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ESTIMATION OF FUNCTIONAL ROOT BIOMASS AND ROOT AND SHOOT RESPONSE OF *ATRIPLEX CONFERTIFOLIA* TO SUMMER RAIN

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ABSTRACT

A technique was developed for separating live from dead roots of shadscale (*Atriplex confertifolia*) based on appearance and turgidity. The procedure was applied to roots retained by a 1-mm sieve in the analysis of soil cores taken in a monospecific shadscale community. The results indicate that at least 8.3% of the roots were alive, but the estimate is conservative since more than half the root biomass passed the 1-mm sieve as fragments, assumed to be dead. Total root biomass, to a depth of 75 cm, came to 2405 g/m^2. Even though the surface litter was scraped from the soil before coring, leaf and stem fragments in the soil samples occurred at an estimated 1165 g/m^2. Using this technique, the influence of simulated summer rainfall and nitrogen supplement on root and shoot growth of shadscale was examined on the southern shrub site of the Curlew Valley Validation Site. There was no measurable response to nitrogen applied with supplementary water. The irrigation treatment of 25-mm equivalent rainfall was followed by a natural rain of 23 mm the next day. Watering did not promote shoot elongation or an increase in shoot biomass, but there was a modest increase in live root biomass within the watered plants nine days after imposing treatment. The increase amounted to 20.7 g/m^2 as measured by cores taken beneath the watered plants and would presumably be less if spatial heterogeneity of root distribution and root growth is taken into account. A concurrent increment in the dead root compartment appeared to occur in the three weeks following watering; no satisfactory explanation can be offered for this apparent phenomenon. Since root growth was measured after the application of real-plus-simulated summer rainfall, it was concluded that shadscale is not dormant during the summer.

INTRODUCTION

Desert ecosystems are characterized by discontinuous occurrence of precipitation (Noy-Meir 1973). The effectiveness of precipitation events in activating biological processes and in plant biomass buildup may be related to a number of factors, in particular temperature, plant characteristics and intensity and duration of the precipitation event. This stochastic nature of precipitation in deserts is important in the timing of growth responses in plants and is justifiably included in simulation models of desert ecosystems (Goodall 1967).

The cool deserts of the Great Basin are characterized by cold winters and hot summers. In winter, snow often occurs and may form a significant component of annual precipitation. Growth of shrubs in these areas appears to be confined to the spring period when temperatures are warm enough for plant growth and when soil moisture is recharged from snowmelt (Caldwell 1972). Summer rainfall is, on the average, low and extremely variable.

In warmer deserts, rain falling at any time of the year generally induces a plant response, as long as it is above a threshold amount (Went 1949; Adams and Strain 1969). However, preliminary experiments by MacMahon et al. (1975) suggest that even heavy supplementary summer watering of *Atriplex confertifolia*, a common shrub in the Great Basin cool desert, does not increase above-ground biomass. This is somewhat surprising, as the species possesses the C_4 syndrome (Welkie and Caldwell 1970) and is capable of active photosynthesis during high summer temperatures. Even at leaf temperatures greater than 50 C, positive photosynthetic gains occur (Caldwell 1972).

There may be several explanations for this apparent lack of response to additional soil moisture during the summer period. First, absorption of water from the wetted zone following summer showers may be insufficient to promote active photosynthesis because of the lack of viable root surfaces. Second, the surface horizon that becomes wet may be deficient in available nutrients, especially nitrogen, thereby limiting the growth response. Third, active photosynthesis may occur following summer rains, but the majority of the photosynthate may be basipetally partitioned into new root structures. Fourth, there may be no measurable growth response because this species exhibits summer dormancy.

In this project, a technique was developed to distinguish live from aging or dead roots in soil samples, which was then utilized in an experiment designed to test the above hypotheses.

OBJECTIVES

1. Develop and evaluate a method to quantitatively determine the proportion of dead roots in a root sample.
2. Measure the shoot and root growth of *A. confertifolia* response to supplementary water and nitrogen application during summer.
3. Measure the plant water stress and dryness of the soil as influenced by the treatments.

METHODS

Live and Dead Root Separation

Several methods have been used to estimate the proportion of dead roots in a sample. These include differentiation of roots based on color development when stained by 2, 3, 5-triphenyl tetrazolium, C^{14} activity of individual roots and differential density when floated in methanol. Caldwell et al. (1975) discuss the limitations of these methods and conclude that none was really satisfactory, although the flotation method deserved further evaluation and refinement.

