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TEMPORAL AND SPATIAL PARTITIONING OF THE SOIL WATER RESOURCE
BETWEEN TWO AGROPYRON BUNCHGRASSES AND
ARTEMISIA TRIDENTATA

by

Halldor Thorgeirsson

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

of

MASTER OF SCIENCE

in

Range Ecology

Approved:

UTAH STATE UNIVERSITY
Logan, Utah

1985

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Halldor Thorgeirsson

TABLE OF CONTENTS

	Page
ACKNOWLEDGEMENTS.....	ii
LIST OF FIGURES.....	iv
ABSTRACT.....	v
INTRODUCTION.....	1
MATERIALS AND METHODS.....	2
Study site.....	2
Soil water use.....	3
Plant water status.....	4
Root growth dynamics.....	5
RESULTS.....	6
Soil water use.....	6
Plant water status.....	8
Root growth dynamics.....	9
DISCUSSION.....	10
Timing and rate of extraction.....	11
Extent of extraction.....	12
Spatial and temporal resource partitioning.....	12
Plant water status.....	13
Root growth dynamics.....	14
Competitive interactions.....	16
LITERATURE CITED.....	18
APPENDIX.....	23

LIST OF FIGURES

Figure	Page
1. Mean volumetric water content of the top 110 cm of the soil profile in 1981 and 1982.....	24
2. Rate of water extraction from 10-30 cm and 70-90 cm of the soil profile (a), and rate of water extraction by monocultures of <u>A. desertorum</u> and <u>A. spicatum</u> from 50-90 cm of the profile (b).....	25
3. Soil water potential at various depths under monocultures of <u>A. spicatum</u> and <u>A. desertorum</u> in 1981 (a) and 1982 (b).....	26
4. Mean cumulative water extraction by monocultures and mixtures of <u>A. spicatum</u> and <u>A. desertorum</u> with <u>Artemisia tridentata</u>	27
5. Water extraction by monocultures of <u>A. spicatum</u> (a) and <u>A. desertorum</u> , expressed as a percentage of water extraction by mixtures of these grasses with <u>Artemisia tridentata</u>	28
6. Predawn and midday xylem pressure potentials of <u>A. spicatum</u> and <u>A. desertorum</u> in monocultures.....	29
7. Mean length of new adventitious roots per tiller of <u>A. spicatum</u> and <u>A. desertorum</u>	30
8. Number of active tips (a) and rate of elongation of active tips (b) of <u>A. spicatum</u> and <u>A. desertorum</u>	31
9. Mean daily elongation rates for <u>A. spicatum</u> and <u>A. desertorum</u> root tips.....	32
10. Survivorship patterns for elongation of lateral root tips of <u>A. desertorum</u> and <u>A. spicatum</u>	33

ABSTRACT

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Temporal and spatial partitioning of the soil water resource
between two Agropyron bunchgrasses and
Artemisia tridentata

by

Halldor Thorgeirsson, Master of Science

Utah State University, 1985

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Department: Range Science

Dynamics of soil water use by two cool-season Agropyron bunchgrasses during the warm season depletion of soil water reserves were monitored for two years in experimental plots in the field. Agropyron desertorum, an introduced, competitive species from Eurasia, extracted more water from the deeper (> 50 cm) soil layers than the native, less competitive Agropyron spicatum. Agropyron desertorum both extracts this water earlier and to lower soil water potentials than Agropyron spicatum. From the water extraction dynamics of the grasses in monocultures and in their two-way (50:50) mixtures with a shrub they commonly co-occur with, Artemisia tridentata, partitioning of the soil water resource between the grasses and the shrub was inferred. This indicated that Artemisia tridentata and Agropyron desertorum partitioned the soil water resource fairly evenly, while considerable quantities of water in the deeper soil layers under Agropyron spicatum seemed to be available to the shrub without direct competition. The implications of this difference in water resource partitioning for competition of the grasses with Artemisia tridentata are discussed.

