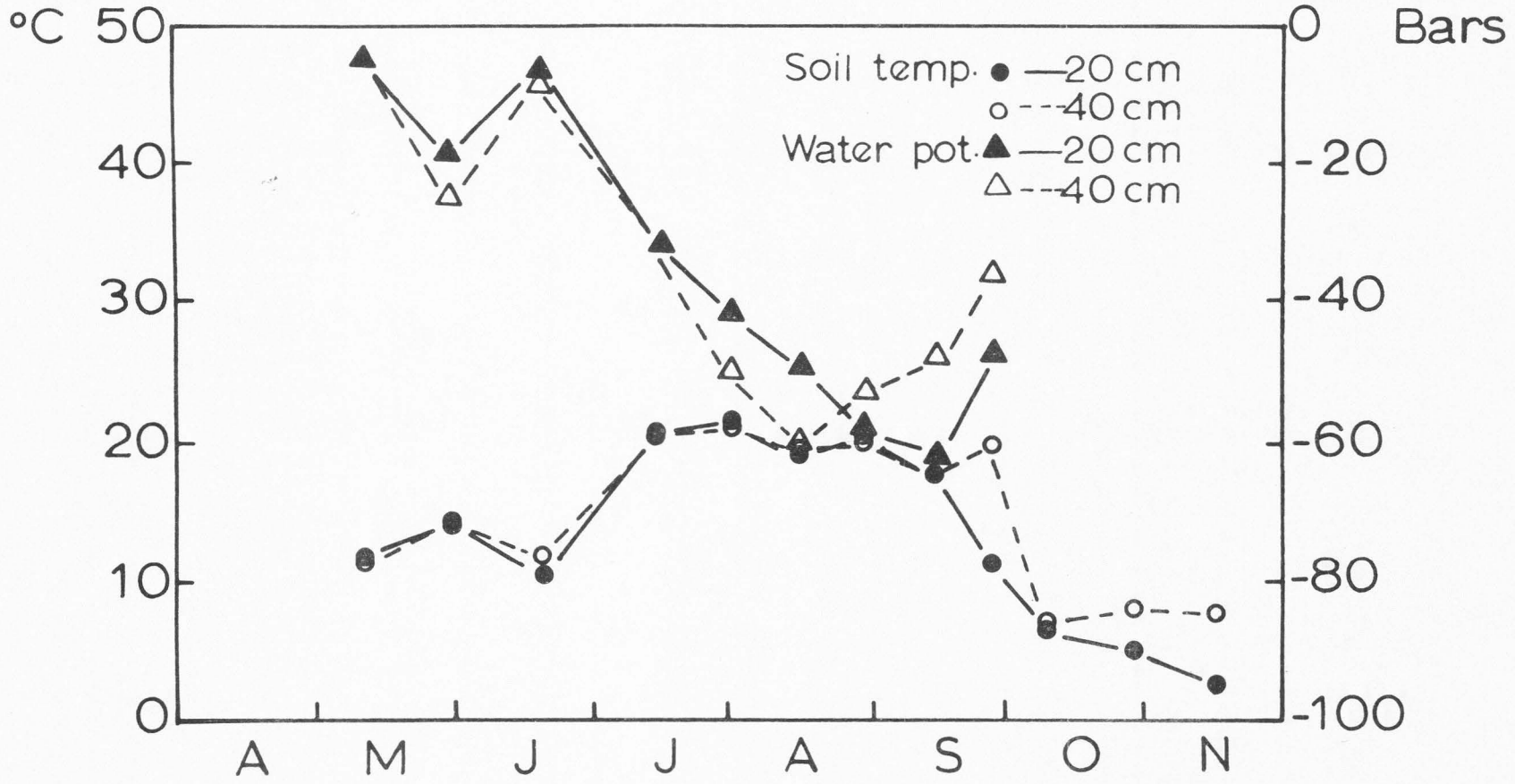


Figure 10. Soil temperature and water potential at 20 and 40 cm depths next to the observation window in the Artemisia tridentata-dominated community.

Soil Ψ_s for 1973 was noticeably higher than recorded the previous year. This is attributed to a higher annual precipitation for 1973 when compared to 1972 (Figure 11).

As a further indication that the observation chambers were causing a minimal disturbance of the soil-root environment, the above-ground phenology of plant whose roots were adjacent to these observation windows was followed in detail during 1972 and 1973. This was done by using the phenological code procedure of West and Wein (1971). The progress of phenological events was not found to differ from nearby plants in the undisturbed community.

Root dynamics

The first roots of Atriplex confertifolia appeared against the Plexiglass surface by 13 June, 1972. Only two small roots were observed for Artemisia tridentata and no roots were recorded for Ceratoides lanata during the 1972 growing season.

During June and early July 1972, growth of primary roots of Atriplex was at a rate of 3 to 5 mm/day. Growth substantially decreased in late July and August but continued in late September and early October. During August Ψ_s was in the range of -60 to -80 atm immediately adjacent to the observation window. After the first week of October no further growth was detected. The pattern of growth for part of one window in 1972 is shown in Figure 11.

For 1973, root growth activity was first observed on March 23 for Artemisia and in the first two weeks of April for the other two species.

Figure 11. Pattern of root growth of Atriplex confertifolia in part of one window during 1972.

At the time that new root growth was first detected for Atriplex in 1973, initiation of shoot activity in the first half of April was indicated by the swelling of apical buds and regreening of over-wintered leaves.

The maximum absolute rate of elongation of 7 mm/d was recorded during April with a predominance of growth near the soil surface. In May growth was noted in all soil layers from 10 to 55 cm depths. Rates of elongation as high as 15 mm/d were recorded, but usually growth was 1 to 5 mm/d. Rapid growth of new laterals also occurred. A flush of root growth activity was observed for late July below the 50 and 60 cm depths, characterized by a large profusion of laterals with growth rates as high as 5 mm/d. Most of the activity appeared to be concentrated in the production of numerous short lateral roots ranging from a few mm to 4 or 5 cm in length. With diminishing degrees of intensity in the lower soil horizons this situation persisted almost to the end of September. At the same time root growth activity was practically nonexistant in the upper soil layers. A significant decrease in the rate of root growth was recorded after September; however, even during November and January new roots were still appearing at the deeper soil layers, although the highest soil horizon was frozen and shoot activity had terminated much earlier. In one of the chambers roots of Atriplex reached the bottom of the observation pane, which is about 1 m in depth. Moisture in these soils rarely appears to penetrate further than 90 cm depth (Gasto, 1969)

Occasionally, the formation of new lateral root was observed originating from roots of the previous season. Resumption of growth of the apical regions of the apparently suberized root tips of these older roots was not detected.

In the first week of April 1973 initiation of shoot activity for Ceratoides lanata was indicated by the initiation of swelling of leaf buds. Roots were observed for the first time against the window on April 9. Growth continued throughout the growing season with small increments of root growth in existing roots detected as late as January, 1974. Root growth was characterized by the predominance of long extension roots with not as many small laterals as in Atriplex. A single root could be followed against the window for as far as 35 cm, frequently being as long as 15 to 20 cm. Early in the season a pattern of high root activity was depicted for the upper soil layers, with root growth increments up to 10 mm/d. Root growth substantially decreased for the upper 50 cm by the end of August, with now new root activity above 25 cm. On the other side root growth was significantly enhanced at deeper soil layers as the season progressed, with an apparent peak of root development below the 50 cm depth in late July. Root growth rate during this period of the year was on the order of 3 to 5 mm/d with a maximum rate recorded of 14 mm/d.

A significant reduction of root growth was observed starting in the first week of September, at a time when Atriplex was still exhibiting a relatively high rate of growth. Late in the season no new roots appeared in the observation windows. New root growth was mainly represented by the extension of some of the main roots deep in the profile.

Few of the principal roots of Ceratoides extended below 70 cm depth, and no new roots were observed below 80 cm.

The first roots of Artemisia tridentata appeared on the transparent pane on March 23, 1973. At this time of the year shoot phenology indicated that buds and leaves were still in winter dormancy, or postdormancy-quiescence.

The general pattern of root growth through the season appeared to be similar to that observed for the other two species. Root growth activity was very high early in the season near the soil surface and tended to increase in the lower soil layers during the second week of May and early June. During June, July and part of August root activity with different degrees of intensity for different parts of the window was occurring for all the soil layers from 10 to 60 cm depth. Vigorous growth of new laterals also occurred. Starting in the second part of August, practically no new root growth was detected in the upper 30 cm.

The highest rate of root extension was from 10 to 14 mm/d during May. Usually rates were on the order of 1 to 5 mm/d.

Root growth activity diminished markedly after August. It was mainly represented by a slow but continuous extension of some of the main roots in the lower soil horizons. Active slow growing root tips were recorded as late as January, 1974.

Only a few roots were below the 60 cm depth. One of the reasons that may contribute to the shallow rooting habit of this species with respect to the other two, could be the presence of a hard calcium carbonate layer at approximately 60 to 70 cm depth (Skujins and West, 1973).

For both Ceratoides lanata and Artemisia tridentata the growth of individual apical meristems were rarely active for more than two or three weeks except for some of the principal extension roots.

Figure 12 depicts the daily average root increment for one of the windows for each species under study, expressed in mm of root elongation per day for each observation interval.

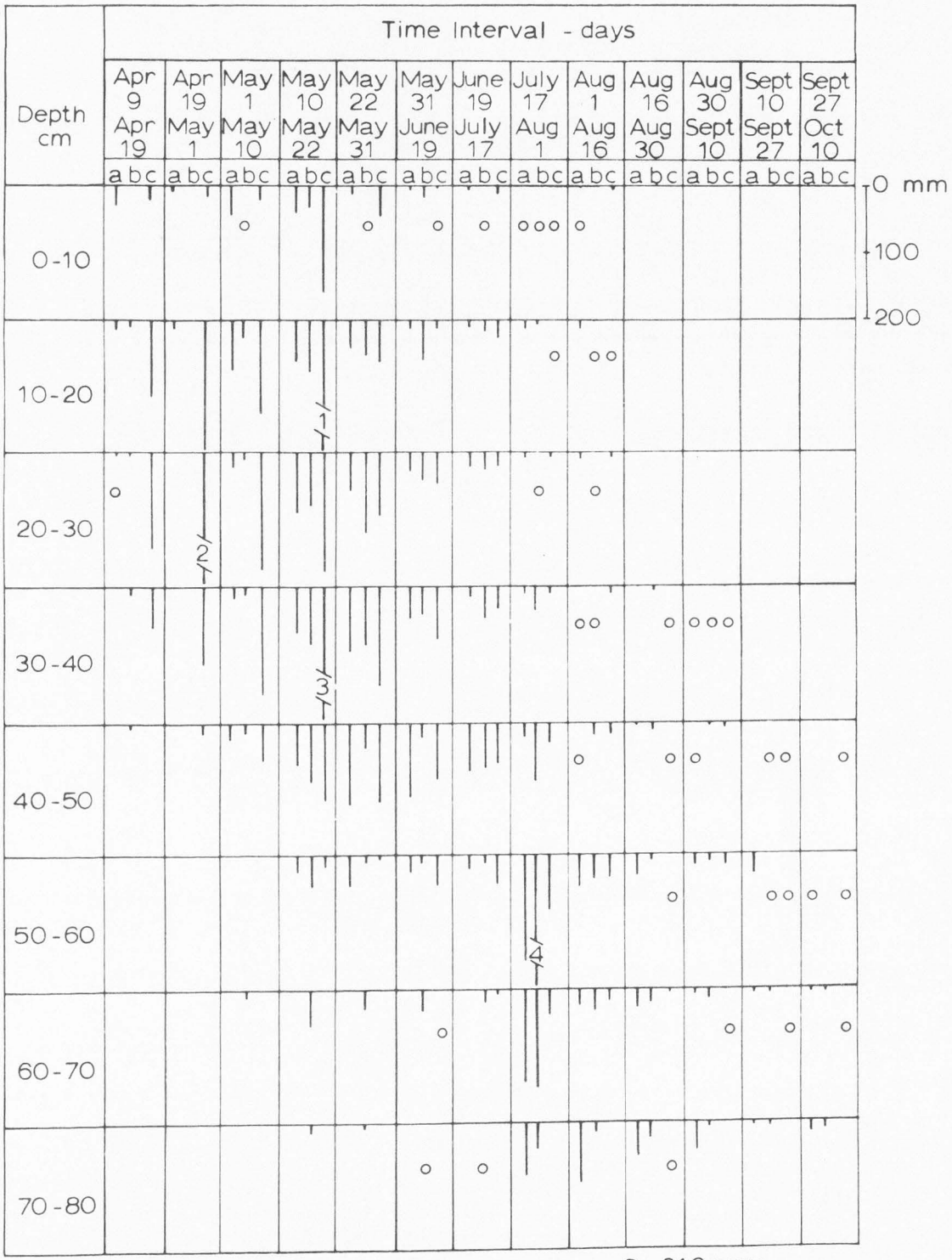
Table 1 indicates that shoot phenological stage for each species at the time that root growth observations were made. Phenological data recorded in this study were supplemented with phenological information recorded during 1973 by N. E. West (personal communication) in the same communities.

Root growth activity for the three species under study is shown in Tables 2, 3, and 4 as relative growth rates, R, in cm of root elongation per cm of existing root mass for the current year, per day. This was calculated in a manner analogous to that of aerial plant parts (Kvet et al., 1971).

$$R = \frac{\ln L_2 - \ln L_1}{t_2 - t_1}$$

where L_1 and L_2 are the total length of roots of the current season visible in the observation window at times t_1 and t_2, respectively.

A certain error may be expected in the exact value for the R index, since the L_2 values account also for some of the new principal roots appearing in the window which were not present at time t_1. This should not materially affect the interpretation of these results of relative root activity.



a = Atriplex confertifolia
b = Ceratoides lanata
c = Artemisia tridentata

o = >5mm
1 = 270 mm
2 = 350 mm
3 = 210 mm
4 = 280 mm

Table 1. Shoot phenology of Atriplex confertifolia, Ceratoides lanata, and Artemisia tridentata at the date of each root observation.

Date	Atriplex confertifolia	Ceratoides lanata	Artemisia tridentata
April 9	Winter dormancy	Winter dormancy	Winter dormancy
April 19	Regreening of leaves and apical buds swelling	Regreening of leaves and apical buds swelling	Regreening of leaves and apical buds swelling
May 1	Regreening of leaves and apical buds swelling Twig elongation	Twig elongation	Twig elongation
May 10	Twig elongation	Twig elongation	Twig elongation
May 22	Twig elongation Floral buds developing	Twig elongation Floral buds developing	Twig elongation Floral buds developing
May 31	Flowers opening	Floral bud developing. Some twig elongation	Twig elongation Floral bud developing
June 19	Flower opening and initiation fruit developing	Flower opening	Floral bud developing
July 17	Fruit developing Male flowers dying	Fruit developing	Flower opening
August 1	Fruit developing	Fruit developing	Fruit developing
August 16	Fruit developing	Fruit developing	Fruit developing
August 30	Fruit developing	Fruit developing Some leaf bud swelling	Fruit developing Some leaf bud swelling
Sept. 10	Fruit developing	Fruit developing Begin fruit dissemination Leaf bud swelling	Fruit developing Begin fruit dissemination
Sept. 27	Fruit developing Leaf bud swelling	Fruit dissemination Leaf bud swelling	Fruit dissemination
Oct. 10	Fruit developing Leaf bud swelling	Fruit dissemination Leaf bud swelling	Fruit dissemination
Oct. 27	Leaf bud swelling	Leaf bud swelling	Leaf bud swelling

By the simple comparison of the indexes it is difficult to deduce if any of the species has the potential of a higher rate of growth per unit root material than the other two. This is because the R values are quite similar and vary considerably with depth for species at any observation time.

The R index provides valuable information on root activity. Their period of maximum growth activity as expressed by the R index occurred early in the growth season for all three species.

The progression of the root growth activity from the upper to the lower soil horizons for these species is clearly depicted in Tables 2, 3, and 4. Atriplex showed the maximum rate of change of root activity in response to depth. At the same time it appeared to have the most active root system later in the season in the lower soil horizons.

Root Branching and Distribution Pattern

It was considered that the number of points of initial contact of growth root tips with the nearly vertical plexiglass pane may give an index of the spatial root distribution in the different soil layers and of the manner in which the soil volume is occupied by the roots of these three species. This approach is very similar to the trench method employed by several investigators (Weaver, 1919; Havis, 1938; Nechaeva, 1968; Kochenderfer, 1972) who had similar objectives.

The average value of root intersection per 100 cm^2 for one root observation box divided in two window panels in increments of 10-cm

Table 2. Relative growth rate for the root growth of Atriplex confertifolia, 1973 growing season.