In the present study, a method based on size, appearance and turgidity was used to differentiate between live and dead roots. This was developed after a microscopic

examination of root parts extracted from soil samples. It was found that the majority of the biomass obtained from soil cores consisted of very fine root fragments (< 1-mm diam.) that could be confidently classed as being dead. The roots that were intact were found to vary in their turgidity when touched by a dissecting needle. On the basis of these observations, the following procedure was used to separate and quantify components of the root biomass: 1) Samples taken from the field were weighed, gently mixed by hand to distribute the roots evenly throughout and all wood and major roots (diam. > 0.5 mm) were picked from the soil and washed. Major roots were examined and if they were brittle and showed signs of decomposition, they were separated and classed as being dead and the remainder were classed as being alive. Both fractions were dried and weighed. 2) A subsample was extracted (approximately 30-40 g) and weighed. All root material was floated from the subsample by repeated washing and decanting with water. Two sieves (1.0- and 0.15-mm openings) were used to retain fine root material. The first retained intact roots 1 mm or more in length and the second retained root fragments and some sand particles. The material passing this second sieve was found, on microscopic examination, to contain no intact roots and consisted of semidisintegrated root parts which were assumed to be separated from the root system and could therefore be classified as dead root material. Because of contamination by sand, the samples of root fragments were combusted in a furnace and the true dry weight was determined. 3) The roots retained on the 1.0-mm sieve were washed onto a filter paper (12.5-cm diam.) on a Buchner funnel. Water was withdrawn slowly with suction and the roots were randomly arranged to cover the paper. A clear plastic sheet (16 x 16 cm) which was marked with a grid with lines 12.7 mm apart, was placed under the paper and both were placed on the lighted stage of a binocular microscope. Using the technique of Newman (1966), as modified by Marsh (1971), the length of roots on the paper was determined by line interception. The 12.7-mm grid allowed direct estimation of root length in centimeters, from the number of interceptions. Each root that crossed a line was classified into one of three categories: alive, senescing or dead, on the basis of touch and appearance. A dissecting needle was pressed onto each root and, if the root was firm with the stele intact, it was classed as being alive; if soft (but not limp) with the stele intact, it was classed as senescing; if collapsed with the stele degenerated or missing, it was classed as being dead. Only a few of the live roots were white or near-white in color. Most of the roots were amber-brown. Following length determination, litter (undecomposed leaves and stems) was removed, the fine roots were carefully scraped from the filter paper and both fractions were dried and weighed.

To test the validity of this approach, an *A. confertifolia* plant was exposed to an atmosphere of $C^{14}O_2$ for 1 hr. This was done by enclosing the shoot in a polyethylene bag into which was released $C^{14}O_2$ from $BaC^{14}O_3$ by addition of lactic acid. A day later, roots extracted from cores were classified as described above and the C^{14} content of individual roots was determined using methods described in Tieszen et al. (1974).

The sampling site was in Curlew Valley, west of the Wildcat Hills, near the same location sampled by Caldwell and Camp (1974). The community was a nearly monospecific stand of *A. confertifolia* (Torr. and Frem.) S. Wats. On August 15, 1975, a transect was laid out and at 12 points, 2 m apart, soil cores were taken with an auger (8.3-mm diam.). Before coring, the litter was scraped from the surface. The depths of sampling were 0-25, 25-50 and 50-75 cm. Soil samples were enclosed in plastic bags and kept cool in polystyrene boxes during transport back to the laboratory where they were placed in a cool room (5 C) and processed within the next two days.

Plant Response to Summer Rain

The study took place on sites 3 and 4 in the ART-ATR-SIT vegetation type of the Curlew Valley Validation Site. This type is dominated by two shrubs, *Artemisia tridentata* and *Atriplex confertifolia*, and a perennial grass, *Sitanion hystrix*.

With One Rainfall Supplementation

During the first week of July 1975, 110 bushes of *A. confertifolia* (of uniform size) were tagged and randomly assigned to one of three treatments. The treatments and number of plants assigned to each were as follows: A) Controls (13); B) 25 mm of supplementary water (53); C) 25 mm of supplementary water plus 200 kg nitrogen/ha (53).

Shoot growth—Ten randomly selected plants from each treatment were used for monitoring shoot length. On July 8, four shoots on each plant were tagged (on the N, S, E and W sides of each bush) and their length measured. On August 13 these same shoots were remeasured. Separately, shoots (4 per plant) on 10 control plants were measured on May 14 and again on August 13 to assess overall extension for the growing season.