Predawn and midday xylem pressure potentials were not different between the two grasses in spite of different fluxes through the plants.

Agropyron desertorum initiated new adventitious roots in fall and early spring while Agropyron spicatum did so only during spring. Observations from a root observation chamber indicated essentially parallel pattern of lateral root elongation during the depletion phase through top 200 cm of the profile. In both species the number of active tips, and the rate of elongation of active tips, decreased as the soil dried out. Root tips at all depths were inactive by the middle of September. Agropyron desertorum maintained root elongation at 50-110 cm for two weeks longer than A. spicatum.

(33 pages)

INTRODUCTION

In variable environments such as the Great Basin cold desert, competitive balance between plants changes in a dynamic fashion with environmental fluctuations. To gain an understanding of competitive interactions under such conditions the pattern of resource use and partitioning between individuals, species or populations needs to be studied. Nearest neighbor analysis (Pielou 1962, Yeaton et al. 1977, Nobel 1981) and differential removal studies (Fonteyn and Mahall 1981, Robberecht et al. 1983, Ehleringer 1984) provide a measure of the intensity of competitive interactions and relative importance of intraspecific and interspecific competition. These approaches do not, however, provide direct information on the dynamics of resource use and how the competing individuals interact in their resource acquisition. The rates of supply and use of clearly defined resources need to be measured and the growth functions of the competing individuals, or populations, with respect to these resources described (Tilman 1980, 1982).

The extensive Great Basin Desert of the U.S. Intermountain West is dominated by two life forms, shrubs and grasses (MacMahon 1979), coexisting in a temporary equilibrium (West 1983). Their phenology, resource acquisition characteristics and stress responses differ, resulting in a changing competitive balance following environmental perturbations. A paucity of summer precipitation gives shrubs a competitive advantage while fire helps the grasses maintain their position in the community. Livestock grazing, introduced by European man, and the concomitant suppression of fire, have changed the

competitive balance in favor of the shrubs leading to suppression of native grasses (e.g. Agropyron spicatum and Festuca idahoensis) and almost exclusive dominance of vast areas by shrubs, in particular Artemisia tridentata. Some introduced grasses (e.g. the Eurasian Agropyron desertorum) are more grazing tolerant, however, and more effective in competing with the shrubs (Caldwell et al. 1981, Caldwell and Richards 1985, Richards et al. 1985).

Our primary objective in this study was to nondestructively monitor the rates of supply and use of soil water by two perennial cool-season bunchgrasses, Agropyron spicatum (Pursh)Scribn. and Smith (bluebunch wheatgrass), and Agropyron desertorum (Fisch. ex Link)Schult. (crested wheatgrass), growing in monocultures and in mixtures with a shrub with which they frequently co-occur, Artemisia tridentata ssp. vaseyana (Rydb.)Beetle (mountain big sagebrush). The dynamics of root growth were also studied and related to the aquisition of water by the two grass species. The expression of competitive interactions between the two grasses and the shrub in shoot and root characteristics, is described in a companion paper (Richards et al. 1985).

MATERIALS AND METHODS

Study site

This study was conducted on a foothill area 4 km northeast of Logan, Utah (41 45'N, 111 48'W, 1460 m a.s.l.). The area was formerly occupied by a native A. spicatum/Artemisia tridentata community, representative of those found throughout the Great Basin (West 1983). Plants of these species and A. desertorum were transplanted in a

uniform matrix with a spacing of 50 cm, either as monocultures of the bunchgrasses or two-way (50:50) mixtures of the grasses with Artemisia tridentata. In the two-way mixtures each individual bunchgrass was surrounded by four Artemisia plants. The A. spicatum and Artemisia tridentata plants were from the neighboring native communities, while A. desertorum was from a pasture in central Utah seeded in 1953. Soils are rocky Mollisols (Typic Haploxerolls) which have been formed on alluvial fan material (Southard et al. 1978).