Depth cm.	Window	cm $cm^{-1} day^{-1}$													
		April 9 April 19	April 19 May 1	May 1 May 10	May 10 May 22	May 22 May 31	May 31 June 19	June 19 July 17	July 17 Aug. 1	Aug. 1 Aug. 16	Aug. 16 Aug. 30	Aug. 30 Sept. 10	Sept. 10 Sept. 27	Sept. 27 Oct. 10	Oct. 10 Oct. 27
0-10	1				0.21	0.03	5.69×10^{-3}	7.98×10^{-3}	5.91×10^{-3}	1.06×10^{-3}					
	2		0.02	0.07	3.60×10^{-3}	2.07×10^{-3}	2.55×10^{-3}	1.91×10^{-3}							
10-20	1				0.10	0.04	0.01	8.42×10^{-3}	8.84×10^{-3}	7.58×10^{-3}	3.29×10^{-4}				
	2		0.05	0.12	0.04	0.01	2.52×10^{-3}	1.04×10^{-3}	2.55×10^{-3}	2.10×10^{-3}					
20-30	1	0.10	8.14×10^{-3}	0.18	0.11	0.03	9.51×10^{-3}	7.34×10^{-3}	3.69×10^{-3}	5.16×10^{-3}					
	2				0.25	0.05	0.02	9.58×10^{-3}	3.34×10^{-3}						
30-40	1				0.16	0.08	0.02	0.01	5.60×10^{-3}	3.50×10^{-4}					
	2				0.15	0.06	0.03	7.70×10^{-3}	7.45×10^{-4}			3.48×10^{-4}			
40-50	1				0.22	0.09	0.05	0.02	3.55×10^{-3}	2.51×10^{-4}	1.17×10^{-3}	3.81×10^{-4}	1.59×10^{-4}		
	2				0.09	0.07	0.02	0.01	3.14×10^{-3}		6.95×10^{-4}	2.01×10^{-4}			
50-60	1							0.04	0.09	4.40×10^{-3}	3.37×10^{-3}	5.36×10^{-4}			
	2					0.10	0.02	0.01	0.04	0.01	7.85×10^{-3}	4.15×10^{-3}	7.25×10^{-3}	4.30×10^{-4}	3.77×10^{-4}
60-70	1									8.62×10^{-3}	3.77×10^{-3}	2.77×10^{-3}			5.05×10^{-4}
	2									0.02	0.01	3.33×10^{-3}	3.59×10^{-3}	2.56×10^{-3}	
70-80	1									0.02	2.41×10^{-3}	2.14×10^{-3}	1.35×10^{-3}	2.52×10^{-3}	1.46×10^{-3}
	2									0.08	0.05	0.01	2.43×10^{-3}	4.59×10^{-3}	5.74×10^{-4}
Total	1	0.10	8.14×10^{-3}	0.27	0.13	0.05	0.03	0.01	0.02	4.46×10^{-3}	1.25×10^{-3}	5.61×10^{-4}	1.62×10^{-4}	2.22×10^{-4}	2.39×10^{-4}
	2		0.03	0.11	0.06	0.04	0.02	7.65×10^{-3}	0.02	9.06×10^{-3}	9.39×10^{-3}	3.58×10^{-3}	2.51×10^{-3}	1.19×10^{-3}	1.95×10^{-4}

Table 3. Relative growth rate for the root growth of Ceratoides lanata, 1973 growing season.

Depth cm.	Window	cm $cm^{-1} day^{-1}$												
		April 9 April 19	April 19 May 10	May 10 May 22	May 22 May 31	May 31 June 19	June 19 July 17	July 17 Aug. 1	Aug. 1 Aug. 16	Aug. 16 Aug. 30	Aug. 30 Sept. 10	Sept. 10 Sept. 27	Sept. 27 Oct. 10	Oct. 10 Oct. 27
0-10	1			0.15	9.11×10^{-3}	0.03	3.05×10^{-4}							
	2		0.06	0.08	8.45×10^{-3}	3.97×10^{-3}	4.85×10^{-3}							
10-20	1	0.05	0.03	0.10	0.02	0.02	4.07×10^{-3}	5.93×10^{-4}	2.69×10^{-4}					
	2	0.08	0.09	0.04	0.04	0.03	4.75×10^{-3}	3.27×10^{-3}						
20-30	1	0.14	0.04	0.10	0.08	0.01	0.01	1.28×10^{-3}	1.70×10^{-3}	8.93×10^{-4}				
	2	0.06	0.12	0.18	0.05	0.02	6.34×10^{-3}							
30-40	1		0.05	0.08	0.04	0.01	0.01	4.86×10^{-3}	6.62×10^{-4}	3.55×10^{-3}				
	2			0.16	0.05	0.02	0.02	0.01	3.07×10^{-4}		2.33×10^{-4}			
40-50	1		0.06	0.11	5.54×10^{-3}	0.01	0.03	0.02	4.55×10^{-3}	2.84×10^{-3}	1.21×10^{-3}			
	2			0.07	0.04	0.01	0.01	0.02	1.96×10^{-3}	9.78×10^{-4}	4.87×10^{-4}	9.15×10^{-4}		
50-60	1				0.05	0.04	0.02	0.11	8.78×10^{-3}	2.58×10^{-3}	2.80×10^{-3}	2.85×10^{-4}		
	2			0.05	5.89×10^{-3}	2.21×10^{-3}	2.53×10^{-3}	0.05	2.24×10^{-3}	2.02×10^{-4}	2.57×10^{-4}			
60-70	1					0.06	0.02	0.05	0.01	8.87×10^{-3}	5.12×10^{-3}	1.80×10^{-3}	1.66×10^{-3}	1.13×10^{-3}
	2			0.11	0.01	0.02	3.38×10^{-3}	0.04	1.12×10^{-3}	1.33×10^{-3}	9.89×10^{-4}	7.51×10^{-4}	7.67×10^{-4}	4.07×10^{-4}
70-80	1								0.04	0.04	5.32×10^{-3}	4.06×10^{-3}	0.01	6.45×10^{-4}
	2				0.04	3.67×10^{-3}	5.51×10^{-3}	0.06	8.02×10^{-3}	0.01	6.11×10^{-3}	5.50×10^{-3}	5.91×10^{-3}	5.51×10^{-4}
Total	1	0.13	0.04	0.11	0.04	0.02	0.01	0.02	5.62×10^{-3}	4.09×10^{-3}	1.80×10^{-3}	4.84×10^{-4}	7.17×10^{-4}	4.63×10^{-4}
	2	0.07	0.14	0.08	0.03	0.02	7.53×10^{-3}	0.02	1.34×10^{-3}	9.69×10^{-4}	7.29×10^{-4}	6.26×10^{-4}	5.28×10^{-4}	9.70×10^{-5}

Table 4. Relative growth rate for the root growth of Artemisia tridentata, 1973 growing season.

Depth cm.	Window	cm cm^{-1} day^{-1}													
		April 9 April 19	April 19 May 1	May 1 May 10	May 10 May 22	May 22 May 31	May 31 June 19	June 19 July 17	July 17 Aug. 1	Aug. 1 Aug. 16	Aug. 16 Aug. 30	Aug. 30 Sept. 10	Sept. 10 Sept. 27	Sept. 27 Oct. 10	Oct. 10 Oct. 27
0-10	1	0.04		$1.83x10^{-3}$	0.14	0.02	$3.72x10^{-4}$	$3.29x10^{-3}$	$1.31x10^{-3}$	$2.15x10^{-3}$					
	2	0.10	0.05	0.05	0.08	$8.99x10^{-3}$	$2.12x10^{-3}$	$4.75x10^{-3}$		$5.09x10^{-4}$	$7.18x10^{-4}$				
10-20	1	0.07	0.06	0.02	0.04	$8.64x10^{-3}$	$2.37x10^{-4}$	$2.68x10^{-3}$	$1.54x10^{-4}$	$2.46x10^{-4}$					
	2	0.07	0.05	0.04	0.03	$3.54x10^{-3}$	$3.06x10^{-3}$	$2.32x10^{-3}$	$1.20x10^{-4}$	$1.20x10^{-4}$	$1.12x10^{-4}$				
20-30	1	0.09	0.08	0.02	0.01	$9.44x10^{-3}$	$4.07x10^{-3}$	$1.54x10^{-3}$	$7.94x10^{-4}$	$8.18x10^{-4}$					
	2	0.07	0.08	0.03	0.03	$7.80x10^{-3}$	$4.08x10^{-3}$	$1.70x10^{-3}$	$6.17x10^{-4}$	$1.86x10^{-4}$		$1.43x10^{-4}$			
30-40	1	0.17	0.07	0.06	0.04	0.02	$5.77x10^{-3}$	$1.37x10^{-3}$	$1.22x10^{-3}$	$1.04x10^{-3}$					
	2	0.03	0.23	0.06	0.07	0.04	0.02	$7.69x10^{-3}$	$1.02x10^{-3}$	$9.32x10^{-4}$	$3.73x10^{-4}$	$7.31x10^{-4}$			
40-50	1			0.11	0.08	0.04	0.02	$7.82x10^{-3}$	$4.54x10^{-3}$	$2.15x10^{-3}$	$2.67x10^{-4}$	$1.52x10^{-3}$	$5.75x10^{-5}$		
	2			0.18	0.11	0.06	0.03	0.02	$2.29x10^{-3}$	$2.54x10^{-3}$	$3.06x10^{-4}$	$4.16x10^{-4}$	$3.21x10^{-4}$	$5.10x10^{-4}$	
50-60	1					0.02	0.05	0.02	0.02	0.02	$2.05x10^{-3}$	$8.98x10^{-3}$	$7.50x10^{-4}$	$9.68x10^{-4}$	$2.79x10^{-4}$
	2					0.03	0.10	0.03	0.03	$5.45x10^{-2}$	$2.23x10^{-4}$	$1.84x10^{-3}$			
60-70	1													0.06	0.02
	2					0.09	0.03	0.06	0.09	0.02	$4.79x10^{-3}$	$3.32x10^{-3}$	$2.37x10^{-3}$	$2.98x10^{-3}$	$4.17x10^{-3}$
Total	1	0.09	0.07	0.03	0.04	0.02	$5.22x10^{-3}$	$3.15x10^{-3}$	$2.09x10^{-3}$	$1.71x10^{-3}$	$1.43x10^{-4}$	$7.08x10^{-4}$	$1.07x10^{-4}$	$1.53x10^{-4}$	$6.14x10^{-5}$
	2	0.07	0.07	0.04	0.04	0.02	0.01	$7.07x10^{-3}$	$5.59x10^{-3}$	$2.17x10^{-3}$	$4.56x10^{-4}$	$6.56x10^{-4}$	$1.59x10^{-4}$	$2.33x10^{-4}$	$2.36x10^{-4}$

depths for Atriplex confertifolia, Ceratoides lanata and Artemisia tridentata is shown in Table 5. The distinction between roots "longer" or "shorter" than 5 cm refers to the total root length against the Plexiglass following initial contact with the pane. This was done in an attempt to obtain some information on the proportion of principal roots and small lateral rootlets. A value of 5 cm was somewhat arbitrarily selected taking into consideration that lateral roots shorter than 5 cm seldomly formed lateral roots themselves.

An assumption has to be made, that the proportion of long principal roots of which only the terminal portion is apparent against the observation pane is small, and about the same for all three species. It is apparent that the short lateral roots produced during 1973 as indicated by the intersection with the window, were rather evenly distributed in the various soil horizons down to 60 cm depth for the Atriplex- and Ceratoides-dominated communities. However, their number tended to decrease with depth for Artemisia. Approximately 60 percent more rootlets were present for Atriplex than for Ceratoides, while the value for Artemisia are noticeably higher than the other two species, but these were only in the upper 40 cm.

The ratio of "roots longer than 5 cm to shorter than 5 cm" as registered in the observation windows during the 1973 growing season, was 1:27 for Atriplex confertifolia, 1:10 for Ceratoides lanata and 1:17 for Artemisia tridentata.

Table 5. Distribution of the roots of Atriplex confertifolia, Ceratoides lanata, and Artemisia tridentata at several depths in the soil. Number of roots per 100 cm^2 in the vertical observation pane.

Depth cm	Atriplex confertifolia		Ceratoides lanata		Atremisia tridentata	
	Larger than 5 cm	Shorter than 5 cm	Larger than 5 cm	Shorter than 5 cm	Larger than 5 cm	Shorter than 5 cm
10-20	2.1	20.7	1.9	19.4	2.4	57.5
	0.5(1)	6.6	0.6	1.3	0.5	8.0
20-30	1.4	38.6	1.6	22.0	3.9	63.7
	0.4	5.1	0.4	1.6	0.7	6.4
30-40	1.7	46.6	1.9	24.4	4.0	51.2
	0.3	2.6	0.6	2.7	0.6	7.0
40-50	1.1	46.5	2.5	28.7	2.9	33.4
	0.4	3.1	0.3	3.1	0.7	2.1
50-60	0.2	44.3	3.6	27.4	0.2	29.5
	0.2	3.3	0.6	1.8	0.4	3.9

(1) Standard error of the mean.

Microscopic studies

Microscopic observations indicated that the active growing root tips of Atriplex confertifolia with a diameter of 0.06 to 0.15 mm are the thinest of the three species under study. In some cases the root apices of this species were a light brown color at the extreme distal portion. A white zone of 2 to 6 mm in length with root hairs was immediately proximal to this tip. Next followed a 3 to 10 mm zone somewhat darker in color and densely covered with root hairs. The remainder of the root was reddish-brown in color and apparently suberized (Fig. 13) but still covered with root hairs. Vigorously growing roots in the early season often had a much longer white zone of several cm in length and densely covered with root hairs.

Active root apices of Ceratoides lanata were generally 0.3 to 0.4 mm in diameter followed by a zone of 2 to 6 mm devoid of root hairs. Next was a region densely covered with root hairs. One problem in mapping or observing the actively growing roots of this species was their almost total lack of pigmentation, which makes them almost transparent and difficult to detect in the observation pane (Fig. 14a).

The change in color associated with suberization appears to be indicated by a slight yellowing with takes place at a distance of 4 to 10 mm from the root tip. The apparently suberized older root surfaces exhibited an intense pale-yellow color which easily contrasted with the soil particles. These suberized roots were almost always densely covered with root hairs (Fig. 14c).

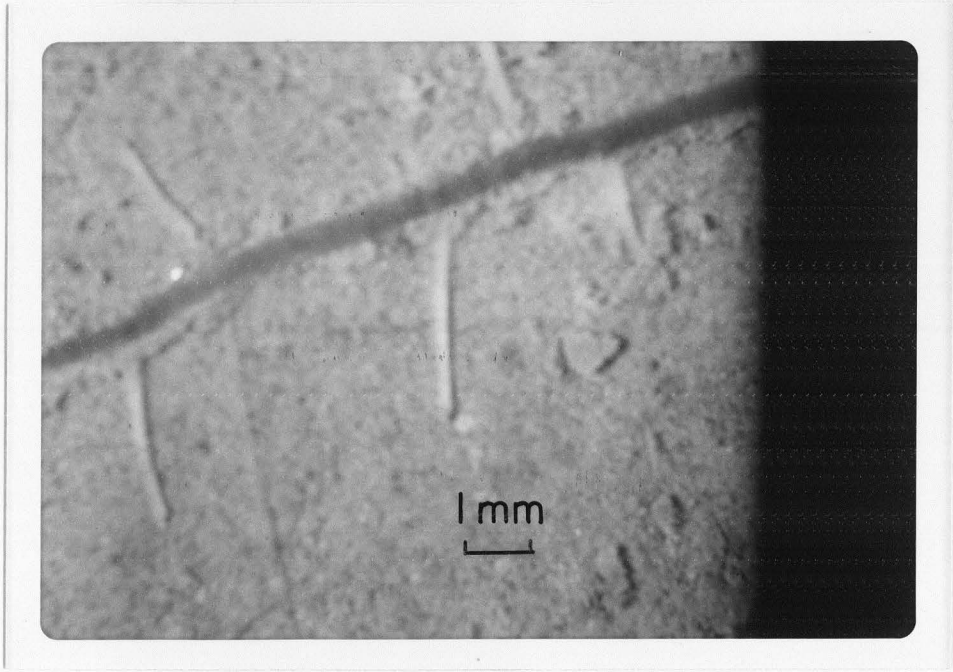


Figure 13. Photomicrograph of the root of Atriplex confertifolia.