Soil water—Soil water potential (Ψ_S) was regularly monitored, using calibrated soil psychrometers. Each psychrometer consisted of a chromal-constantan and a copper-constantan thermocouple mounted in a hollow porous ceramic bulb. Three plants were randomly selected from each of the three treatments, and in early July three psychrometers were installed under each of these nine bushes at the depths of 7.5, 15.0 and 22.5 cm. Each psychrometer was installed 12 cm away from the plant center. Microvolt readings were converted to water potentials (— bars) using individual calibration factors and a correction for soil temperature. Ψ_S at 50 cm was measured in the same manner, using psychrometers that were installed two years previously in the same vegetation type and within 50 m of the present experimental site.

Watering treatment—The application of supplementary water to the 106 plants in treatments B and C was conducted on July 9. Metal collars, 40 cm in diameter, were pushed about 5 cm into the soil around the selected bushes and water was sprinkled over the area. The amount of water sprinkled around each plant was equivalent to a 25-mm rainfall occurring within the 40-cm (diam.) collars, which were removed as soon as the surface water soaked

into the soil. All watering took place in the late afternoon of July 9. For treatment C, the nitrogen was applied as NH_4NO_3 dissolved in the irrigation water, which represented a nutrient supplement at the rate of 200 kg/ha within the confines of the metal collars.

A day after the water had been applied to the 106 test plants, a natural rainstorm occurred which added 23 mm to both the control and irrigated plants. This rain fell on the evening of July 10. The impact on the experimental design was to virtually double the watering treatment on the irrigated plants (making a total of 48 mm of equivalent rain over a 36-hr period), and to promote the status of the "control" plants to the level of soil water conditions originally planned for treatments B and C. This effectively blurred the disparity in soil water potential intended between the control and irrigated plants.

Plant water potential—Xylem pressure potential (Ψ_p) of control plants was measured using a Scholander-type pressure chamber (Ritchie and Hinckley 1975). Terminal portions of shoots were used in the measurements. Dawn and noon readings were made to obtain the minimum and maximum potentials for the plant population on a particular day.

Shoot and root harvest—On eight occasions over a 60-day period, shoots and roots of the irrigated plants in treatments B and C were sampled. The shoots were cut off at ground level, the leaves were separated from stems, oven-dried and then weighed. Roots under the bushes were then sampled using an auger (8.3-mm diam.). Two soil cores were taken from under each bush on the north and south sides at a distance of 12 cm from the stem base and at two depths, 0-15 and 15-30 cm.

The density of "alive," "senescing" and "dead" roots (< 0.5-mm diam.) in the soil cores was estimated in the same manner as described above.

With Repeated Rainfall Supplements

Beginning July 29, and repeated on August 5 and 12, a group of six plants was watered in the manner described in the above section. Each time the application was equivalent to 25 mm of rainfall occurring within the metal collars encircling the plants. The control plants for this second irrigation experiment were the group of 13 plants selected for controls in the preceding experiment (treatment A).

On the final irrigation date (August 12), the control group of 13 plants was divided into two halves and one half was given a watering treatment of 25-mm equivalent rainfall.

Plant water potential measured by a Scholander pressure bomb was recorded for the controls from July 6 at intervals until August 6, and for half the group on August 13 and 15. The July record was obtained as treatment A of the above section. Dawn and noon readings for the repeated watering experiment were made the day after irrigation, viz., July 30, August 6 and 13, and again on August 15. The exception to this schedule was the postponement of noon readings planned for August 6 to August 8.

RESULTS

Separation of "Live" and "Dead" Roots

The proportions of roots sampled from under the bush exposed to $C^{14}O_2$, that contained a C^{14} content significantly above a background level, were 0, 7 and 27%, respectively, for "dead," "senescing" and "alive" roots. This distribution of isotope activity in the root classes suggests that root sections whose metabolism attracted and retained labeled assimilate tend to be classified as "alive" in the visual/touch technique. The low proportion of labeled roots in the "alive" category (27%), however, means that potentially three-fourths of the "alive" roots could be senescing or dead, if the C^{14} assimilate distribution is the sole criterion of discernment.

The analysis of roots in cores taken in a pure shadscale community indicates that only 8.3% of roots were "alive," based on the visual/touch technique (Table 1). A large component (54%) of the total root biomass fell into the "fragments" category caught between sieves of 1.0- and 0.15-mm pore size. This fraction was assumed to be "dead," and was therefore not inspected for separation into "alive" and "dead" categories. Since the root fragments represent more than half the total root weight, it would require only a small fraction of these fragments to be classified as living material in order to substantially affect the amount of "alive" roots in the soil. In fact, if only 18% of the root fragments were alive, the proportion of living roots would be doubled.