Soil water use

Soil water content was determined weekly with a neutron moisture probe (Campbell Pacific Nuclear, Model 503). Two access tubes were installed in each of the monoculture plots of the two grass species. A total of seven tubes were installed in three monoculture plots of A. spicatum and Artemisia, and a total of five in two mixture plots of A. desertorum and Artemisia. Because rocks restricted the depth of the tubes, analysis of the data was limited to the top 90 cm, unless otherwise noted. Air voids adjacent to the access tubes (Richardson and Burroughs 1972), were prevented by pouring a soil slurry down along the tubes. Standard calibration curves developed by the manufacturer were used. These calibrations assume that all hydrogen is in the form of water. This is a fair assumption for these limestone-derived soils which are low in organic matter. Any deviations from the standard calibration curve caused by local soil characteristics, would affect the absolute reading rather than the sensitivity of the instrument. Due to lack of local calibration and 30 to 40 % volumetric rock content of the C horizon (starting at 30-50 cm), soil water is expressed as a

percentage of total water reserves. The water reserves were calculated for each tube at each depth as the difference between the minimum and maximum measured volumetric water content (Rambal 1984). Rate of water extraction was calculated as the difference in water reserves between two points in time.

Soil water potential was measured weekly using single junction, screen-cage thermocouple psychrometers (J.R.D. Merrill Specialty Equipment, Logan, Utah). They were installed in undisturbed soil in the two grass monocultures approximately 25 cm horizontally from a root observation chamber (at 20, 40, 60 and 100 cm in 1981, and at those depths plus 140 and 180 cm in July 1982). The soil psychrometers were within 1.5 m of one of the two neutron access tubes in the monocultures. Two psychrometers were installed 10 cm apart at some depths to provide information on local variability. A microvoltmeter (Wescor Inc., Logan, Utah) measured psychrometer output following application of an 8 mA cooling current for 15 s when the profile was wet, or for 25 s when the soil water potential was < -1.5 MPa. Readings were corrected to 25 C. Soil temperatures ranged from 14 to 25 C. Psychrometers were individually calibrated using the same instrumentation (Brown and Bartos 1982).

Plant water status

Plant xylem pressure potentials were measured in 1982 on plants growing by the root observation chamber using a pressure chamber (PMS Instrum. Co., Corvallis, Oregon). Measured plant parts were enclosed in small bags to prevent rapid water loss (Turner and Long 1980). Measurements were made on leaf blades while they were available, but

after they had all senesced inflorescences were used.

Root growth dynamics

Initiation of new adventitious roots was determined by successive harvests of uniform plants of both species and census of new roots and total tillers per bunch. Total new root length per tiller was calculated as the product of mean number of new roots per tiller and the average length of roots less than 10 cm. Roots longer than 10 cm were not counted because they were often broken during excavation, preventing reliable determination of length. Elongation of first-order lateral roots was observed through glass windows of a root observation chamber. Root elements were named using developmental (starting from the top down) root-element terminology (Rose 1983). Vertical roots initiated from the base of the plant were termed axes, those arising from the axes and growing horizontally were termed first-order laterals. In these species axes and first order laterals constitute nearly the entire root system. The root observation chamber was installed in the winter of 1980-81, following the procedure of Fernandez and Caldwell (1975). It had six glass viewing panels (60 x 200 cm each), three facing a monoculture of A. spicatum and three facing a monoculture of A. desertorum. The small spaces (15 cm) between the panels and the pit walls were backfilled with the excavated soil, which had been sieved to remove stones. Soil horizonation and bulk density were duplicated as closely as possible during the backfilling. Roots of A. spicatum appeared to have grown fully to the windows, while considerably fewer A. desertorum roots were visible through the glass.

Lateral root elongation and the number of active tips was recorded

using transparent 10x30 cm acetate sheets. Roots were observed daily in July of 1981 and weekly from June 24th through September 15th in 1982. The weekly rates cannot be compared directly with daily rates since individual root tips only elongate for a short period of time (see Results).