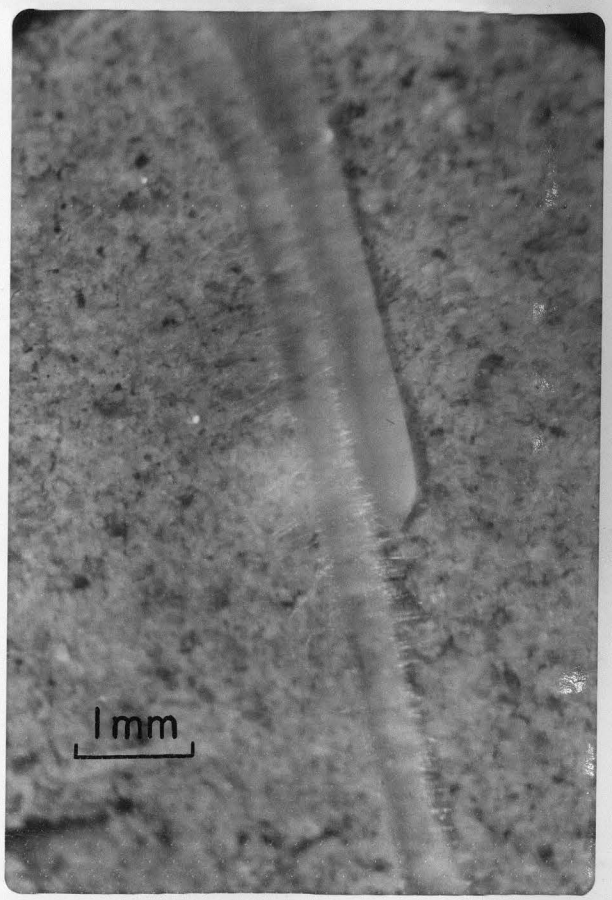
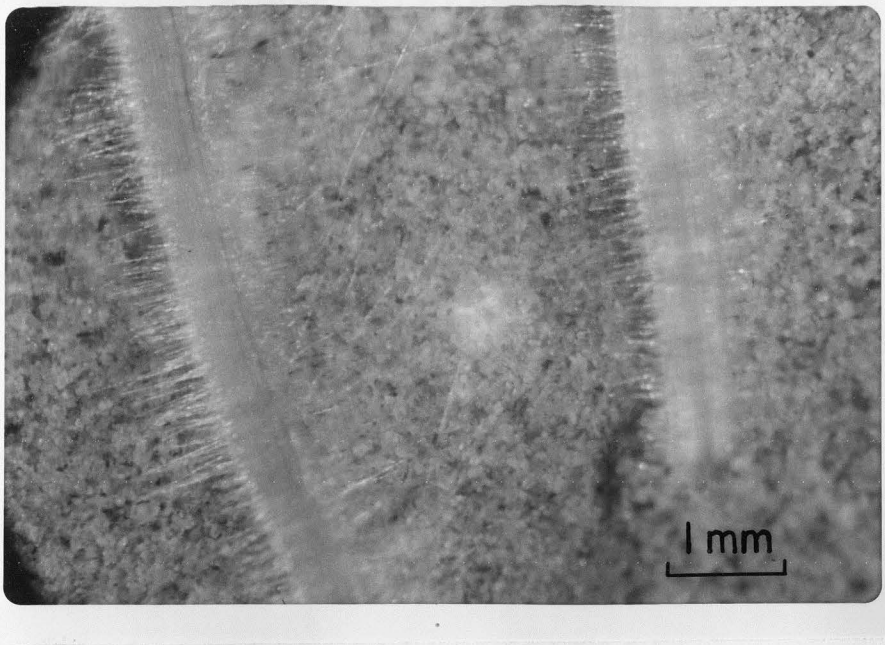
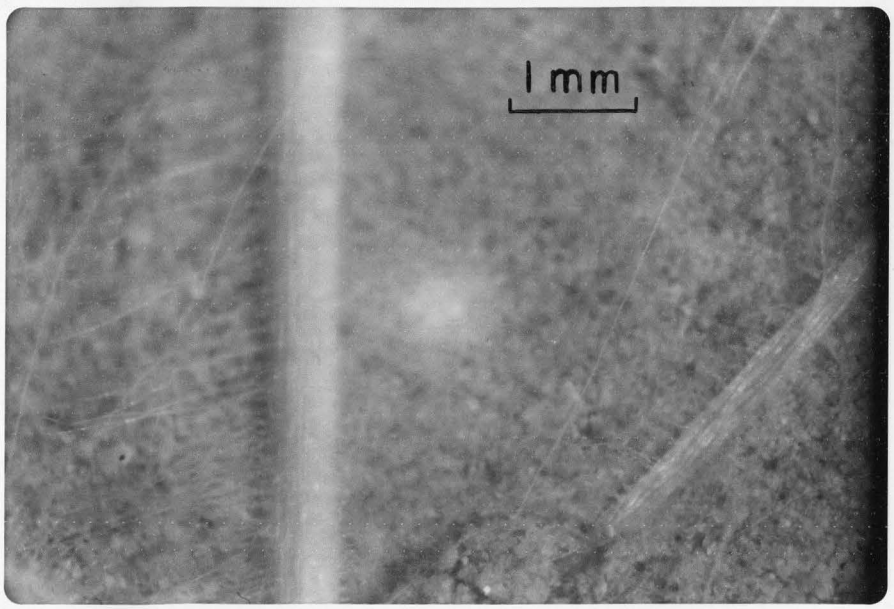


Figure 14. Photomicrograph of the root of Ceratoides lanata.
a) Details of root tips.



b) Densely root hair covered area next to the root apex.



c) Presence of root hairs in apparent suberized root portions.

Growing root tips of Artemisia tridentata were of similar diameter and morphology to Ceratoides. Characteristic of this species was the existence of numerous lateral roots which started to differentiate at a distance of 2 to 4 cm from the root tip. These laterals were usually smaller in diameter. The roots were typically dark-brown in color and apparently were suberized a few mm or sometimes several cm from the root tip. But, as was the case with the other two species they were still covered with root hairs (Fig. 15). A characteristic observed for Artemisia was the differentiation of a distinct brown cap at the extreme tip of the roots associated with the cessation of root growth (Fig. 15b). This phenomenon, known as metacutization has been noted in other species (Wilcox, 1954; Romberger, 1963; Mason et al., 1970).

For both Ceratoides and Artemisia vigorously growing roots early in the season exhibited a much longer white zone following the root apex which was usually densely covered with root hairs.

For all three species darkening of the roots associated with suberization appears to follow new root extension by 7 to 15 days early in the season. However, from August on, it was apparent that less time was required for suberization to take place following root extension.

The apical meristem of the main extension roots of these species may remain active for a considerable time, while rapidly growing lateral arising from these main roots seldomly were active longer than one or two weeks.

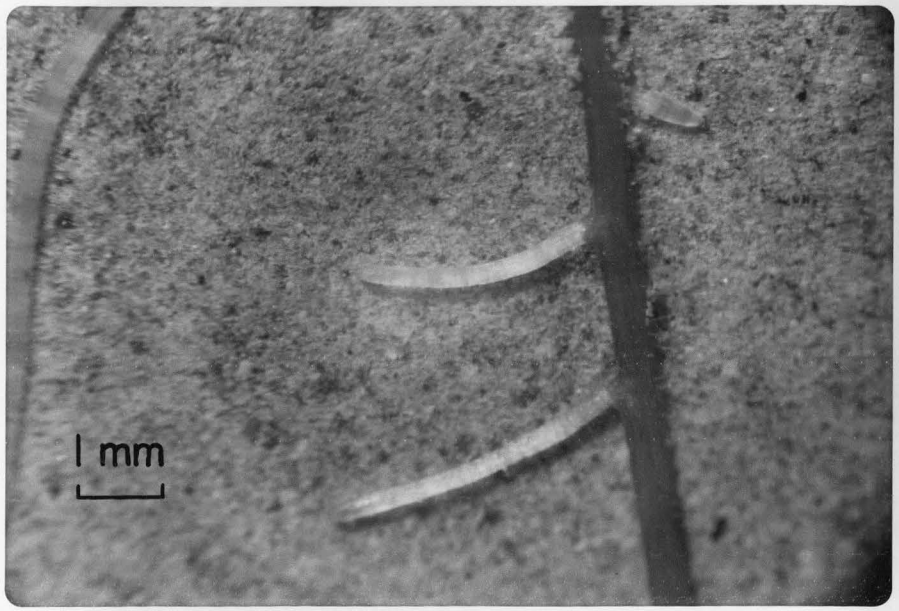
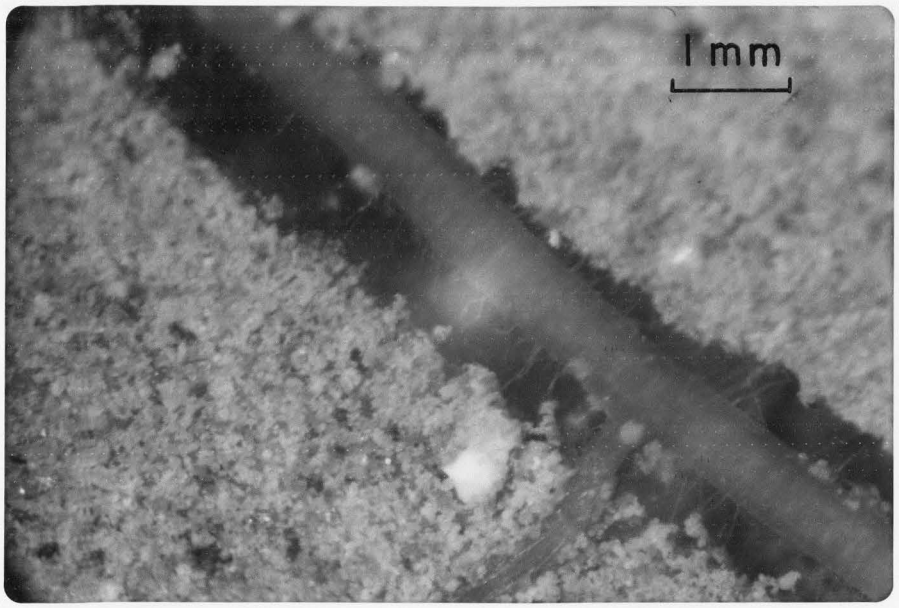


Figure 15. Photomicrograph of the roots of Artemisia tridentata.
a) Apparently suberized root with actively growing new laterals.

b) Rootlets showing metacutization-type layer covering the root apex.



c) Apparently suberized root showing persistant root hairs.

Some of the main extension roots and a few of their laterals tended to increase in diameter. Root thickening was also observed in roots in which apical growth had already ceased. The maximum rate of thickening was observed for a single root of Atriplex which appeared in the window on May 10 and by the end of the season was over 2 mm in diameter. This represents more than a 10-fold increase in diameter; however, growth in diameter during the growing season for these three species was usually on the order of no more than two or three times the initial diameter. It is apparent that the main roots and some of their lateral elements are primarily responsible for extension of the root system.

The short rootlets may grow from a few mm to a few cm in length, but usually they do not show any significant increase in thickness.

Active and inactive apical meristems were easily detected with the microscope. An inactive meristem was apparently completely suberized including the root apex. Moreover, cessation of meristematic activity was indicated by a light brown color for Atriplex and the metacutization zone in Artemisia, which remains visible for some time because the rest of the root tends to darken slowly.

A noticeable feature of the roots of all three species was the presence of root hairs over most of the root surface, including the apparently suberized portions. Persistence of root hairs for long periods of time has been observed by Jeffrey and Torrey (1921) in woody species of Aster and by McDougall (1921) in several woody legumes. A similar report was given by Whitaker (1923) for various

members of the Compositae family. Roots totally covered by root hairs in three grasses were mentioned also by Dittmer (1938)

Root hairs in Atriplex confertifolia were still visible during 1973 for suberized roots of the previous year.

Near the root tip, the newly formed root hairs are whitish or colorless for the three species (Fig. 14a,b and 15a). Root hairs in suberized older segments appeared stiff and rigid and sometimes broken through the microscope. Their color was light brown for Atriplex and Artemisia and pale yellow for Ceratoides. In the latter species these persistent root hairs were longer than in the other two species.

There were also some places on the roots where these hairs were absent, probably because of replacement of the epidermis or movement of the roots through the soil which resulted in sloughing of the root hairs.

Discussion

The plants whose roots were under study were growing in their natural habitat with no indication of disturbance due to the presence of the boxes, except for the obstruction imposed by the observation panes.

Two physical factors are recognized as particularly important in influencing root growth. They are availability of water and temperature. No significant differences were found between the temperature and Ψ_s in the undisturbed soil community and in the soil next to the observation window. The internal temperature of the

chambers was controlled by the temperature of the soil surrounding five sides of the chambers. During the winter they were covered above by snow.

One factor that could affect the Ψ_s in the soil-window interphase could be water from precipitation running down the outside face of the window pane where it interfaces with the soil profile. This effect was never observed in this study. Root visibility was never blurred during the two years of observation.

Initiation of significant growth activity in the spring occurred a few days earlier for roots than for aerial plant parts for the three species under study. A similar conclusion has been reported by Fedorova (1968) for sand desert shrubs. Active root growth extended into the first week of September for Ceratoides and Artemisia and almost one month later for Atriplex. However, small increments of root growth were recorded as late as January 18, 1974, when the soil surface was frozen, although active shoot growth for the three species ended much earlier in July. This observation would indicate that the root system of these species is never completely dormant during the winter. Uninterrupted activity of root growth during the winter at soil temperatures near freezing has been recorded by Collison (1935) for apple trees. Bahr et al. (1970) reported that root growth of Prunus cerasifera continued through the winter in Canada.

The soil provides a reasonably stable environment for roots. The seasonal trends of temperature and Ψ_s are repeated each year, although the timing and magnitude may vary from year to year. There are no sudden or drastic changes in temperature as occurs in the aerial

environment, although changes in Ψ_s can be quite considerable during the growing season. Once the surface of the soil is frozen it acts as a protective barrier against further cooling of underground layers. For example, the temperature inside the chambers never was below freezing. The temperature of the soil next to the window at 65 cm depth was in the range of 6 to 8°C during the second week of November, while at 95 cm it was 1 to 1.5°C higher. Similarly, the soil temperature was around 3 and 4°C at the 65 and 95 cm depths respectively during the first week of January, 1974.

The changes in root growth activity with time and the progression of root growth from the upper to lower soil horizons during the season, as expressed by the relative growth rate or the absolute quantity of new roots recorded for each observation date, would indicate a cyclic change of root growth with depth through the growing season for the three species. The cyclic root growth activity of perennial plants has been reported for fruit trees (Rogers, 1939b; Kolesmikov, 1968; Rogers and Head, 1969) and forest trees (Wilcox, 1954; Lyr and Hoffman, 1968; Ovington and Murray, 1968; Fedorova, 1968; Mason et al., 1970; McDougall, 1916). However, no reports have been found which would indicate a vertical change in root activity with depth as suggested by this study.

The response of root growth activity through the growing season as related to progressive depths appeared to be more conspicuous for Atriplex than for the other two species. Moreover, Atriplex exhibited the most root system activity in the season at the lower soil horizons.

The pattern of root growth activity observed for these species through the growing season with increasing depths could be associated in part with the cyclic changes in temperature and Ψ_s in the soil. The rapid initial root growth near the soil surface early in the spring was related to the abundance of water after thawing of the upper soil layers in combination with a rapid increase of soil temperature in that region. In general, root growth slowed as the soil water potential decreased in each layer of the soil profile. Soil water potentials reached minimum values during the month of August, being slightly higher at lower depths (Moore and Caldwell, 1972). However, small increments of root growth were recorded even at Ψ_s around -70 bars at 40 cm depth during August, 1972. None of the three species interrupted their root growth at the lowest water potentials around -60 bars registered during the 1973 growing season. It is evidence that these species are capable of extracting enough moisture to transpire at water potentials at which mesophytic plants cannot survive (Moore, White and Caldwell, 1972). Cowling (1969) reported root growth for up to 60 days in Atriplex vesicaria if another portion of the root system was in a more favorable moisture condition. He did not, however, determine water potential in these soils.

The limited root activity near the soil surface after June and July was correlated not only with the lower Ψ_s observered there when compared to the deeper soil layers, but also with the higher temperature of the soil near the surface (Figs. 8, 9, and 10). Cessation of root growth attributed to higher temperatures in the upper soil level during the hottest months seems to be a common occurrence for some grasses (Brown, 1939; Stuckey, 1941).

The soil temperatures at which maximum root activity was registered for these three shrub species appear to indicate that the optimum temperature for root growth may be in the approximate range of 13 to 18°C. Root growth activity will tend to slow down at lower temperatures. Lyford and Wilson (1966) found that the rate of growth of red maple root tips was highly sensitive to temperature change. They also estimated that the optimum temperature for root growth appeared to be around 12 to 15°C.

Although the root system of these three species as a whole grew actively for a span of several months, the growth of individual apical meristems was usually limited to one to several weeks depending on the time of the year and whether or not it was a rootlet or a primary extension root.