Although litter was scraped from the soil surface before coring, the amount of leaf and stem litter in the soil samples was high (mean of 1165 g/m^2). This suggests that to obtain a reasonable estimate of root biomass in routine sampling, some method of accounting for litter contamination should be used.

In determining the weight of alive minor roots, it was assumed that both intact dead and living roots had a similar weight/length relationship. The mean diameters of the subsamples of dead and alive roots were 0.326 and 0.315 mm, respectively. Since most of the dry weight of roots is structural material, it is unlikely that there would be a significant error in the determination of the weight of live roots. The conversion factor for dry weight from length of small roots is therefore 1.38×10^{-4} g/cm.

The value for the total below-ground biomass is higher than that reported by Caldwell and Camp (1974) from a sampling of the same area in 1973, 1871 vs. 2405 g/m^2, but differences of this order would be expected due to variation in seasonal conditions. It is considered that the sampling method yielded a reasonable estimate of the total root biomass as the coefficient of variation for this was 17%.

The below-ground biomass (Table 1) and density of minor roots (Table 2) were highest in the 25-50 cm horizon. Other studies in the same community (Bjerregaard 1971; Fernandez 1974) have reported that the highest biomass and concentration of roots occur in the top 25 cm of the profile. No explanation can be offered for this disparity.

Table 1. Biomass (g/m^2) of root components separated from soil at three depths. For comparisons between depths, means followed by the same letter are not significantly different at the 5% level

Component	Depth (cm)				% Total Roots
	0-25	25-50	50-75	(0-75)	
"Alive"					
a) tap root*	-	-	-	(48)*	8.3%
b) major (> 5 mm)	25ab	38b	9a	(72)	
c) minor (< 5 mm)	12a	42b	25ab	(79)	
"Dead"					
a) major (> 5 mm)	27ab	51b	19a	(97)	91.7%
b) minor (< 5 mm)	155a	390b	274c	(819)	
c) fragments	456a	486a	348a	(1290)	
TOTAL	675a	1007b	675a	(2405)	

* Value taken from the data of Caldwell and Camp (1974).

Table 2. Density (cm/cm^3) of fine roots (< 5-mm diam. and categorized into alive, senescing and dead) at three depths, under and between bushes. Asterisks indicate under and between bush means that are significantly different ($P < 0.05$). For depth comparisons, means followed by the same letter are not significantly different at the 5% level

Category	Sampling Site	Depth (cm)		
		0-25	25-50	50-75
		A	B	C
Alive	Under	0.09 a	0.5 b	0.18 ab
	Between	0.03 a	0.21 b	0.11 ab
Senescing	Under	0.34 a	1.09 b	0.80 ab
	Between	0.21 a	*0.41 a	*0.26 a
Dead	Under	4.50 a	11.94 b	8.13 ab
	Between	4.44 a	10.21 b	7.57 ab
TOTAL	Under	4.92 a	13.54 b	9.11 c
	Between	4.69 a	10.83 b	7.94 ab

The cores taken from under shrub canopies (n=7) were considered separately in Table 2 from those taken from between shrubs (n=5). All values for roots sampled from under shrubs were higher than those taken from the interspaces, but because of the variation there was a statistically significant difference only at two depths for roots classed as "senescing."

Response to Summer Rain

Rainfall, Soil and Xylem Water Potentials

With one irrigation event—During the experimental period, little rain fell except for a heavy fall of 23 mm one day after commencement of treatments (Fig. 1 [a]). This rainfall added 23 mm to the 25-mm irrigation treatments (B and C) and watered the controls to the level originally intended for the treatments. The two applications of water, one natural and one by hand, are quite different in circumstances and conditions. The irrigation was applied to metal-ringed enclosures surrounding individual plants in one dose in late afternoon. The rainfall occurred over several hours during the night and, of course, fell evenly over the soil surface. The effectiveness of the 25 mm of irrigation water may have been less than the effectiveness of the 23-mm rainfall for the following reasons: 1) Some of the irrigation water may have traveled laterally into drier soil after it had infiltrated below the level of the metal flashing, thus reducing the water content in the zone immediately beneath the plant. 2) The irrigation water was applied during high evaporative conditions, whereas the rain fell during a spell of high humidity. Whatever the correct explanation may be, there was no significant difference in plant water potential at any time between the plants receiving 25-mm supplementary water one day prior to the rainfall and those plants (control) which were not irrigated but received the 23-mm rainfall. Xylem water potentials for control plants at dawn and noon (DSCODE A3UMJ05) are shown in Figure 1 (f). Application of water (either rainfall or irrigation water) increased dawn values of xylem pressure potentials from —30 to —15 bars. Thereafter, there was a steady decrease to —56 and —62 bars at dawn and noon, respectively, at the middle of September.