RESULTS

Soil water use

In the cold semi-desert environment of the northern Intermountain region precipitation falls primarily during the cold season. During the two years of this study (1981 and 1982) 87.0 % and 90.9 % of the 468 mm and 816 mm annual precipitation fell from September through May. Water accumulates in the soil profile during this time and is extracted by plants during the warm season (Fig. 1). The dynamics of soil water consist essentially of: a recharge phase and a depletion phase. Fig. 1 shows a depletion phase and the beginning of a recharge phase for 1981 and 1982. During the depletion phase change in volumetric water content is almost exclusively due to extraction by plants. The depletion phase started in the first week of June in 1981 and the first week of May in 1982. The rate of extraction peaked by the middle of July in 1981 and the middle of June in 1982. The recharge phase started with the fall rains in October in 1981 and September in 1982. Each event thus occurred one month earlier in 1982.

Soil water was first extracted from the surface layers and then from progressively deeper layers as the water was depleted (Fig. 2a). The rate of extraction from 10 to 30 cm was highest during May of 1982.

After that the rate was higher from deeper layers.

During May and the first part of June the two species extracted water from the deeper (50 to 90 cm) soil layers at comparable rates, by the middle of June, however, A. desertorum showed a sharp increase while A. spicatum rates increased to a much lesser extent and did so one week later (Fig. 2b). This difference in rate of extraction of deep soil water resulted in markedly lower soil water potentials under A. desertorum than A. spicatum (Fig. 3). At 100 cm the water potential under A. desertorum reached a minimum of -2.6 MPa in 1981 and -3.7 MPa in 1982, while under A. spicatum the minima were -0.5 MPa in 1981 and -1.2 MPa in 1982. The soil water potential below 140 cm remained at saturation levels throughout the season, suggesting minimal water extraction at that depth.

The slight difference in the time the two species show an increase in the rate of extraction of deep soil water reinforces the difference in extent (depth) of extraction. These together assume considerable importance when the dynamics of water extraction by the grasses when competing with a shrub are considered. The lack of spatial separation of the thoroughly intermingled root systems (Caldwell and Richards 1985), makes it difficult to unequivocally attribute extraction of water from any soil volume to a particular plant. This can be done indirectly, however. The relative contribution of the grasses to the total water extraction by a grass-shrub mixture can be inferred by comparing the dynamics of water extraction by the grasses in monocultures to that of a grass-shrub mixture. One parameter describing these dynamics is cumulative extraction of deep soil water (50 to 90 cm) during the depletion phase (Fig 4). The A. spicatum monoculture

extracted water slower than its mixture with Artemisia during most of the depletion phase, while the A. desertorum monoculture extracted water at similar rates alone as its mixture with the shrub. The grasses have the same phenology and timing of biomass accumulation in mixtures as they do in monocultures, indicating that their water extraction dynamics are the same in both plottypes. This makes it possible to infer the partitioning of the soil water resource in the mixtures between the grasses and the shrub, by comparing the cumulative water extraction of the grass monocultures at a point in time to that of the mixtures. This was done for the first two thirds of the depletion phase, i.e. before the end of June, when A. spicatum sharply increased its rate of extraction (Fig 5). Agropyron spicatum utilizes only a portion of the soil water below 50 cm that both A. desertorum and the grass-shrub mixtures do.

Plant water status

The grasses do not show signs of water stress at our study site until June (Caldwell et al. 1981, Nowak and Caldwell 1984a, D. A. Johnson et al. unpublished). By July of 1982 their midday xylem pressure potentials were approximately -3.0 MPa, but predawn water potentials did not fall below -1.9 MPa in either species (Fig. 6). Xylem pressure potentials were not significantly different between species from July through September. Agropyron spicatum appeared, however, to be able to maintain slightly higher midday xylem pressure potentials than A. desertorum after July 14th. At that time 29% more water by volume remained in the top 110 cm of the soil profile in the A. spicatum plot than the A. desertorum plot.