At any soil depth not all the roots were growing at the same time. Even during the periods of maximum root growth activity, only a fraction of the roots were actively growing. A flush of root activity below the 50 to 60 cm depth was observed for Ceratoides lanata and Atriplex confertifolia during the second half of July, as indicated by their respective relative growth index (Tables 2, 3 and 4) and their absolute increments in root growth (Fig. 12). This enhancement of root activity appears to be associated with changes in shoot phenology occurring at that time. For both species it appeared to be correlated with the transition from the phenological stage of flowering and fertilization to that of fruit development.

There is no doubt that root growth is influenced by the physical environment, but in addition it is governed by the distribution of photosynthates between the roots and the aerial plant organs. The

development of the shoot shows a substantial variation during the growing season and will seemingly alter the balance of energy partitioning between shoot and root. It seems reasonable that shoot energy requirements are higher during the active flowering process than later during fruit development, where there is no other significant growing vegetative activity occurring except the filling of the small seeds.

After fertilization occurs increased quantities of assimilates can be diverted to the underground organs, as was indicated by a second seasonal peak of root activity observed at that time at lower depths.

The size and spatial distribution of the root system and the relative abundance of root elements in the different soil layers determine the volume of soil which can be exploited. Heredity plays an important role in characteristics such as distribution, degree of branching and physiological attributes. The extent to which the hereditary characters are expressed may depend on environmental conditions such as soil physical properties, available moisture, impermeable soil layers, and the inherent plasticity of each species. Cannon (1911) and Dittmer (1948) concluded that heredity played a more important role than edaphic conditions determining the pattern of root distribution in the soil. The significance of the genetic variation among plant root systems has been treated in detail by Throughton and Whittington (1969).

It is known that the capacity for water and nutrient uptake is more related to root length and surface area than to total biomass of roots. The thin rootlets represent the most active absorption

organs of the root system. The root absorbing ability for these species will be dependent on their absorbing capacity per unit root area and their rate of extension in the soil. These concepts are analogous to net assimilation rate and relative growth rate indices of foliage. Gardner (1964) and Cowan (1965) discussed the significance that the total root length per unit soil volume has in the absorption of water. Miller (1916) attributed the greater drought resistance of sorghum as compared to maize to the fact that the former had a much more finely divided root system.

An indication of the root density and distribution in the soil in 1973 for these species as recorded in the root observation chambers is given in Table 5. Atriplex and Ceratoides have a rather uniform rate of root distribution down to considerable depths, while root density rapidly decreases for Artemisia. The data collected during 1973 suggest that Atriplex tends to explore the soil volume at greater depths with a more profuse system of small lateral rootlets than the other two species.

One factor that may contribute to the shallower root habitat of the roots of Artemisia tridentata could be the presence of a calcium carbonate layer much nearer the soil surface (Skujins and West, 1973). Moore and Caldwell (1972) also reported a considerable increase in the salt content of these soils at depths of 60 cm. High concentrations of salts may limit root penetration in the soil since Artemisia is not considered a halophyte.

The underground organs have an important bearing in the photosynthetic activity of plants of arid regions. Stomata aperture is ultimately controlled by water absorbed through the root system.

DePuit and Caldwell (1973) reported that the amount of available moisture seems to be a major factor affecting photosynthetic rates in Artemisia throughout the growing season. Plants growing in the same place may have developed different capacities for the extraction of water in desert soils, which would be dependent on their strategies for root distribution, total length of roots per unit soil volume, as well as the rate of root extension and root phenology during the growing season.

Patterns of photosynthetic activity and transpiration have been previously studied for Atriplex and Ceratoides in Curlew Valley (Caldwell, 1972). It has been observed in those studies that Ceratoides curtailed almost all photosynthesis and transpiratory activity by the first part of August, while photosynthesis continued much later in the season for Atriplex. It can be hypothesized that the cessation of transpiration of Ceratoides in contrast to continued transpiratory activity for Atriplex may be related to "root factors", since aerial environmental conditions were similar for both species. Limitations in water uptake may be a prime factor forcing Ceratoides into a stage of summer dormancy. The noticeably higher proportions of rootlets per unit soil volume observed for Atriplex in comparison to Ceratoides (Table 5) could suggest a greater capacity for water extraction from the soil and therefore more transpiration later in the season. Moreover, root growth activity appeared to be more pronounced later in the season for Atriplex than for the other two species.

It could also be, that the root systems of Atriplex and Ceratoides undergo different phenological phases. Water absorption by the roots

of the latter species could be limited by a stage of reduced absorptive activity as a part of the normal phenological cycle.

The high root/shoot biomass observed for plants of cool desert habitats (Rodin and Bazilevich, 1965; Federova, 1968; Shalyt and Zhivotenko, 1968; Sveshnikova, 1968) and for *Atriplex* and *Ceratoides* in this study and earlier by Bjerregaard (1971) is not unexpected since due to the low moisture availability of these soils the efficiency of water extraction per unit root-absorbing surface will tend to diminish.

Since in order to carry on photosynthesis, plants are commited to transpiration, each unit of shoot transpiring surface requires a larger root surface in contact with the soil than would be the case for plants under more mesic environments.

Even though the shoot and root biomass calculations for *Atriplex* and *Ceratoides* in this study and those of Bjerregaard (1971) showed some differences, both studies are constant in indicating a much higher root/shoot ratio for *Ceratoides* than for *Atriplex*.

A common characteristic of the root system of these three species was the presence of root hairs covering most of the root surface including the apparently suberized areas. Dittmer (1949) reported that root hairs can be quite persistant structures which are able to withstand the effects of considerable secondary thickening before being sloughed off. Cross sections of persistant root hairs made by McDougall (1921) in *Gleditsia triacanthos* showed that they were thick-walled root hairs which were stiff and rigid and did not shrivel when exposed to the air. They are not structures related

exclusively to xeric conditions since they may be present in plants from very different habitats.

It is generally accepted that the presence of root hairs is correlated with the process of absorption of water and salts. No attempt was made in the present study to investigate the functional characteristics of these structures, so it is difficult to evaluate their ecological importance. The length of the time these hairs could remain alive and functional in the soil as well as their anatomical characteristics deserve further research.

The formation of a brown cap over the root tip was often observed within a few days after growth ceased in the roots of Artemisia tridentata. The formation of this layer was referred to as Metakutisierung by German workers (Romberger, 1963). This process has since been Anglicized by Wilcox (1954) to "metacutization". No detailed studies have been conducted on this phenomenon of apparent metacutized root tips for Artemisia, except for the microscopic observations through the Plexiglass panes. However, the browning and anatomical changes recorded for the root tips of this species are similar to those reviewed by Romberger (1963) when he discusses this process in detail. The browning appears to be associated with a dual process of lignification and suberization which forms a continuous sheet over the whole apex isolating the root tip from the external environment. Metacutization is associated more with dormancy than with root senescence. Wilcox (1954) observed in Abies procera that root growth may be reinitiated by breaking through the root cap. He also associated the presence of these suberized layers with a protective function for the resting meristem.

Root tips of Atriplex were occasionally observed to be light brown in color and opaque whereas the root apex of Ceratoides was always clear or milky white and almost transparent.

An attempt to detect endotrophic and ecotrophic mycorrhizal hyphae on the roots of Atriplex confertifolia growing under similar conditions in the glasshouse was not successful. However, it cannot be concluded that they do not exist in the field. Since the functioning of higher plant roots appears to be in intimate association with the rhizosphere microbes, research on this point is certainly needed. In over 37 species studied by Dittmer (1949) there was not a single one which did not have associated fungal hyphae.

At the lower Ψ_s of these soils during much of the growing season, negligible water movement in the soil would be expected. Water and nutrient uptake then most probably occurs through new root growth into unexplored soil regions. Kramer (1940, 1969) considered that the capillary movement of water by itself is not enough in many occasions to adequately supply a plant with water, as an important factor in water availability to plants is given by continuous exploration of the soil by means of new root growth. The mechanism of water flow from the soil to the root surface has been treated in detail by Klute and Peters (1969).

The short duration of active growth exhibited by many of the rootlets in the species under study may be associated with the depletion of water in the immediate vicinity, which may induce metabolic changes affecting the root meristematic activity. Street (1969) reported that increased amounts of hormone-like growth factors at the root meristem may have an inhibitory effect on root growth.

The thick, perennial, well-suberized root system may develop gradually in each of these species depending on their genetic potential, age, and the limitations imposed by environmental factors. The primary absorbing surfaces are most certainly the small rootlets in the main root system. It is postulated in this study that periodic sloughing and replacement of new rootlets is most likely the mechanism whereby the root system extends into new soil areas or may repeatedly re-explore areas occupied previously.

The principle of continual death and renewal of small roots in perennial species is not new. It has been suggested by botanists since the end of the last century (Romberger, 1963). However, it has not yet been clearly demonstrated.

Head (1971, 1973) observed the rotting of individual small rootlets. Small rootlets may decay in fruit trees after several months or sometimes after 2 or 3 years, or the whole network may decay at one time. A natural cyclic renewal of roots has been proposed by Kolesnikov (1968) for fruit trees.

Although individual roots were observed for Atriplex during two years and during the growing season of 1973 for the other two species, it was impossible to discern root death. The low water potential of these soils is probably not conducive to a rapid rotting of dead roots. Extensive root decay was never observed in any of the windows. Most of the rootlets of Atriplex in 1972 were still present in 1973. However, a few of them were obviously rotting away and others had totally disappeared. This phenomenon was only occasionally observed for Ceratoides lanata or Artemisia tridentata.

CHAPTER IV

PARTITIONING OF ^{14}C-PHOTOSYNTHATES

Introduction

The success of a plant community in a given habitat can in part be related to an appropriate balance in the utilization of available energy for survival and reproductive processes. The mode of this utilization has been fixed for each species with different degrees of environmental plasticity through genotypic selection. Energy allocation can be considered a hereditary phenological event (Cody, 1966), whose expression, to a greater or lesser extent, can be modified by environmental conditions.

A reasonable knowledge of plant community energy fixation and distribution to the above-ground and below-ground plant organs is one of the requisites for an understanding of plant community energetics.

Complete information for any given plant species rarely exists. A study by Harper and Ogden (1970) on the partitioning of dry matter and energy in Senecio vulgaris is probably one of the most detailed works on this subject. The knowledge of the carbon balance of plants has recently been thoroughly reviewed by Mooney (1972).

Because carbon allocation represents the distribution of energy trapped during photosynthesis, carbon-14 tracer techniques offer a unique opportunity for the study of the utilization and transfer of energy on an individual plant or a whole community basis. In this study ^{14}C distribution and accumulation in the different plant parts was used as a basic index of photosynthate allocation (Kortschack et al., 1965; Evans and Wardlaw, 1966; Dahlman and Kucera, 1967; Hansen, 1967; Hartt and Kortschack, 1967; Gordon and Larson, 1968; Marshall and Sagar, 1968; Ursino et al., 1968; Hofstra and Nelson, 1969; Kriedeman, 1969; Easting, 1970; Lovell and Lovell, 1970; Quinlan and Weaver, 1970; Dochel et al., 1972).

Monospecific stands of Atriplex confertifolia and Ceratoides lanata were selected for this study. This was the only way to assume that the root samples collected during this work were only those of a single species. These communities were defined by distinct alternes. Their respective areas were calculated and found to be approximately 6000 m^2 for Atriplex and 3000 m^2 for Ceratoides.

The study of the seasonal pattern of photo-assimilated ^{14}C transfer from foliage to the different plant parts was done three times during the growing season, in April, July and September. The study of the quantitative allocation of fixed carbon to above- and below-gound plant parts on a community basis was done only in July and September.

Materials and Methods

Labeling of the plants with ^{14}C

To conduct this study on a community level basis a 4.8-m^2 plot in each community was selected for application of $^{14}CO_2$. Working with individual plants was impossible because it was not feasible to extract all the roots of a single plant. Also this would not be representative of underground biomass unless numerous plants were extracted. To treat isolated plants is also unrealistic since they do not represent plants in the community interacting with other plants.

At three times during the growing season, air-tight plastic film tents were erected over these 2.2 x 2.2 m plots in the Atriplex confertifolia and Ceratoides lanata communities (Fig. 16). Labeling coincided with significant phenological events in the growing season: early spring regrowth, reproductive organ development and immediately following cessation of shoot growth.

Labeling the plants was initiated at dawn with the radiocarbon liberated inside the polyethylene tent. Five mC of $^{14}CO_2$ gas was released by reacting labeled barium carbonate with an excess of lactic acid solution. Plants were allowed to assimilate the $^{14}CO_2$ for four to five hours during which time a small fan provided air mixing inside the enclosure. Soil, air and leaf temperature inside the tent were recorded with thermocouples.

In July and September, the tent was removed when leaf temperature reached 45°C to prevent heat damage

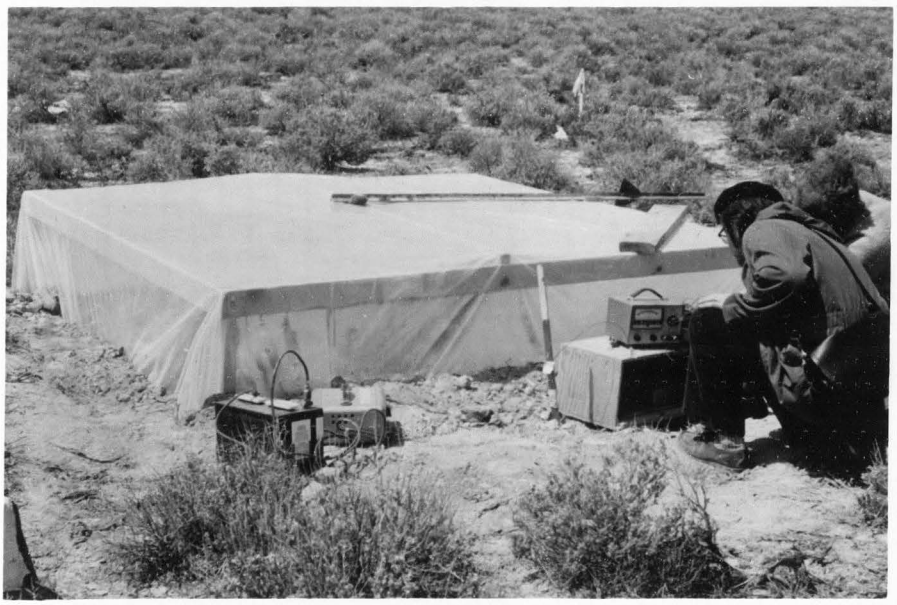


Figure 16. General view of the plastic film tent employed for tagging the experimental plots with $^{14}CO_2$.

to the plants. It was found that the use of one or two layers of cheesecloth screening over the tent was efficient in delaying temperature increase.

This technique permitted the labeling of a rather large experimental plot *in situ* with minimal disturbance of the site. No expensive equipment was needed for temperature control and no residual undue damage was noted on the plants during the remainder of the growing season. With some modifications this method is similar to that employed by Dahlman and Kucera (1965, 1968) on a tall grass prairie.

The tagged plants in each plot were utilized to gather information on the partitioning of ^{14}C-photosynthates to various plant parts and the total allocation of this carbon to above- and below-ground productivity on a community basis. Different procedures and techniques were employed in collecting and preparing the samples for analysis of radioactivity for each of these two objectives.

For reasons of convenience in this work the term "partitioning" is used to refer to carbon distribution to plant parts on the basis of unit weight of dry tissue, while "allocation" is used to denote carbon transport and accumulation in a community ground area basis.

To determine deployment of ^{14}C to several organs of the plants 72 hours after labeling, three plants were completely harvested, including their root system and immediately chilled with ice. In order not to disturb the soil for subsequent root core sampling as is explained below, only plants outside of a central 1.2-m^2 plot were collected for this purpose.

The harvested samples were brought into the laboratory and samples were taken manually from the different plant parts: new

leaves, old leaves, buds, flowers, different branch categories, etc. (Figs. 17 and 18). For this purpose, roots were separated and classified according to their diameter in the following categories: more than 5 mm, 2-5 mm, 1-2 mm, .2-1 mm and less than .2 mm.

The assessment of living and dead roots was accomplished for individual roots by means of differential density of root tissues in methanol, as is explained later.

Following the separation of shoot components and root size classes for each plant, the tissue samples were dried for 48 hours at 85°C, finely ground and stored for subsequent combustion and radioactivity determination.

Grinding was performed in a modified hand operated coffee mill, isolated in a transparent 'Plexiglass' box, operated under negative pressure from the outside by means of attached gloves.

The ^{14}C evaluation of these samples indicates concentrations of carbon translocated from the leaves to the different plant parts on unit dry weight basis. However, this does not render information about the total amount of carbon per unit ground area in the community allocated for each of the plant organs. Because of the magnitude of the task involved in determining biomass per unit ground area of individual plant organs, such as buds, flowers, leaves, twigs of various ages, spines, etc., a different sampling procedure was employed to estimate allocation of fixed carbon on a community basis.