Soil water potentials (A3UMJ04) experienced a change after watering (Fig. 1 [b-e]) with soil near the surface reaching 0 bars after the rain but rapidly drying out to exceed —60 bars from the end of July. Water from the rainfall penetrated to a depth of at least 22.5 cm and probably deeper under those plants that received supplementary water. At a depth of 50 cm, Ψ_s steadily decreased from —20 to —40 bars during the summer period, almost certainly as a result of water uptake through roots.

With repeated irrigation—The repeated irrigation effect (three, 25-mm equivalent precipitation at 1-week intervals) on plant water potentials is illustrated in Figure 2. The control plants are those designated as treatment A in the single irrigation experiment. The curves for control (dawn and noon data) in Figure 2 are identical to the curves in Figure 1 (f) for the period from July 16 to August 15.

Application of repeated irrigation inhibited the decline in dawn-measured xylem potential but did not reverse it. After the second watering (August 5), the noon plant potential values showed a response to the irrigation, increasing from —51.5 on August 8 to —43.5 on August 15.

A single application of 25 mm of water on August 12, to previously unwatered plants, increased Ψ_p within 24 hr. This suggests that at least some of the roots in this surface horizon were capable of immediately absorbing water from the wetted soil. The further increase in Ψ_p two days later may be attributed to increased absorptive ability of the existing live roots and/or deeper penetration of the water to root surfaces lower in the profile.

Shoot Growth

There was no detectable response in shoot growth, whether measured by shoot length, stem or leaf weight, as a result of wetting the soil profile in early July (Fig. 3). Analysis of variance showed that none of the treatments induced any significant response in above-ground biomass.

Elongation of shoots occurred only during the spring and probably commenced in early May (West and Gunn 1974).