Root growth dynamics

Root elongation is closely linked to the dynamics of water extraction from dry soils. Two aspects of the root growth of the two grasses were studied: 1) The initiation of new adventitious roots in fall, late winter and spring, and 2) cessation of lateral root elongation as the soil dried out.

The annual growth cycles of A. desertorum and A. spicatum begin with the initiation of new tillers and production of a small amount of green foliage following fall rains. At this time A. desertorum produces more new adventitious root length per tiller than does A. spicatum (Fig. 7). This is due to both a greater number and length of roots on A. desertorum tillers. In the late winter and spring A. desertorum also has more new root length/tiller than A. spicatum (Fig. 7). The difference is greater than the data suggest since many new roots on A. desertorum were longer than 10 cm by this time, and thus were not measured and included in the mean length values presented.

As spring shoot growth proceeds, new lateral roots are initiated from previous years' adventitious roots. When observations of the elongation of these lateral roots started in the middle of June of 1982 they had been growing for two to three months. By that time more growing tips were located in the 50 to 110 cm region of the profile than closer to the surface (Fig. 8). By July 9th tips above 50 cm were all inactive. Soil water potentials were then -2.1 to -2.7 MPa in that part of the profile. Agropyron spicatum roots were all inactive at 50 to 110 cm by July 25th while A. desertorum roots remained active at this depth into August. Roots below 110 cm grew until the first part of September, but all activity was terminated by September 11th. By this

time essentially no green leaf or stem area remained on the plant. The rate of elongation of active tips also declined as the soil dried out (Fig. 8). Similarly, observations of daily rates of elongation in July of 1981 showed high rates of elongation deep in the profile while the root elongation at the surface was slow (Fig. 9). The data from neither year indicate a significant difference in root phenology between the two species during the depletion phase. The period of elongation of individual lateral roots was limited to a maximum of nine days, but most laterals were active for only 4 or 5 days (Fig. 10). There was no difference between the species in this characteristic.

DISCUSSION

Precipitation patterns during the depletion phase in 1982 were more typical than in 1981, when 119 mm fell in May, delaying the warm-season depletion of soil water that year by one month (Fig. 1). No estimate was made in this study of deep water drainage. Comparison with work of Holmes (1984) and Rambal (1984) suggested minimal drainage during the depletion phase. Depletion of soil water was thus exclusively attributed to extraction by plants.

During the depletion phase water stored in the soil profile is the sole source of water to the grasses and the shrubs. This period of the year, while not the time of highest productivity due to low water availability and high evaporative demands, is important for competition between the two life forms. The soil water is equally accessible to either of the closely intertwined root systems of adjacent plants. The portion of this water resource captured by any one plant is thus not only determined by its own resource acquisition characteristics, but

also by that of its neighbors. Of these characteristics timing, rate and extent of acquisition are the most important. Differences in the timing of resource acquisition, indicated by the point at which the rate becomes greater than zero, and the rate of this acquisition, can result in markedly different division of shared resources. Extent of resource acquisition, however, determines how much of a resource is available to a plant. Ability to extract water at low soil water potentials or from deep in the profile, for example, makes additional water available to a plant. All three resource acquisition characteristics were found to be different between the two grasses.

Timing and rate of extraction

Agropyron desertorum started earlier to extract water from the deep (50-90 cm) soil layers (Fig. 2b). The two lines in Fig. 2b represent the dynamics of two independent monocultures plots, not of directly interacting plants. The water content and soil water potentials in the upper part of the profile, prior to the observed divergence in the rate of extraction of the deeper soil water, were slightly lower in the A. spicatum plot. Assuming that extraction of the less accessible deep water only starts after the more accessible shallow water has been exhausted, this fact suggests an even greater difference in the timing of the two species. The difference in timing of extraction is also reflected in the fact that while cumulative extraction by the A. spicatum monoculture lagged behind the other plots early in the depletion phase, the total extraction during the depletion phase by this species was only 20 % less than that of the A. desertorum. Total extraction by a plant in monoculture, however,

measures the potential of the plant for resource acquisition, a potential that might or might not be realized once the plant is growing in a mixture with plants of another species. Artemisia tridentata extracts water from deep in the profile, starts early and continues extraction through the warm season (Campbell and Harris 1977). The timing of water extraction by the grasses can thus affect their ability to compete with the shrub.