The above-ground portion of four labeled plant was harvested and immediately chilled with ice. In the laboratory these plants

Figure 17. Diagramatic representation of plant parts sampled for ^{14}C for *Atriplex confertifolia*.

1. Apical new buds.
2. New expanding leaves
3. Mature leaves of previous year.
4. New braches of the current year.
5. Secondary branches of previous years.
6. Primary branches, previous years.
7. Main stem and crown.
8. Flowers and fruits.
9. Axilary vegetative buds.
10. Fully expanded leaves, current year.
11. Spines.
12. Main tap root.
13. Lateral roots, 5-10 mm diameter.
14. Lateral roots, 2-5 mm diameter.
15. Lateral roots, 1-2 mm diameter.
16. Lateral roots, 0.2-1 mm diameter.
17. Lateral roots less than 0.2 mm diameter.

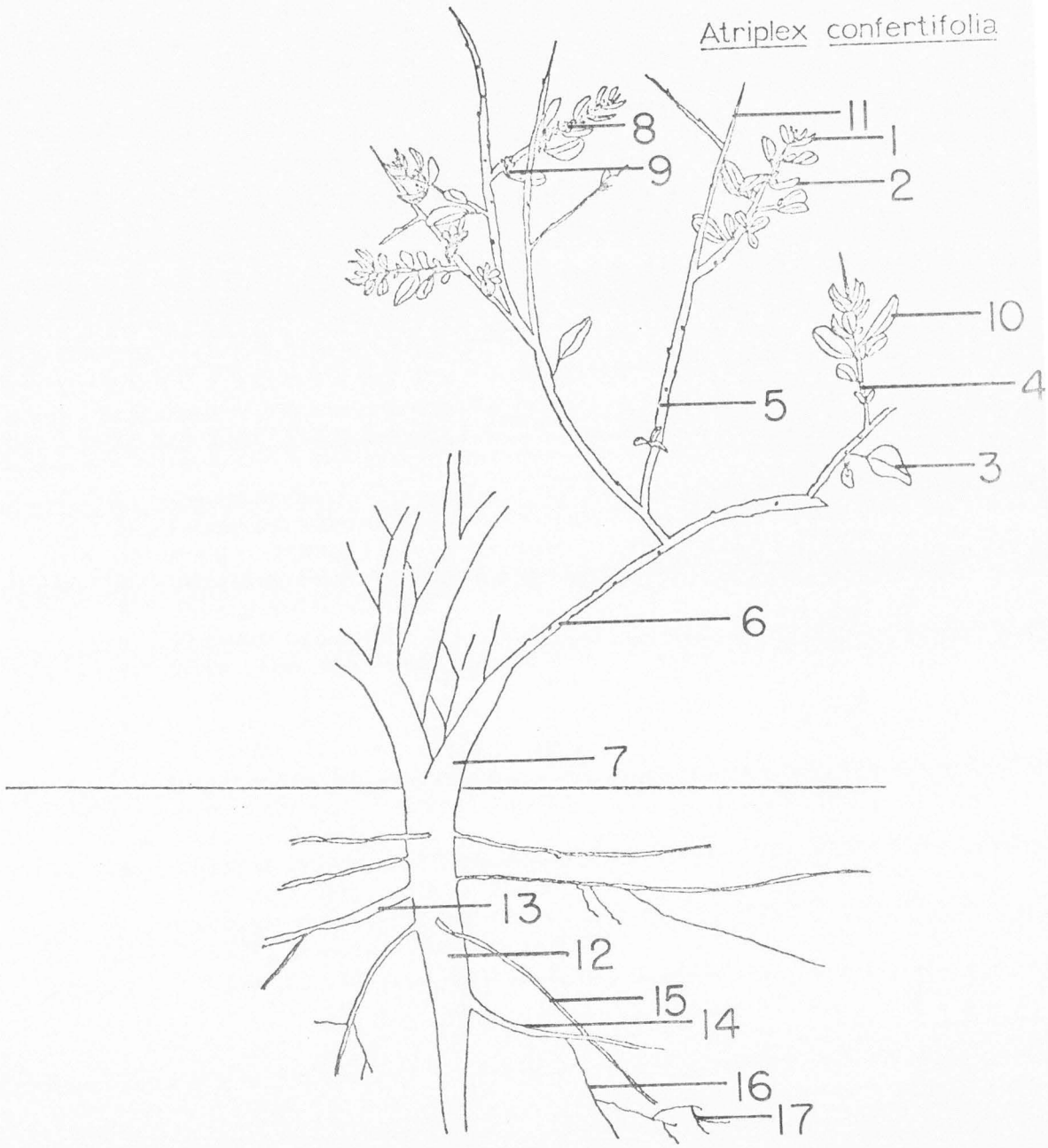

Atriplex confertifolia
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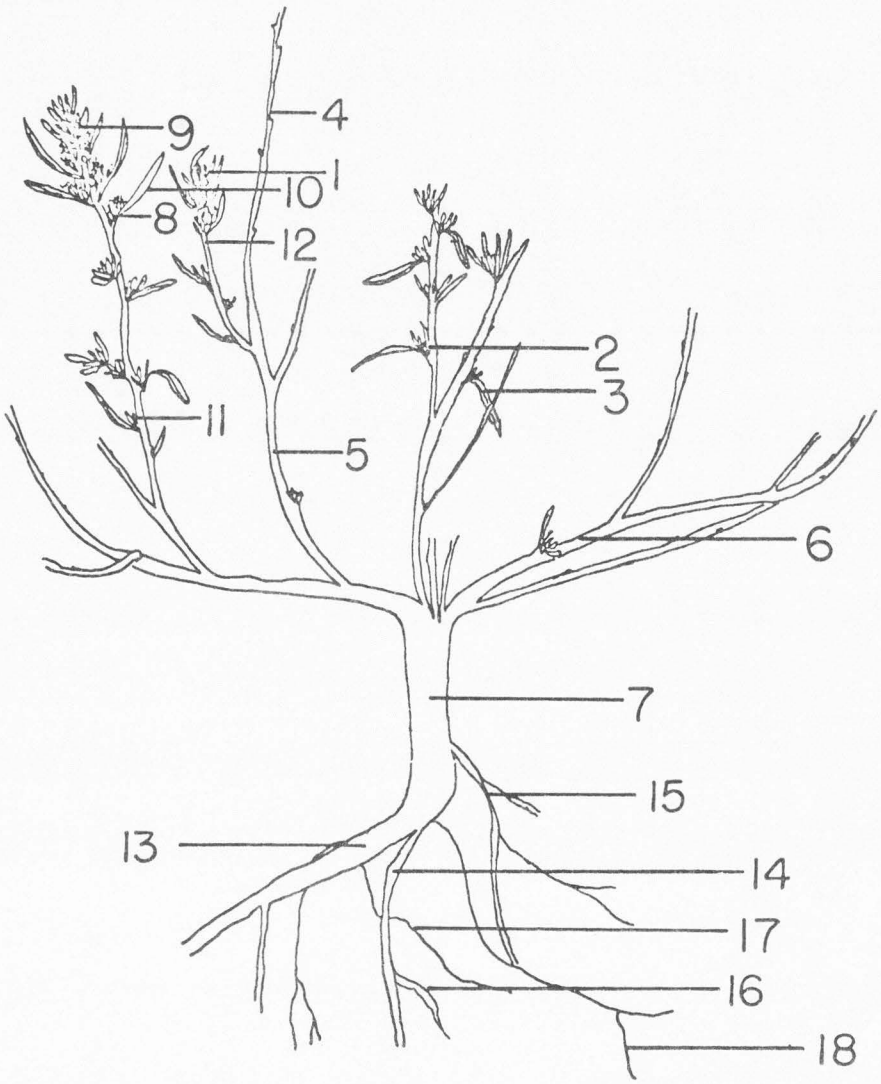
Figure 18. Diagramatic representation of plant parts samples for ^{14}C for Ceratoides lanata.

1. Upper buds.
2. Lower axilary buds.
3. Mature leaves, previous year.
4. Tertiary branches, holding buds.
5. Secondary branches.
6. Primary branches.
7. Main stem and crown.
8. Flowers, female.
9. Flowers, male.
10. Expanded leaves, current year.
11. Vegetative axilary buds.
12. New branches, current year.
13. Main tap root.
14. Lateral roots, 5-10 mm diameter.
15. Lateral roots, 2-5 mm diameter.
16. Lateral roots, 1-2 mm diameter.
17. Lateral roots, 0.2-1 mm diameter.
18. Lateral roots less than 0.2 mm diameter.

Ceratoides lanata



were separated into current year's and previous year's growth fractions, dried at 85°C during 48 hours, ground and stored for subsequent radiocarbon assay. Whole plants of Ceratoides were treated in this way, whereas with Atriplex, a considerably larger plant, only half of the plant was employed.

To estimate the allocation of fixed carbon to the underground plant system, root material was harvested within each of the labeled plots by soil coring using a 8.35-cm diameter orchard auger. Sample cores were only taken within the undisturbed central 1.1 x 1.1 m area of the labeled plot where all the roots were presumed to derive from plants within the 4.8-m^2 treated plot.

Roots and soil mixtures from 5-30 cm, 30-50 cm, 50-70 cm depths were placed in separate plastic bags to prevent desiccation. If root separation was not done immediately, the roots were stored in a freezer.

Complete separation of the roots was carried out using the same technique employed for calculation of root biomass for each community, as explained below.

Plant biomass sampling

To extrapolate the concentration of C^{14} recorded for the current year's growth, previous year's growth, and root samples to amount of carbon per unit ground area, it was necessary to determine plant biomass for each of the communities under study.

Shoot biomass was sampled by selecting a series of random plots of 4.8 m^2 in the Atriplex community and 1.2 m^2 in the Ceratoides stand. Because plants of Atriplex are larger and

less evenly distributed and Ceratoides are relatively small and more evenly distributed, a much larger plot size was necessary for Atriplex.

All above-ground biomass was separated into current year's growth and previous year's growth fractions, dried for 48 hous at 80°C and weighed.

Underground root biomass was calculated by soil cores chosen at random in the same plot where shoot biomass was collected. Soil core samples containing the roots from 5-30 cm, 30-50 cm, and 50-70 cm depths were individually placed in plastic bags and stored in the freezer until root extractions from the soil were made.

Plant plot and core sample sizes were increased until the successive values of the standard deviation for each new sample addition tends to level off. At this point the coefficient of variation was about ±15 percent. Sixteen plots were used in the Atriplex-dominated community and 12 in the Ceratoides-dominated area. Five soil cores were collected in each plot.

The employed techniques for biomass determination followed closely those of Bjerregaard (1971).

Complete separation of the roots from the soil was achieved by flotation (McKell, 1961: Bjerregaard, 1971) in a saturated NaCl solution. A simple apparatus was developed to allow a complete and rapid separation of the roots from the soil (Fig. 19). It consisted of an inverted 1 ℓ erlenmeyer flask with its bottom removed. This was attached to the top of a 3 ℓ flask. After addition of about 400 ml of water and enough NaCl to make a saturated solution, the soil sample was introduced into the apparatus. By using a piece of tubing extending to the bottom of the flask, water was added under pressure to fill the apparatus to within one or two cm

Figure 19. Apparatus employed for the separation of roots from the soil.

from the top of the inverted erlenmeyer flask portion. This produced a vigorous stirring action very effective in liberating the roots from the soil. Additional agitation was also obtained by the use of a rigid plastic tube enlarged and flattened at the end which is manually rotated to stir the soil at the bottom of the flask. A variation of this which was sometimes used in that water was added through the plastic tube having various perforations near the end. This rendered a vigorous mixing by the movement of the rod and the water coming through the perforations under pressure. The separation of the roots from the soil was facilitated by the silty to sandy loam texture of the soils in the study plots.

After decanting for a few moments, the clean root samples were floating at the top of the apparatus. Roots were separated from the water by tilting the apparatus over a 100 mesh sieve which retained even the finest root elements. The shape of the apparatus retained the soil in the flask and did not allow it to spill over when the water in the erlenmeyer flask portion was poured out.

Soil samples contained at the bottom of the apparatus were observed under the microscope and were apparently free of all root materials. With a series of four to five of these units working simultaneously, this technique allowed a rapid processing of a significant number of soil samples in a short time.

Separation of dead and live roots for partitioning studies

Information on root productivity and turnover under field conditions has been hampered by the lack of suitable techniques for quantitative measurements of living root biomass.

A number of methods have been described which attempt to differentiate between a functional and non-functional and presumably dead roots. To diagnose the vitality of root segments of several weeds, Greenhan and Cole (1949, 1950) measured resistance and capacitance of the root tissue. In a few cases vital staining techniques based on the reduction of 2,3, 5-triphenyltetrazolium chloride (TTC) have been employed (Jacques and Schwass, 1957; Aimi and Fujimaki, 1958). The method seems to be satisfactory for young nonsuberized roots. Knievel (1973) adapted the TTC staining technique to separate dead and live tissue in a large number of samples. This technique requires the preparation of standard curves based on known live/dead ratios of the root materials under study. Moreover, TTC reduction appears to also be influenced by the age of the roots.

Carbon-14 labeled plants were used by Ueno et al. (1967) and by Singh and Coleman (1973) for the detection of functional roots through autoradiography. The latter authors calculated the total root biomass of $^{14}CO_2$ treated plots by relating their specific ^{14}C activity of core root samples with the percentage values of a regression constructed by mixing known proportions of functional and nonfunctional roots as identified individually by autoradiography. This procedure assumes that the specific ^{14}C activity for the very thin root is equal to the activity of larger roots. In this study it was found that the root fraction of less than .2 mm in diameter constitutes an important part of the total root biomass and that its specific radiocarbon activity significantly differed from the larger root fractions.

Carbon tracer techniques constitute one of the most reliable methods for the distinction of dead and live root tissue. However, Ueno et al. (1967) pointed out two main problems that may exist in the use of radiocarbon. The radioactivity of the roots would depend on the downward translocation of assimilates which can vary greatly through the season. Also, the uneven distribution of photoassimilates in the root system could result in the possibility that some living roots might be undetected.

One technique involving the separation of roots by differential density in methanol was reliable for the individual separation of the dead and live root segments of Atriplex confertifolia which were used to evaluate carbon partitioned to the different root categories. The same technique was employed for the root samples of Ceratoides lanata; however, in this case the assessment of dead and live roots was supplemented with color and physical appearance.

Root segments of about one to two cm in length were placed in a large test tube containing 95 percent methanol. They were considered alive if the root segments sunk and considered dead if they floated. A few of the root segments remained in suspension or sunk very slowly. These were discarded for radiocarbon assay. It did not seem to make any different if the root segments were fresh or air or oven dried before testing in methanol.

An indication that this technique may be useful in distinguishing living from nonliving root material was obtained when over 200 segments for a variety of root sizes of Atriplex that sunk in methanol and 160 which floated were autoradiographed. The results showed that 98 percent of the root which sunk in methanol were radioactive while 95 percent of those which floated were not radioactive.

Similar treatments with the roots of Ceratoides showed 82 percent and 86 percent confirmative values for the sinking and floating root samples, respectively.

There were a few conflicting samples in which one end of the root sunk and the other floated.

The physical principle utilized for the separation of the two categories of roots is similar to that employed by soil scientists in which different inorganic components from a soil sample are separated by their retention in liquids of different density (Mateleski, 1951). In this case organic solutions of densities greater than 1.0 are generally used. Since, when roots are placed in water always floated independtly of being dead or alive, the idea was to test them in liquids whose density was inferior to that of the water.

Later, an attempt was made to use this technique for the whole root sample derived from a soil core. Since at that time a good part of the core root samples were already analyzed for radioactivity, this line of work was not carried further and is only presented here as an indication of the possibilities that this technique may offer. Part of the core root sample originating from a labeled Atriplex plot was dispersed in methanol after the roots had been dried. As illustrated in Figure 20 the two distinct root fractions were clearly separated in the test tube containing the methanol.