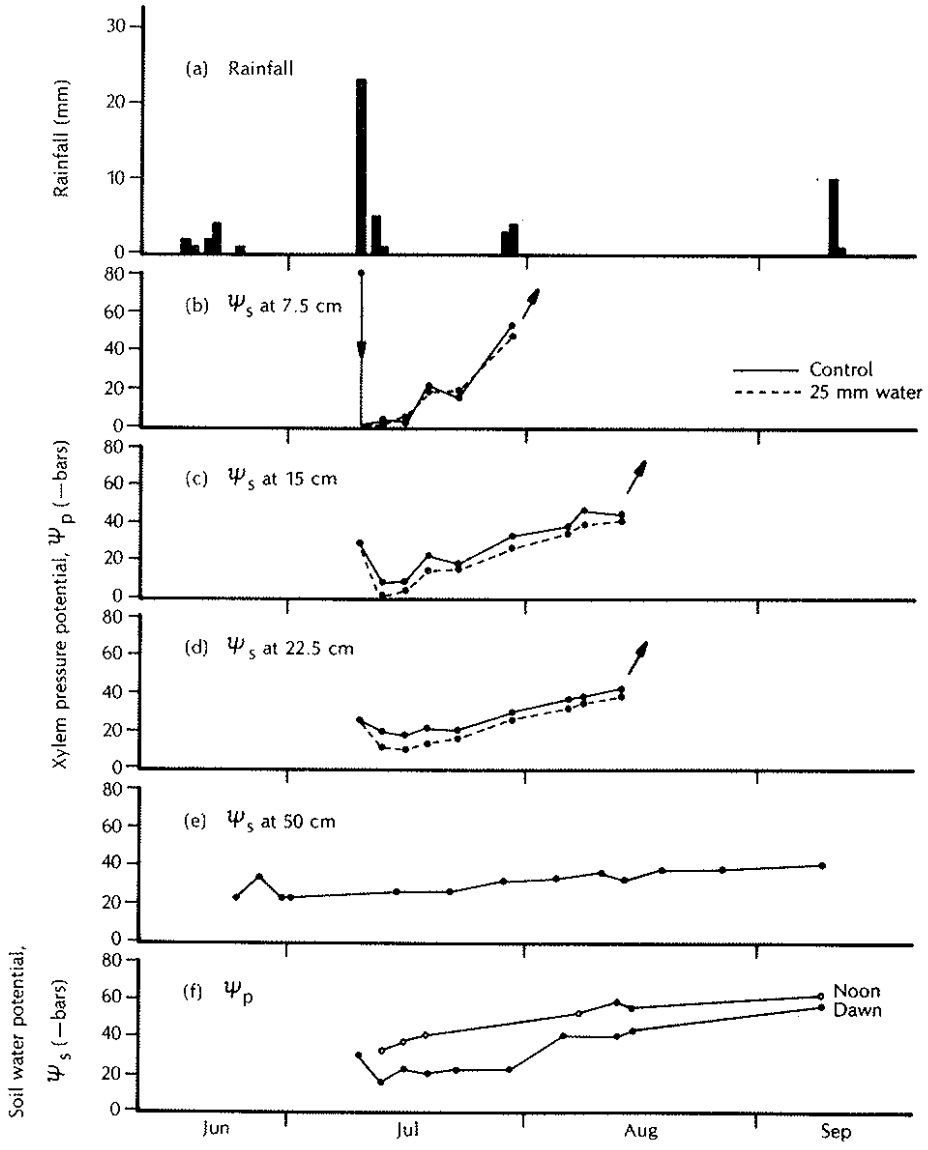

Figure 1. Rainfall (a) and soil water potential (Ψ_s) at 7.5 cm (b), 15 cm (c), 22.5 cm (d) and 50 cm (e) below the surface at the study site (DSCODE A3UMJ04). Ψ_s beneath bushes receiving 25 mm of supplementary water is represented by the broken line. Xylem pressure potentials (Ψ_p) at dawn and noon for the control plants are shown in (f) (A3UMJ05).

Root Growth

Root data were collected from plants in treatments B and C (irrigation, and irrigation with nutrient supplement), but not from plants in treatment A (controls). Analysis of variance showed that there were no statistically significant first-order interactions for the three root categories, nor any significant differences between treatments or depths except for the senescing root category where the density was significantly greater ($P < 0.05$) in the 15-30 cm than in the 0-15 cm depth. The root density data in Figure 4 are means of treatments B and C, and of the two sampling depths.

The combined watering (natural rainfall plus irrigation) is associated with a significant increase in density of live roots, from 1.1 to 1.6 cm/cm^3, nine days later. A more substantial increase in the dead root category was recorded during the three weeks after watering -- 6 to 8.5 cm/cm^3 -- but variance was high.

DISCUSSION

The results obtained in this study indicate that summer rains are ineffective in stimulating shoot growth of the shrub *A. confertifolia* when growing in a cool desert. Reasons for this nonresponse in shoot biomass are now discussed within the framework of the four hypotheses presented in the Introduction.

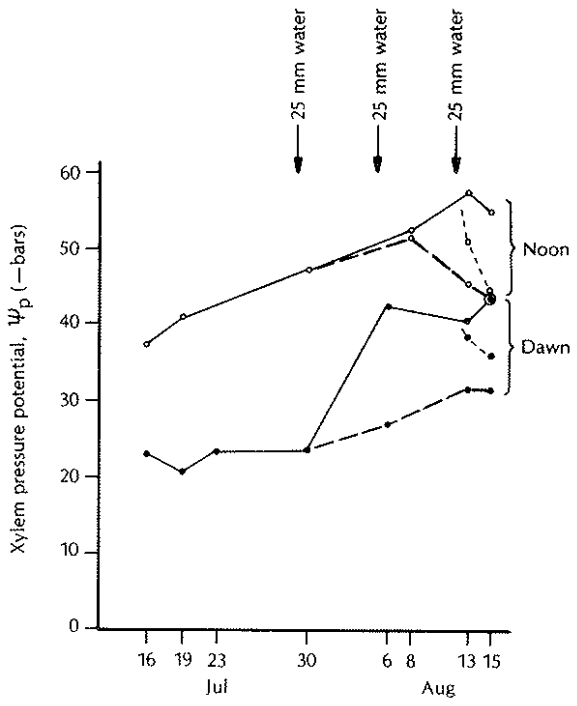

Figure 2. Xylem pressure potentials (Ψ_p) at dawn and noon for shadscale plants that received no supplementary water (————), were irrigated with 25-mm equivalent rainfall on July 29, August 5 and 12 (— — —) and were irrigated at the rate of 25 mm once on August 12 (------). All plants received 23 mm of rainfall on July 9.

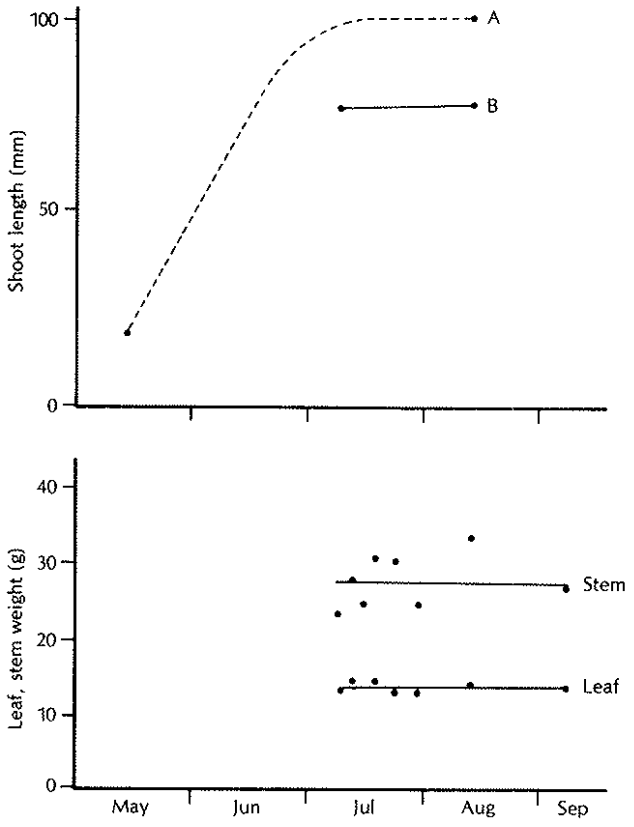

Figure 3. Shoot length for two groups of plants (treatments A and B) and stem and leaf dry weights of bushes of *A. confertifolia*.

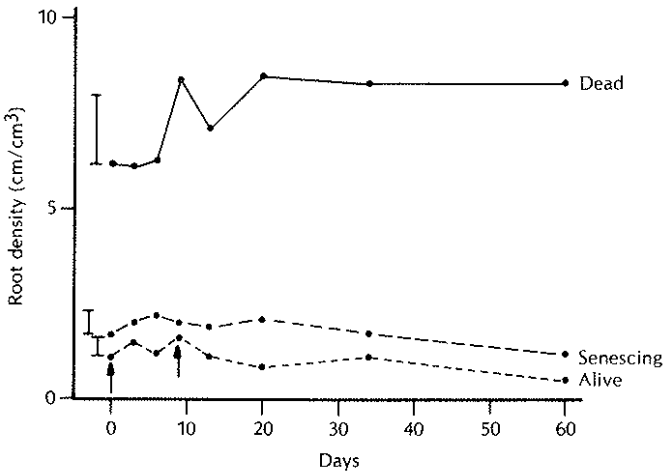

Figure 4. Density of dead, senescing and alive fine roots in the 0-30 cm horizon following watering. Bars are LSD's ($P < 0.05$) for comparing means over time. Arrows indicate means statistically different from one another in the "alive" curve.

The first hypothesis, that growth was limited because of insufficient viable root surfaces in the wetted soil, could not be satisfactorily answered without further experiments. The main problem is in knowing what constitutes an adequate viable root surface for individual shrubs of this species during the summer months. An indirect means of assessing the adequacy of the root surfaces for water uptake is to follow the effect of adding water to the soil on the plant water status. The 23-mm rainfall on July 10 (Fig. 1 [f]) increased Ψ_p from —30 (measured July 9) to —16 bars (dawn values) by July 12, but later in the summer, dawn Ψ_p was not increased (Fig. 2) with a weekly watering treatment but, rather, decreased from —24 to —31 bars. Since dawn values of Ψ_p are considered to be equilibrium values, in which the water potential in the xylem sap is in equilibrium with the soil water potential (Ritchie and Hinckley 1975), then it may be argued that the plants were under water stress as a result of inadequate root surface. Since soil water potentials were more than —10 bars down to a depth of 15 cm (Fig. 1 [b, c]) after the rainfall, Ψ_p (dawn) values near 0 bars might have been expected.

Dawn values of Ψ_p in the order of —20 to —30 bars have also been reported for other halophytes when regularly watered during midsummer (Cary 1971).

The second hypothesis, that growth was limited by a deficiency of available nitrogen in the wetted soil, is not supported by the data. Although measurements of available N in the soil sampled were not made in this experiment, data of Charley and West (1975) indicate that the percentages of N and P in these soils are low with highest levels being in the surface crust. Goodman (1973) found that nitrogen fertilization in the spring produced no immediate apparent effect on shoot biomass, but Jurinak et al. (1975) detected a small, but significant, increase in shoot elongation following spring application of nitrogenous fertilizer at a nearby site. *A. confertifolia* appears to have adapted to grow under conditions of low available soil nitrogen and, as suggested by Caldwell (1974), this is probably achieved by efficient nitrogen uptake and metabolism.