When the radioactivity of the floating and sinking fractions was measured it was found that the former was either not radioactive or was barely above the background count; whereas the root fraction that

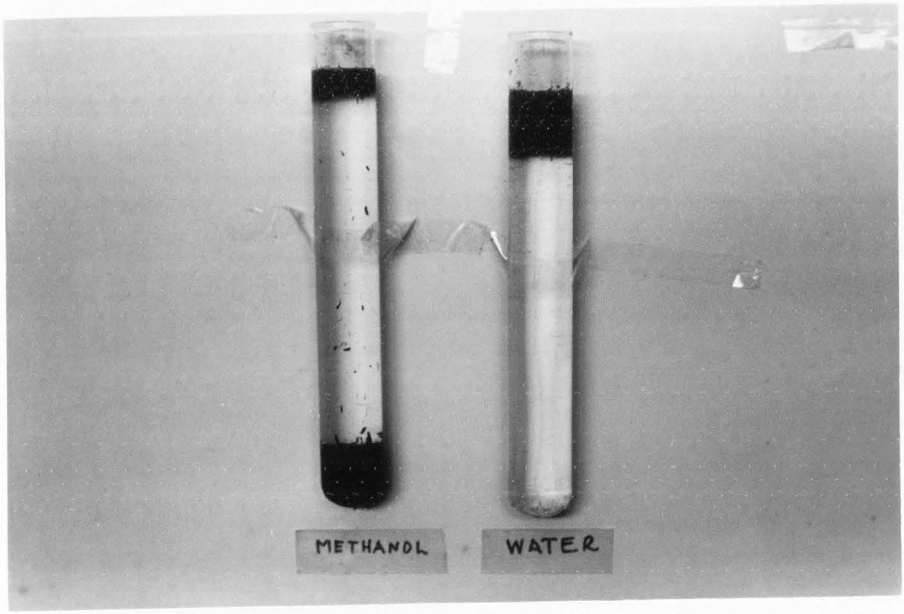


Figure 20. Separation of Atriplex confertifolia root portions by differential density in methanol as compared to water.

sunk was always markedly radioactive, the specific activity depending on the date of treatment.

Observations under the microscope of the floating fraction showed it to be mainly composed of organic detritus and root fractions in various stages of decay. This fraction could be discarded and considered as not part of the functional root system. One important question that still remains is if the root sample portion that sunk was always composed of live tissue or if it is still mixed with nonfunctional material.

The same procedure was used with root core samples originating in the Ceratoides ^{14}C-labeled plots. However, when the sinking and floating fractions were tested for radioactivity, a much less clear-cut result was obtained. The floating root fraction exhibited sometimes as much specific radioactivity per unit dry weight as the sinking portion. Some of the probable reasons for this discrepancy between the root samples of these species are discussed later.

The physical principle upon which this technique is based, provides an approach to the problem of living and non-living root separation that deserves further investigation. Different compounds whose densities are inferior to water should also be tested. Other physical factors besides density, such as wetting properties of root materials may be significant for a basis of separation. A combination of methanol, or other convenient low density liquid solutions, with centrifugation, may also provide a superior separation of dead and live root tissue fractions.

Radiocarbon assay of plant tissue

An oxygen flask combustion technique from Gupta (1966) modified by L. B. Camp (personal communication) was used throughout this study.

Samples of 150 to 200 mg were weighed and wrapped in a black thin tissue paper. The sample was suspended in a 500 ml suction flask by means of a heat resistant wire attached to a rubber stopper in the neck of the flask. This suction flask has a side arm to which a small balloon was attached. This was done for safety reasons due to expansion during combustion. The rubber stopper had a piece of glass tubing inserted through it on which a syringe cap could be sealed.

Before combustion the flask was thoroughly flushed with pure oxygen and immediately closed. The next step was to ignite the sample with a focused light beam from a modified slide projector. Combustion of the sample was completed in a few seconds. Usually there was no smoking observed prior to the flash ignition. After combustion was terminated the flask was set aside for 5 to 10 minutes to cool and allow mixing of the gas. Next a 20 ml aliquot of gas was removed with a syringe and injected into a syringe-capped scintillation vial to which negative pressure had previously been induced by removing part of the air with a syringe. One and a half ml of ethanolamine (CO_2 absorber) was injected through the serum cap of the vial with a glass syringe. After an absorption period of approximately 10 hours the syringe cap was removed and 20 ml of scintillation grade solution was added to the vial which was then

closed with a cap containing a teflon liner. The scintillation "cocktail" contained 460 ml of toluene, 270 ml of methanol, 5 g of PPO, and 100 g of POPOP.

The vial was allowed to set for at least 6 hours to eliminate any chemiluminiscence and then analyzed by a liquid scintillation counter (Nuclear Chicago) for carbon-14 content.

The counting efficiency for each vial was determined by the channels ratio method and DPM were calculated. The calibration curve was established with a toluene base quenched standard set.

The combustion technique explained here was found to be rapid and simple for the analysis of a reasonably larger number of samples. In all cases, three replicates were combusted for each plant sample.

Results

Partitioning of photosynthates to plant organs

The pattern of distribution of ^{14}C to the different plant organs is summarized in Tables 6 and 7. This is represented in terms of actual disintegrations per minute (DPM) of ^{14}C per mg dry weight of plant sample tissue.

The columns labeled April, July and September, indicate the results of ^{14}C partitioning 72 hours after photosynthetic incorporation of $^{14}CO_2$. The columns September-April and September-July, represent the ^{14}C content of samples taken in September from plots originally tagged in April and July, respectively.

The variability among the same plant part samples for each of the three species used are shown in these tables. The trends of

Table 6. Partitioning of photosynthates to plant parts in Atriplex confertifolia.

Shoots	April			July			September			September April Treatment			September July Treatment		
	Plant 1	Plant 2	Plant 3	Plant 1	Plant 2	Plant 3	Plant 1	Plant 2	Plant 3	Plant 1	Plant 2	Plant 3	Plant 1	Plant 2	Plant 3
	DPM/mg dry wt.			DPM/mg dry wt.			DPM/mg dry wt.			DPM/mg dry wt.			DPM/mg dry wt.		
Apical new buds	18552	19739	21035												
	51.8[1/]	166.2	179.1												
New expanding leaves	13470	13709	16078												
	109.3	84.0	234.3												
Mature leaves previous year	2073	2368	2798												
	22.5	6.7	24.3												
New branches current year	11200	10315	12640	1699	2060	1763	116	115	149	871	619	627	1123	1407	1220
	38.5	170.8	66.5	14.5	12.7	4.7	9.3	13.4	6.0	4.6	2.1	3.0	7.3	13.6	11.1
Secondary branches previous year	713	872	1022	824	620	797	96	76	95	412	328	426	549	707	590
	2.0	4.1	12.7	5.0	14.6	5.6	0.6	0.3	0.3	6.5	18.5	6.5	5.8	7.2	4.1
Primary branches previous year	594	560	768	777	609	526	60	49	51	365	208	290	482	509	500
	8.0	20.5	18.5	7.5	10.4	4.1	1.5	6.1	2.5	3.0	3.8	5.2	6.9	5.6	6.8
Main stem and crown	321	201	563	421	386	220	35	41	38	177	205	200	218	258	190
	9.6	13.0	22.0	7.0	16.4	3.4	0.3	1.5	0.6	3.5	2.6	9.1	3.6	10.1	7.0
Flowers and fruit (female plant)				1319	1236	1318	139	146	116	98	123	107	635	806	666
				8.1	59.0	19.0	2.0	4.0	0.6	1.2	0.3	0.6	4.0	11.1	8.1
Axilary vegetative buds				1028	1161	988	169	203	171	214	179	149	478	518	440
				4.0	14.9	50.6	3.6	1.2	0.6	4.1	0.6	4.9	4.1	6.1	0.6
Fully expanded leaves				598	674	649	153	156	169	420	371	360	492	587	490
				15.5	2.6	8.8	0.6	6.2	6.6	7.0	2.0	9.9	6.4	2.8	5.8
Spines	145	121	164												
	2.0	0.5	4.3												
Roots															
Main tap root	390	470	401	401	577	402	19	18	16	101	119	75	237	343	
	6.9	10.1	7.6	4.5	4.6	20.2	0.3	1.5	0.3	1.1	5.2	9.4	9.0	3.6	
Lateral 5-10 mm diam.	460	580	380	320	671	202	15	19	16	145	161	96	241	278	
	2.5	7.3	6.1	7.0	28.1	2.6	1.0	0.0	2.8	1.5	2.5	3.0	5.2	4.3	
Lateral 2-5 mm diam.	147	120	220	430	744	462	26	18	14	99	89	90	226	187	
	2.6	8.1	7.7	5.2	8.5	8.0	0.3	0.8	0.3	0.3	1.7	1.7	6.1	1.5	
Lateral 1-2 mm diam.	171	127	120	543	608	621	20	45	20	88	101	66	280	206	
	4.6	2.8	0.6	6.7	5.9	7.4	0.3	0.6	1.2	0.5	2.5	1.0	3.0	3.0	
Lateral .2-1 mm diam.	277	307	201	521	486	541	41	125	47	138	163	140	381	256	
	2.5	3.4	1.5	5.6	21.7	23.6	2.5	3.6	0.5	9.1	3.2	2.7	6.0	8.7	
Lateral less .2 mm diam.	220	341	198	411	836	520	46	76	49	150	181	129	428	267	
	1.1	2.5	3.5	7.5	2.5	2.0	2.6	0.3	1.1	2.3	1.5	6.2	10.5	2.1	

[1/] Standard error of the mean.

Table 7. Partitioning of photosynthates to plant parts in Ceratoides lanata.

Shoots	April			July			September			September April Treatment			September July Treatment		
	Plant 1	Plant 2	Plant 3	Plant 1	Plant 2	Plant 3	Plant 1	Plant 2	Plant 3	Plant 1	Plant 2	Plant 3	Plant 1	Plant 2	Plant 3
	DPM/mg dry wt.			DPM/mg dry wt.			DPM/mg dry wt.			DPM/mg dry wt.			DPM/mg dry wt.		
Upper buds	4450	4610	4517				206	214	227	21	20	18	686	643	702
	74.6[1]	208.4	13.6				1.5	1.5	2.3	0.5	0.3	0.8	5.5	10.7	3.5
Lower axilary new buds	4207	5172	4218												
	11.2	168.0	7.8												
Mature leaves, previous year	1107	971	878												
	115.4	12.5	121.8												
Tertiary branches (holding buds)	209	323	226	1770	1966	2120	91	79	82	71	67	66	726	691	696
	1.7	4.0	3.4	39.5	13.2	82.6	0.5	1.5	3.2	1.3	0.8	2.0	13.2	6.1	8.1
Secondary branches	152	144	135	1662	1657	1447	63	76	69	69	60	42	575	456	471
	10.1	4.6	3.7	10.3	5.1	2.0	2.0	0.5	1.1	1.5	0.6	0.8	6.6	9.0	0.6
Primary branches	56	203	48	743	952	485	78	87	57	31	19	26	430	334	388
	3.1	12.3	2.5	10.1	2.6	3.2	0.5	0.8	1.0	0.8	2.3	0.3	6.0	5.6	14.3
Main stem and crown	27	122	61	455	543	413	56	39	33	27	25	31	161	198	157
	1.5	3.4	9.1	4.0	2.6	2.0	0.6	0.6	6.4				0.3	2.5	4.1
Flowers (female)				975	1048	934									
				8.0	4.5	1.5									
Flowers (male)				440	532	528									
				2.0	6.0	2.5									
Expanded leaves, current year				970	853	1041	194	194	205	28	20	27	395	341	401
				9.0	9.5	4.1	3.0	1.3	5.6	1.0	3.2	1.5	4.6	2.5	2.6
Vegetative axilary buds				1443	1580	1645	219	196	187	26	25	30	777	846	860
				30.7	5.2	3.0	0.5	1.6	2.1	0.3	0.6	0.3	4.0	4.1	6.2
New branches, current year				1966	1491	1890	166	188	186	66	54	51	898	861	866
				7.1	5.2	11.0	2.0	0.6	4.4	3.7	7.4	6.5	3.5	3.0	8.5
Roots															
Main Tap Root	65	26	36	410	535	365	40	32	51	12	19	16	178	101	151
	1.2	2.5	4.7	8.1	20.5	10.9	1.5	0.6	3.2	0.8	0.3	1.7	5.6	5.8	11.6
Lateral 5-10 mm diam.	42	22	40	378	514	376	52	62	41	11	17	14	153	129	175
	6.0	0.6	2.3	4.3	6.1	4.5	1.5	3.0	0.6	0.3	0.3	0.3	2.0	2.0	3.0
Lateral 2-5 mm diam.	67	45	32	496	432	385	91	70	96	21	28	17	175	252	201
	1.5	3.2	1.7	2.3	3.0	5.0	1.6	0.6	2.0	0.3	0.6	0.3	2.5	7.5	2.3
Lateral 1-2 mm diam.	45	29	62	382	593	351	19	30	27	19	30	27	249	176	271
	2.3	0.7	2.0	6.5	2.0	4.3	0.6	1.5	0.3	0.3	0.3	0.6	4.5	2.5	4.5
Lateral .2-1 mm diam.	69	54	86	548	614	752	24	36	22	24	36	22	313	341	370
	2.5	2.0	6.0	4.1	9.5	4.5	1.1	1.0	2.0	1.0	3.6	0.3	5.6	7.8	1.1
Later less .2 mm diam.	41	52	39	686	764	1107	56	67	76	56	67	76	362	551	450
	0.6	1.5	2.5	7.1	3.3	4.6	0.6	1.0	1.0	2.3	4.8	1.5	8.1	4.9	9.0

[1] Standard error of the mean.

seasonal change for any particular time period are quite consistant for each individual plant of both species.

Figure 21 depicts the average percentage distribution of carbon per unit dry weight among various plant parts 72 hours after each treatment took place. These values were derived from the data included in Tables 6 and 7, and the information collected for the above-ground plant phenology for the Atriplex and Ceratoides dominated communities (Table 1). The standard error for these values are in the vicinity of 1 to 5 percent.

The data of Table 8 show the percentage distribution of ^{14}C, per unit dry weight tissue, on plant samples taken in September from plots tagged in April and July. These values were calculated from the data included in Tables 6 and 7.

A relatively significant amount of radiocarbon appeared in the leaves and reproductive structures of Atriplex confertifolia which was not present at the three days after exposure to $^{14}CO_2$ in April.

The partitioning of photosynthates to plant parts, based on unit dry weight of plant tissue, yields only the relative trends for preferential deployment during the annual plant growth cycle. These data do not provide information on the total amounts of carbon allocated at the community level on an area basis.

Allocation of carbon on community basis

Tables 9 and 10 show the total relative allocation of ^{14}C photosynthates, on land area basis, for the current year's shoot growth

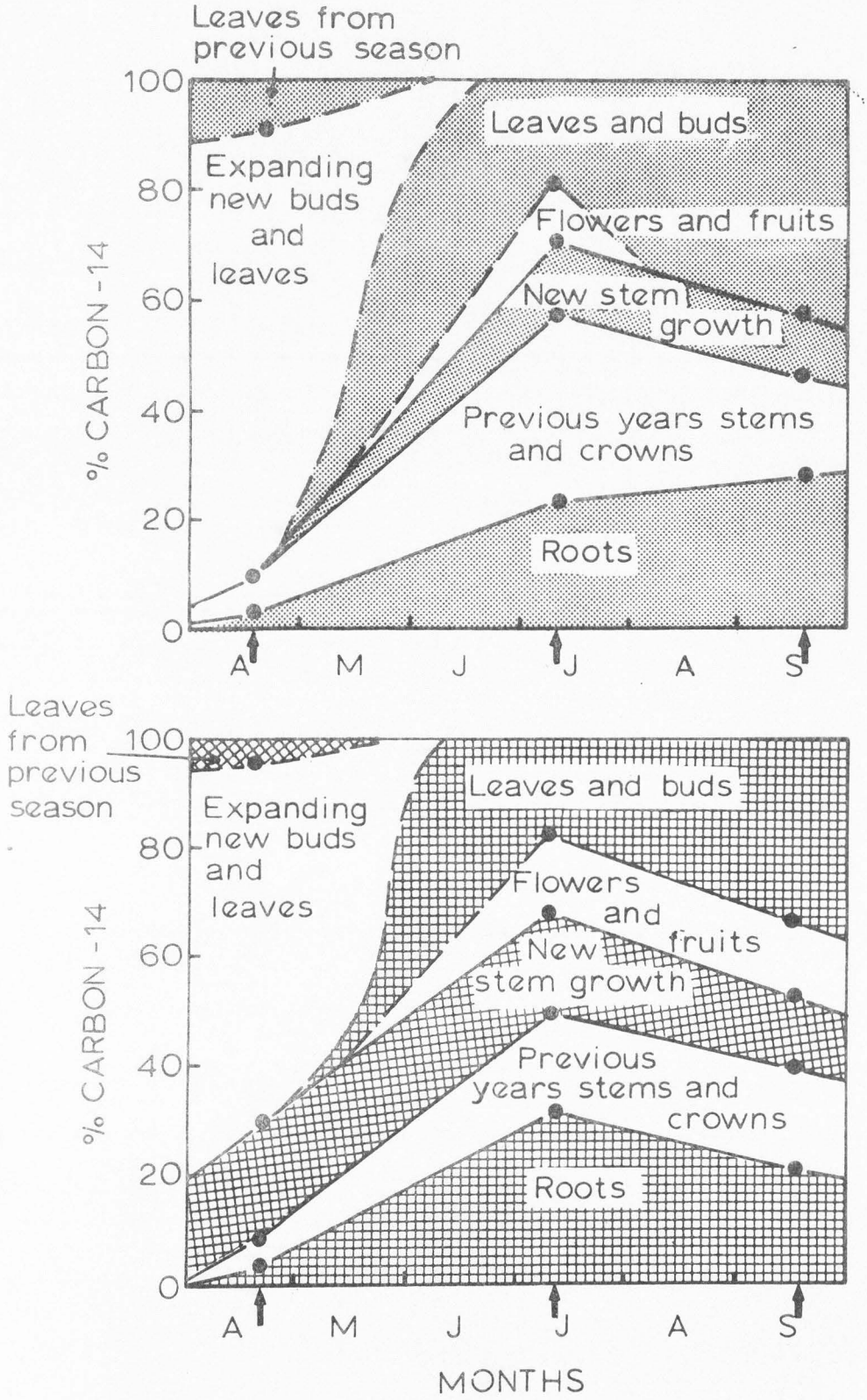


Figure 21. Percentage partitioning to plant parts on a mg dry weight basis, of ^{14}C-photosynthates in April, July and September, 72 hours after $^{14}CO_2$ photoassimilation in a) Ceratoides lanata and b) Atriplex confertifolia. Arrows indicate date of treatments.