It was anticipated that there may have been a root growth response to added nitrogen since studies by Hackett (1972) show that nitrate, locally applied to roots of wheat plants, increased the density and rate of extension of laterals. The failure to induce a detectable response may have been related to the short duration of high soil water potentials, but it suggests that root growth is related to soil moisture status (temperature permitting) rather than nutrient availability.

The third hypothesis, that photosynthate is partitioned into root rather than shoot growth, is supported by the data. Photosynthesis and transpiration measurements in the field on leaves of this shrub (Caldwell 1972; Moore et al. 1972) have shown that active net photosynthesis occurs during the hot and dry summer period and into the autumn.

It seems likely that the majority of the photosynthate produced during the summer is partitioned into root growth after the plant's respiratory demands have been satisfied.

The fourth hypothesis, that this species exhibits summer dormancy, does not appear to be supported by the data. Although shoot growth did not occur, leaves must have been photosynthetically active to account for the root response to water application. Thus, the plant could not be classified as being summer-dormant since total plant weight would have increased following rainfall.

The absence of shoot growth is most likely to be associated with phenological development. At the time of watering, fruits were developing; that is, reproductive development was well advanced. It is probable that further shoot growth and leaf initiation are prevented by internal plant factors.

The horizon of soil in which root growth occurs would appear to be directly related to the soil water status in that horizon. Using root observation chambers, Fernandez and Caldwell (1975) showed that, during summer, quite active root growth occurs below 60 cm. This growth would enable absorption of water from deep in the profile and, hence, continued photosynthesis. In the present study, root growth occurred in the surface horizon following 48 mm of combined natural and irrigation watering. Although there was no set of control plants which remained under dry soil conditions, with which the effect of watering could be compared and its impact observed, the authors assume that the root growth measured by the increase in living roots nine days after watering was the result of the 48-mm "precipitation." It is difficult to imagine any other explanation for the live root increment. On this assumption, then, it follows that the fine roots in the surface soil are not all killed as a result of the low soil water potentials and that some remain viable. Studies of the root systems of *A. vesicaria* show a similar situation (Cowling 1969). Using a split root system, it was found that fine roots remained viable and took up Cl^{36} from extremely dry soil as long as another portion of the root system was located in moist soil.

Concurrent with the increase in living roots, there was far greater increase in dead root material. While the "alive" category root density rose from 1.1 to 1.6 cm/cm^3, the "dead" root compartment jumped from 6.5 to 8 cm/cm^3 three weeks after the watering. If all the new roots died within those three weeks, this would account for only one-third of the increase in dead roots. There are two possible explanations for this enigma: 1) There was a rapid turnover of living roots in the first few weeks of favorable soil conditions. This could have been accounted for by either (a) the total demise of roots living before the watering period, with subsequent replacement by new roots, some of which die within a couple of weeks, or (b) a high mortality of new roots produced in response to the watering. In both cases, there would need to be substantial death of new roots, which is most unlikely in the light of work by Fernandez (1974) on shadscale root growth. 2) The measurement of "alive" roots did not accomplish a complete separation from the "dead" category and, therefore, underestimated the

living fraction and overestimated the dead. This second explanation sounds reasonable when the technique for separation, based on visual and touch characteristics, is reviewed. The procedure permitted a large error in estimation of living roots if the root fragments (passing a 1.0-mm pore sieve) are all assumed to be dead.

The conservative nature of the estimation of root growth in response to "rainfall" indicates that *at least* a 0.5 cm/cm^3 increment in living roots occurred. The extent to which this figure may be an underestimate is unknown. Furthermore, although the data show a rise in dead roots of 1.5 cm/cm^3 (Fig. 4), the variance associated with these data is so high that little confidence can be placed upon the difference between means on two dates (note, for example, the oscillation in values between days 9 and 20). The amount of living roots that may have fallen into the dead root category could be a function of age of roots, so that likelihood of misidentification, based on visual features and "feel," would increase or decrease depending on length of time after root growth initiation.

Based on a root growth increment of 0.5 cm/cm^3 in response to 48 mm of water, and using a density to dry weight conversion factor of 1.38×10^{-4} g/cm^3, the weight of new root growth would be 0.69×10^{-4} g/cm^3. Applying this only to the 0-30 cm horizon, the new root production would be 20.7 g/m^2 in soil beneath shadscale plants. If root response to watering is not as great in soil between plants -- a reasonable assumption -- then root growth on a community basis would be less that 20.7 g/m^2, if the community was pure shadscale.

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