Table 8. Relative percentage of photosynthates partitioned to plant parts at the end of the growing season for the April and July treatments.

Plant Structure	September - April		September - July	
	Atriplex confertifolia	Ceratoides lanata	Atriplex confertifolia	Ceratoides lanata
	$\%C^{14}$		$\% C^{14}$	
Leaves and buds	19	27	17	30
Flowers and fruits	4		12	
New growth	24	12	21	14
Old growth	29	37	22	31
Roots	24	28	36	25

(new shoot growth), previous year's shoot growth (old shoot growth) and roots, 72 hours after exposure to $^{14}CO_2$ in July and September and at the end of the growing season for the April and July treatments. These values were derived from the proportion of ^{14}C translocated to various plant parts multiplied by the amount of biomass in these components of the plant community.

At the time this study was performed no technique was suitable for the separation of living from nonliving root tissue from the soil core samples. Later the technique involving the separation of the two root fractions by differential density in methanol was developed which appeared to be promising for future work with Atriplex roots. However, at the same time, the technique appears to have some restrictions for its use with the roots of Ceratoides.

In order to be consistent with the methodology used for both species in this study, the values of total carbon allocation to roots, in terms of unit community biomass, were estimated by using the total root biomass including both dead and live root components. Nevertheless, since the same technique was employed for the separation of the roots from the soil cores in the ^{14}C-labeled plots and the plots in the rest of the community used for root biomass estimation, the values in both cases are comparable. The carbon values calculated for the underground plant system represent the true total allocation of energy translocated from the shoots to the roots independent of the actual proportion of dead and live root tissue.

Since the changes of living and non-living tissue in the roots during the growing season could not be followed, underground biomass was determined only once during the growing season. The determination of

Table 9. Total allocation of photosynthates to shoots and roots on a land area basis for the Atriplex confertifolia-dominated community.

Date	Plant Component	Biomass kg/ha	DPM mg^{-1} dry wt.	DPM dm^{-2}	Total DPM dm^{-2} plant component	Percent allocation
July	New shoot growth	1,542±60.9[2/]	1,200.0±127.9	1,850,400	1,850,400	63.3
	Old shoot growth	1,214±47.6	442.0± 29.3	536,588	536,588	18.3
	Root system					
	5-30[1/]	9,224±295	33.0 ± 2.9	304,392		
	30-50	5,469±152	21.3 ± 3.1	116,490		
	50-70	4,010±158	29.3 ± 4.0	117,493	538,375	18.4
September	New shoot growth	1,163±70	98.0 ±10.3	113.974	113,974	51.4
	Old shoot growth	1,201±62	47.0 ± 4.8	56,447	56,447	25.4
	Root system					
	5-30	9,224	2.5 ± 0.3	23,060		
	30-50	5,469	3.5 ± 0.3	19,142		
	50-70	4,010	2.3 ± 0.2	9,223	51,425	23.2
April-Sept.	New shoot growth	1,163	308.0 ±22.0	358,204	358,204	36.5
	Old shoot growth	1,201	233.0 ±25.8	279,833	279,833	28.5
	Root system					
	5-30	9,224	21.5 ± 2.1	198,316		
	30-50	5,469	19.0 ± 2.7	103,911		
	50-70	4,010	10.0 ± 1.4	40,100	342,327	35.0
July-Sept.	New shoot growth	1,163	759.0 ±58.8	882,717	882,717	49.7
	Old shoot growth	1,201	314.0 ± 6.8	377.114	377,114	21.2
	Root system					
	5-30	9,224	39.3 ± 5.8	362,503		
	30-50	5,469	15.3 ± 2.4	83,676		
	50-70	4,010	17.5 ± 3.3	70,175	516,354	29.1

1/ Depth in centimeters.

2/ Standard error of the mean.

Table 10. Total allocation of photosynthates to shoots and roots on a land area basis for the Ceratoides lanata-dominated community.

Date	Plant Component	Biomass kg/ha	DPM mg^{-1} dry wt.	DPM dm^{-2}	Total DPM dm^{-2} plant component	Percent allocation
July	New shoot growth	638±26 [2]	1,017.0±62.6	648,846	648,846	42.0
	Old shoot growth	823±35	359.0±35.1	295,457	295,457	19.1
	Root system					
	5-30[1]	7,103±445	49.5± 4.9	351,598		
	30-50	5,176±283	25.0± 1.7	129,400		
	50-70	3,807±258	31.5± 3.4	119,920	600,918	38.9
September	New shoot growth	548±40	131.0± 4.5	71,788	71,788	41.9
	Old shoot growth	818±52	35.0± 1.8	28,630	28,630	16.7
	Root system					
	5-30	7,103	4.8± 1.0	34,094		
	30-50	5,176	3.8± 0.6	19,669		
	50-70	3,807	4.5± 0.6	17,131	70,894	41.4
April-Sept.	New shoot growth	548	68.0± 1.5	37,264	37,264	13.9
	Old shoot growth	818	68.0±12.1	55,624	55,624	20.8
	Root system					
	5-30	7,103	15.5± 0.6	110,097		
	30-50	5,176	8.0± 0.7	41,408		
	50-70	3,807	6.0± 0.4	22,842	174,347	65.3
July-Sept.	New shoot growth	548	479.0±41.0	262,492	262,492	32.3
	Old shoot growth	818	310.0±34.5	253,580	253,580	31.9
	Root system					
	5-30	7,103	12.3± 2.1	87,367		
	30-50	5,176	30.5± 3.9	157,868		
	50-70	3,807	13.5± 1.3	51,395	296,630	36.5

[1] Depth in centimeters.

[2] Standard error of the mean.

root biomass in July was considered the most representative for the year, and this value was used for all further calculations.

There may exist a margin of error in using this single value for the September labeling. However, this will not alter the conclusions or the relative trend of carbon allocation observed in this study on a community basis.

Allocation of total carbon-14 in July showed that over 60 percent of the ^{14}C is retained in new shoots and the rest is distributed in approximately equal amounts between old shoot growth and roots. Similar results were obtained in September, with the exception that there was 10 percent less carbon-14 retained in new shoot growth. The percentage allocation for Ceratoides showed that significantly larger amounts of carbon were being channeled to underground plant parts. Over 80 percent of the new incorporated carbon was found in approximately equal amounts in roots and new shoot growth. Very much the same scheme of ^{14}C allocation was registered in September.

In making these comparisons it must be pointed out that the absolute amounts of carbon-14 fixed and deployed to various plant structures were many times greater in July than in September, when photosynthetic activity was reduced (Caldwell, 1972).

Plant samples taken in September from the plots tagged in April and July indicate that a considerable proportion of carbon fixed at those times was later deployed to the root system. This was particularly noticeable for Ceratoides lanata.

Discussion

Partitioning of photosynthates to plant organs

Partitioning of carbon at different times during the growing season in Atriplex confertifolia and Ceratoides lanata seems to correspond reasonably well with the expected ontogenic patterns of development through the year (Fig. 21 and Tables 6 and 7). A marked seasonal variation in the preferential sinks of carbon on a unit weight basis was observed for both species.

Regions of active growth are consumers of building materials. To varying degress, they act as sinks for photosynthates. Carbon fixed by the leaves is distributed in varying proportions to the terminal meristematic regions, expanding leaves, cambium, reproductive structures or storage organs (Jones et al., 1959; Brouwer, 1962; Hale and Weaver, 1962; Thrower, 1962; Webb and Gorham, 1964; Biddulph and Cory, 1965; Balatinecz et al., 1966; Lupton, 1966; Hansen, 1967; Gordon and Larson, 1968; Ursino et al., 1968; Ryle, 1970; Schier, 1970).

In the April treatment, the concentration of labeled carbon was highest in buds and new leaves, indicating that these plant structures were apparently the primary sinks of photoassimilate consumption. Once the buds break in the spring and the new leaves

start expanding there is a sizeable demand for photoassimilates which are utilized primarily in the construction of new cellular structures and in respiration.

The source of carbon utilized for this early vegetative shoot growth may be either stored reserves or current photosynthesis. The sizeable radioactivity of these organs and the fact that for both species the optimal rate of photosynthesis was exhibited during April and May (Caldwell, 1972) would strongly suggest that the early shoot growth of Atriplex and Ceratoides relies principally on current photosynthate. It has been reported (Kozlowski and Winget, 1964; Kozlowski and Clausen, 1965) that current photoassimilates can be an important source for the new above-ground growth in the spring of evergreen species. However, the source of energy at the initiation of the growing season varies considerably depending on species and environmental conditions (Merrill and Kilby, 1952; Mochizuki and Hanada, 1958). Early shoot growth in Pinus appears to take place principally at the expense of stored materials (Kozlowski, 1964). In deciduous trees reserve carbohydrates also appear to be the source of energy for the early spring growth (Priestley, 1962; Ziegler, 1964; Hansen, 1967).

A change in the rate of radiocarbon distributed per unit dry weight to other plant structures in July with respect to April would indicate that the rate of growth of one organ appears to be favored at the expense of another. A switch in the translocation of photosynthetic products takes place when the new leaves change from

importers of assimilates to exporters. Changes in the rate of assimilate utilization from one plant organ to another can occur in a short period of time (Stoy, 1969).

The elongation of new shoots appears to be completed earlier in Atriplex than Ceratoides, but for both species it was essentially terminated during the first half of June.

The development of floral buds marks the initiation of a new pattern in the utilization of available energy resources, introducing a new demand on the allocation of photoassimilates (Brouwer, 1962; Harper and Ogden, 1972). Figure 21 indicates that the total carbon investment per unit weight of tissue gradually increased as flowering buds developed, fertilization occurred, and fruits started to mature. The maximum carbon-14 concentration for the reproductive structures was only the result of a single observation during the summer. However, it did correspond with the time of fertilization and initiation of fruit development in July.

The reproductive effort, expressed as the amount of carbon allocated per mg of dry tissue weight indicates a different pattern of energy deployment for Atriplex and Ceratoides. Both species flowered almost at the same time. However, Fig. 21 would indicate that after fertilization the reproductive structures of Atriplex exhibited a similar proportion of ^{14}C activity in July and September, whereas Ceratoides rapidly declined. These differences could be attributed to the fact that Ceratoides disseminates its seeds much earlier during August, while the fruits of Atriplex persists on the plant much longer falling to the ground during late fall. Fruits of Atriplex were present during the September labeling and their green fruit bracts were most probably photosynthetically active.

In terms of relative carbon allocated to plant parts per unit dry weight tissue, it appears that Ceratoides is able to accomplish reproduction with a much lower expenditure of energy than Atriplex. The short reproductive period of Ceratoides can be associated with the completion of reproduction before significant net photosynthesis ceases by the middle of August.

The proportion of carbon allocated to new stems in Atriplex is remarkably constant during the growing period and apparently independent of the succession of plant phenological stages.

Apparently carbon channeled to new stem growth is utilized first in the elongation of new branches and much later in the season for secondary growth in addition to stored reserves. New stem elongation during the April labeling treatment was just incipient in Ceratoides. It should be noted that the $^{14}CO_2$ exposure for this species was done a few days earlier than for Atriplex. The results of the July and September treatments show again a reasonably constant proportion of photosynthates partitioned to new stems.

The amount of energy expended in the more perennial parts of the shoot system (main stem, primary and secondary branches) appears to be quite significant. For both species a low relative rate of newly synthesized assimilates utilization early in the spring for these plant parts is followed by increasing amounts in July and September.

The larger proportion of carbon retained in the foliage in September could be in part related to the lower rate of photosynthetic

activity for this species at that time (Caldwell, 1972) which proportionally would increase the amount of carbon retained for the leaves.

The low concentration of radioactive carbon in the roots in the April treatment, when the root observation chambers were indicating a maximum of root growth activity, suggests that this new root growth might have taken place at the expense of stored reserves, presumably in the root system itself.

The zone of high meristematic activity in the expanding buds and leaves in the spring may have placed a demand on the photosynthates which would take preference over the root system. It has been reported (Porter, 1966; Hansen, 1967) that the intensity of transport of assimilates is dependent on the proximity of leaves to the carbon sink and also on the relative demands of these sinks. Carbohydrate storage and its utilization in plants has been treated with greater detail by various authors (Kramer and Kozlowski, 1960; Cook, 1966; Kozlowski and Keller, 1966; Priestly, 1970; Zimmerman and Brown, 1971).

For both species the relative concentration of carbon, in terms of unit weight of root tissues, partitioned to the underground plant system significantly increased later in the season. Atriplex reached a maximum value during July followed by a decline in September, the relative concentration of ^{14}C in the roots of Ceratoides increased in September.

Table 8 indicates that relative concentration of C^{14} in plant samples taken in September, from plots originally labeled in April and July, respectively. These values can be considered to represent

the final destination of energy incorporated in the plant in April and July before the initiation of the winter shoot dormancy period. Roots appeared to receive a significant relative proportion of the carbon fixed in April and July.

Total allocation of photosynthates on a community basis

The partitioning of photoassimilates based on unit dry weight of plant parts, illustrates the relative trends of carbon deployment. Since these values only render the concentration of radioactive carbon in the plant structure analyzed, they are of limited utility when considering allocation of carbon on a community basis. Therefore, allocation assessments were also conducted whereby concentration of ^{14}C to above- and below-ground plant parts could be multiplied by a factor of total biomass per unit area in these different components.

An analysis of the energy allocation at the community level for these stands dominated by Atriplex confertifolia and Ceratoides lanata 72 hours after treatment with $^{14}CO_2$ in July and September is given in Tables 9 and 10. It is apparent that the relative values of carbon allocation to the plant structures under study varied significantly for each community.

Approximately 60 and 50 percent of the recently photoassimilated carbon in July and September, respectively, appeared to be localized in the new shoot growth of Atriplex. The remaining portion was distributed in nearly equal amounts between the old shoot growth and the root system. The scheme of energy utilization in Ceratoides

showed similar patterns of carbon deployment in the July and September treatments. Approximately 80 percent of the fixed carbon in the community was distributed in similar amounts between the new shoot growth and the underground structures with the rest allocated to the previous year's growth.

A generalized pattern of carbon balance for a plant is given by Porter (1966). He estimates that 25 percent of the carbon photoassimilated goes to the roots, 25 percent is exported to the stems, 10 percent is channeled from mature leaves to developing leaves, while the rest will remain in the fixation leaves. This would differ for different plants during the year and with changes in environmental factors. In some evergreen species in which leaves act as reservoirs of assimilates, greater proportional amounts of carbon might be retained in the leaves (Larson, 1964; Kozlowski and Winget, 1964; Gordon and Larson, 1968; Dickman and Kozlowski, 1970).

Unfortunately, total allocation on a community basis was not calculated at the beginning of the growing season. However, the data reported for the partitioning of photosynthates to plant parts per unit dry weight in the spring 72 hours after labeling with ^{14}C (Tables 6 and 7) provide the basis for an assumption that for both species most of the fixed carbon at that time would be allocated to the new shoot tissue, with presumably minimal amount being channeled to the underground plant parts.

The amount of total carbon allocated to the new growth of shoots was highest in July for Atriplex. This may be associated

with a greater proportional new growth biomass and the high energy demands of the reproductive effort occurring at that time. Conversely, substantially lesser amounts of carbon were allocated to the new shoot growth of Ceratoides, presumably due to the lower proportional new shoot biomass and apparently lower energy requirements for seed production.

In general, results of the total ^{14}C allocation studies on a community basis indicate a reasonable consistency with the values of biomass per unit area and the pattern of preferential partitioning of radiocarbon in terms of unit weight of plant parts during their annual growth cycle.

The final determination of carbon allocation at the end of the season from plots originally tagged in April and July (Tables 8 and 9) showed that there was a significant change in the energy distributed to new shoot growth, old shoot growth, and the root system.

In all cases there appeared to have been a higher relative distribution of energy to the root system. This was particularly prevalent in the Ceratoides-dominated community in which 65 and 36 percent of the carbon photoassimilated in April and July, respectively, and was still remaining in the plant, appeared to be located in the underground plant structures. Similarly, in the Atriplex community, 35 and 29 percent of the total carbon incorporated in the April and July treatments, respectively, appeared in the root system.

The higher proportion of carbon located in the underground biomass of the Ceratoides community is consistent with the higher root/shoot biomass ratios of this community.

The noticeably high carbon content of the new growth of Atriplex at the end of the growing season for the April and July ^{14}C labeling treatments, may in part be attributed to the presence of the fruits at the time the last sample was taken in September.

If it is assumed that the intense root growth activity observed in April depends principally on a source of energy from stored photosynthates and not from current photosynthesis, the large proportion of carbon allocated to the roots before the winter season began can be interpreted as a strategy of energy storage for the next season's root growth. The importance of the root system of these two species as a reserve of photoassimilated materials has been stressed by Coyne and Cook (1970).

Redistribution of photoassimilated carbon appears to have an important role in the manner in which energy is selectively allocated to plant structures. This is apparent because of the high values of total radiocarbon present, on a community basis, in the new shoot tissues of these two species in September which was not present at the time $^{14}CO_2$ photoassimilation occurred in April. It can, therefore, that be postulated temporary pools of photosynthates in which carbon is retained as a transient reserve of energy do exist.

A hypothesis of this kind could imply that during the growth stages which have high energy demands, that both the energy of current photosynthates and that of stored reserves from photosynthesis of the same season may be tapped. The use of stored reserves in Atriplex when the fruits were approaching maturity has been reported by Coyne and Cook (1970).

There most likely exists a flexible scheme of use of these pools of available current photosynthates in cool desert shrubs. Under normal situations this reserve of resources is in part selectively devoted to satisfy the high energy demands of reproduction. Environmental stresses, such as predators, diseases, drought, may, however, change the mode of utilization of this energy. Fluctuations in the pattern of carbohydrate reserves and their utilization in Atriplex and Ceratoides attributed to environmental factors has been previously reported (Coyne and Cook, 1970).

Figure 22 indicates that from the total amount of radiocarbon distributed to the new shoot growth, old shoot growth, and roots in terms of plant biomass per unit ground area 72 hours after $^{14}CO_2$ photoassimilation occurred in July, only slightly over 60 and 50 percent was retained in the plants in September for Atriplex and Ceratoides, respectively. For both species the greatest ^{14}C reduction occurred in the new growth fraction. These values were calculated from the data of Tables 9 and 10. The recorded carbon losses are closer to the values observed by Hansen (1967) in apple trees and by Ursino et al (1968) for young pine plants.

Once carbon has been photoassimilated it can be lost from the plant tissue through respiration, litter, herbivore consumption, and root and shoot exudation. In part, the significant amounts of radioactivity lost in the new shoot growth biomass for both communities can be accounted for by the sheddingof the reproductive structures and leaves, which were highly radioactive and constituted a significant proportion of the new shoot growth at the moment

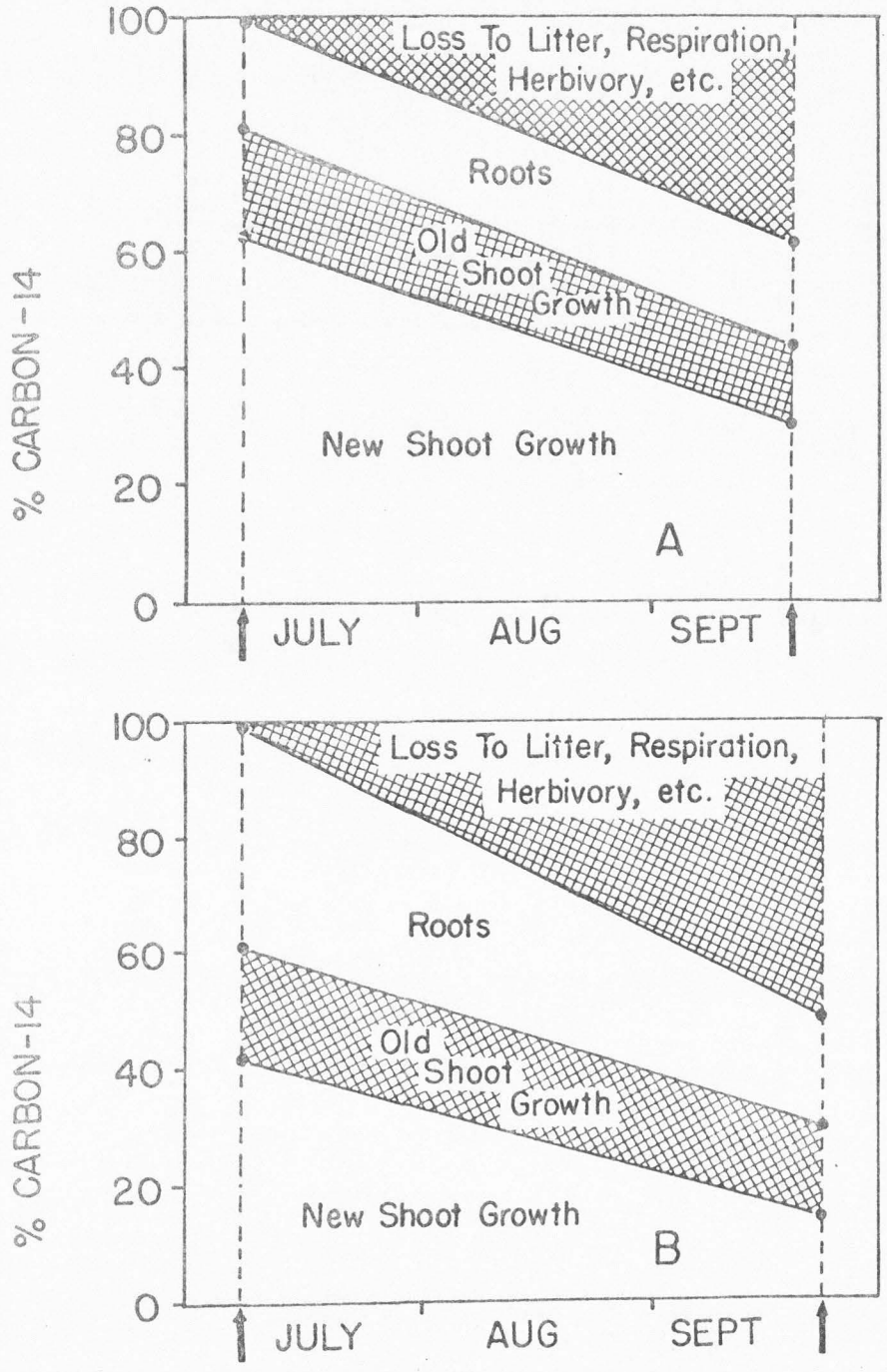


Figure 22. Total relative allocation of ^{14}C-photosynthates in terms of plant biomass 72 hours after $^{14}CO_2$ photoassimilation in July and at the end of the growing season in a) Atriplex confertifolia and b) Ceratoides lanata. Arrows indicate date the plant samples were taken.

of the ^{14}C labeling in July. Data of N. E. West (unpublished data) showed that the loss of plant materials between July and September amounted to approximately 58 percent and 66 per cent, respectively, of the total litter production for these species during the 1973 growing season for Atriplex and Ceratoides communities.

Translocation of photosynthates to other plant structures may also account for the loss of ^{14}C in the new shoot tissue.

A lesser reduction of radiocarbon allocated to old shoot growth and roots is apparent for these species between July and September.

Care must be taken in the interpretation of these figures, as they most probably represent the net balance of ^{14}C translocation in these structures three months following $^{14}CO_2$ assimilation. Losses through respiration and other pathways could be compensated by ^{14}C-photosynthate translocation from other plant parts. Carbohydrate reserves appear to accumulate in the roots and crowns of Atriplex and Ceratoides plants especially late in the growing season (Coyne and Cook, 1970). Increased transport of ^{14}C towards the root system during the fall in perennial plants has been reported for other species was well (Hansen, 1967; Ursino et al., 1968).

Future research for the differentiation of dead and live roots in the soil

Calculation of root biomass and rates of root system turnover present special problems. There exists no single satisfactory technique for determining the underground turnover rates in natural

undisturbed communities. The growth observation chambers discussed earlier, although valuable for determining the timing and extent of root activity, do not permit quantitative determination of underground biomass turnover.

In the root system of perennial plants it is very difficult to differentiate between new and old root growth or dead from living roots on the scale required for community biomass studies.

Dahlman and Kucera (1965) estimated for a grassland prairie that the differences between the highest value of below-ground biomass and that found early in the season represents the annual net root growth for the season under field conditions. Additional root growth may still occur and further decay processes may reduce later measurements. An additional complexity is presented when the underground system is composed of roots of different species which may differ in their phenology and in the rate of their turnover.

The method for the separation of dead and living roots by differential density in methanol discussed earlier was found to be satisfactory for the testing of individual roots. It was also shown to be a promising technique for the separation of dead and living root fractions of Atriplex confertifolia originating from whole soil core root samples.

Several root core samples of Atriplex originating from the July root biomass studies were treated with the separatory methanol technique. It was found that approximately 83 percent of the total weight of each sample corresponded to the fraction that sank. The

remainder could be considered to be composed mainly of inert organic materials. This information would indicate that at least approximately 17 percent of the total root biomass found in this study consisted of non-living material. However, the question still remains as to the proportion of non-living root core materials that might have still been mixed with the sinking root biomass.

When the same procedure was applied to the root core samples of Ceratoides lanata, it was observed that 30 percent of the total root biomass of each sample floated and the remaining 70 percent sunk. However, as was reported in the Results Section, the distribution of radioactivity between the sinking and the floating components was not so clear cut.

These differences in the results for the root core samples originating from the Atriplex- and Ceratoides-dominated communities were most intriguing. They were probably associated in part with the processes of root decay for each species in the soil. Further studies along this line would demand the development of new techniques and were beyond the scope of this project. Nevertheless, some additional observations were made since they may be of interest for future research.

From the moment a root dies to its total disintegration in the soil, there may exist a gradient in its change in density, which would make it float or sink in methanol. Sometimes, too, it might either sink very slowly or remain in suspension.

Two phenomena were observed which may have a significant bearing on the manner in which roots of cold desert shrubs decay in the soil.

First, it was noted that although a root might be attached to the main root system, there is no guarantee it is alive. This could be important when roots are detached from the plants for study. Secondly, root decay in both species, at least in part, is a process that appears to occur beginning within innermost parts of the root. In other words, there were clear indications that xylem tissue may disintegrate earlier than the external phloem and cortex. Frequently examples were found of roots which were empty, exhibiting an internal hollow core with the peripheral cortex intact. These were dead root remnants. However, the fact that on occasion small rootlets were attached to these hollow-core root segments, suggests that the root cortex may stay active even though the decay processes in the interior of the root tissue have been initiated much earlier.

One microscopic observation of root segments of Ceratoides in varying apparent degrees of decay suggested that fungal mycelia appeared to be present in most cases.

The mode of root decay in the soil for Atriplex and Ceratoides may be a reason for the different root core sample results when the roots were treated with the alcohol density separation technique. The processes of root decomposition in the soil may also be different for the same species under different soil conditions.

Studies on the mechanisms of root shedding and decay could contribute to an understanding of root turnover and energy partitioning in the different compartments of the belowground ecosystem. Understanding of root decay may also help in devising methods for the separation of dead and living root tissue in the soil.

CHAPTER V

SUMMARY AND CONCLUSIONS

Survival of Atriplex confertifolia, Ceratoides lanata and Artemisia tridentata in the cool desert environment could not be possible without the ecological adaptations that allow them to cope with the effects of very low soil and plant water potentials and the great fluctuation of daily and seasonal temperatures.

The results of this study give some insights on the nature of different evolutionary strategies of energy allocation and root growth dynamics followed by the three cool desert shrubs of this work.

Certain major patterns of root growth activity appear to be common for the three species. For example, the root growth chambers indicated that root growth activity of these species preceded elongation of new shoots in 1973; furthermore, the growth period of the root system was longer than for the shoot system in the fall. Moreover, roots of all three species showed some degree of growth activity during the winter season. Maximum absolute root growth rates for all three species were found to take place in the spring near the soil surface. This is the period during the growing season when soil Ψ_s is highest following the melting of the snow and thawing of the upper soil layer. A rapid increase in soil temperature is also noted in this soil region at that time.

Root growth activity later during the growing season for all three species appears to be principally influenced by the interaction of

soil water availability and soil temperatures. The pattern of root activity observed at progressive depths in the soil during the course of the season may be primarily an adaptation corresponding to cyclic seasonal changes of Ψ_s and temperature of the soil. A strategy of this nature will allow this species to have always at least part of its root system functioning within a physiologically suitable range of Ψ_s and temperature in the soil, even though other parts of the root system may be limited in activity because of less favorable temperature and water conditions.

Different adaptative interspecific differences become apparent for the root growth activity of Atriplex in August and September with respect to the other two species. In effect, while Ceratoides and Artemisia significantly reduce their root growth activity after the second week of August, Atriplex still maintains a noticeable pattern of new root growth. The extended period of root growth activity during the year for Atriplex may be advantageous for this species. This may represent an adaptative strategy for water uptake association which enables Atriplex to extend the period of significant net photosynthesis well into the fall (Caldwell, 1972).

The high root/shoot ratios observed for Atriplex and Ceratoides may perhaps be viewed as part of the adaptative mechanism which will allow these species to overcome the problem of low moisture availability in the soil, which tends to diminish the efficiency of water extraction per unit of root absorbing surface. The primary absorbing surfaces of the root system of these shrubs are most probably the small rootlets. It is postulated in this work that a periodic sloughing of and replacement is the meachanism whereby roots repeatedly re-explore the same soil mass.

Certain major patterns appear to have evolved for Atriplex confertifolia and Ceratoides lanata in the proportion of energy allocated to the various plant structures, both in terms of unit weight of plant organs or on a total community basis. These patterns suggest that the schemes of energy utilization and allocation of these species would differ quantitatively more than qualitatively. The seasonal variation in the partitioning of photosynthates to plant organs during the 1973 growing season, in terms of unit weight dry tissue, appears to correspond reasonably with the development of the different organs during the plant annual growth cycle. Growth is dependent upon the availability of energy to the growing structures. It can be considered that each ontogenetic seasonal plant stage of development will demand a certain amount of energy which must be applied at the proper time, combining a program of carbon partitioning in response to plant genetic constitution and changes of environmental factors. In Ceratoides the reproductive effort expressed in terms of relative carbon allocated per unit dry weight tissue appears to be a relatively less energy demanding process. It is suggested that this phenomenon may be associated with the shorter reproductive period for this species.

Judging by the values of ^{14}C allocated to above-ground and below-ground plant structures, in terms of plant biomass per unit ground area, 72 hours after $^{14}CO_2$ photoassimilation occurred in July and September (Tables 9 and 10), Ceratoides appears to allocate larger amounts of energy to the root system. This conclusion appears to be confirmed by the data in Chapter IV which also indicate that as much as 65 percent and 36 percent of the $^{14}CO_2$ photoassimilated

in April and July, respectively, and still present in the plants by September, was localized in the underground structures of the Ceratoides-dominated community. For similar dates and treatments only 35 percent and 29 percent of the total carbon incorporated in April and July was present in the underground structures of the Atriplex-dominated community. The higher proportion in the Ceratoides-dominated community are consistant with the higher root/shoot biomass ratio strategy of this species.

The results on root growth dynamics and allocation of energy in the three shrub species of this study no doubt reinforce the concept that survival of this plant community under the cool desert environment must greatly depend on ecological adaptative strategies taking place in the underground plant structures.

Atriplex possesses the C_4 photosynthetic pathway whereas Ceratoides possesses the more common C_3 pathway (Welkie and Caldwell, 1970). It has been reported that C_4 species have higher photosynthetic rates than C_3 species (Hatch and Slack, 1970). However, Caldwell (1972) reported that under cool desert environments rates of net photosynthesis for Atriplex were similar or sometimes less than those of Ceratoides. Under desert conditions, yield of photosynthetic rates does not necessarily have to represent an index of ecological success in terms of survival. It may entail higher transpiration. The adaptative characteristics to the detrimental effects under extreme conditions may bear more importance than actual photosynthetic rates under favorable conditions. On an annual basis Atriplex has greater photosynthesis per unit land area than Ceratoides. This is due in part to more foliage per unit surface, also because of the ability

of this species to maintain a low but positive rate of net photosynthesis (Caldwell, 1972) in dry periods. Atriplex confertifolia has greater photosynthesis per unit land area than Ceratoides lanata.

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