Extent of extraction

The extent (depth) of water extraction by A. desertorum was greater than by A. spicatum. This was primarily due to greater extraction from deep soil layers by A. desertorum (Figs. 2b and 4). It also extracted water to lower soil water potential (Fig. 3). The former is more important in terms of production while the latter may have important implications for plant survival and competitive exclusion.

Spatial and temporal resource partitioning

Our inferences of resource partitioning in mixtures from monoculture water use dynamics, indicated that the water resource was evenly partitioned between A. desertorum and the shrub (Fig. 5b), while significant quantities of water in the deeper soil layers under A. spicatum seemed to have been available to the shrub without direct competition (Fig. 5a). This is mainly due to difference in the extent of extraction by the two grasses, but differences in timing and rate are also important. Walter (1971, see also Soriano and Sala 1983) has hypothesized a spatial separation of resource use between coexisting shrubs and grasses. He suggests that while both life forms compete for

water in the upper layers of the soil, shrubs exclusively use the deep soil water. Our results indicate that this holds for Artemisia tridentata and A. spicatum, while resource use by A. desertorum and Artemisia tridentata seems to overlap, at least through 110 cm of the profile (Fig. 4 and 5). More intensive competitive interactions would thus be expected between the introduced A. desertorum and the shrub than between the shrub and A. spicatum that has evolved with it. Differences in the biomass of Artemisia growing next to the two grass species at our study site indicate that this is the case (Richards et al. 1985).

Plant water status

There was essentially no difference in xylem pressure potential of the two species monocultures during May and June and only slight difference in July (Fig. 6) even though the water flux through the plants was different. Extensive measurements of the xylem pressure potential of the two grasses when grown in mixtures with Artemisia tridentata at our study site similarly showed that species difference only developed late in the depletion phase (Caldwell et al. 1981, Nowak and Caldwell 1984a, Johnson, D. A., et al. unpublished).

Xylem pressure potential is an instantaneous measure of the water deficit of the plant. It does not necessarily reflect the rate of water flux through the plant. Increased water availability can result in increased leaf area and total flux through the plant with no or only slight change in xylem pressure potential. In studies of resource competition a distinction needs thus to be made between resource use and stress. Ehleringer (1984) showed that Encelia farinosa shrubs

almost doubled their biomass in 21 months following removal of neighbors, while midday xylem pressure potentials only improved by a maximum of 0.5 MPa. Similarly Artemisia tridentata plants at our study site were at the same xylem pressure potentials growing next to either of the two grass species (Link, S.O., unpublished), while the plants growing next to A. desertorum were significantly smaller (Richards et al. 1985). This has important implications for differential removal studies where xylem pressure potential is used as the primary response variable (see e.g. Fonteyn and Mahall 1981).

Root growth dynamics

Root phenology has been suggested to be an important factor affecting the partitioning of water resources between competing plants (Harris 1976, Gulmon et al. 1983). Earlier initiation of adventitious roots during the cold season by A. desertorum correlates with greater foliage area per tiller of A. desertorum during that period (Nowak and Caldwell 1984b). This root growth during the cold season, when resources are highly available, potentially affects the ability of A. desertorum to compete for water during the depletion phase. This species has been shown to have 50 % higher root density (length of root per volume of soil) by July than A. spicatum (Caldwell and Richards 1985). This difference is primarily a result of finer root elements in A. desertorum, while the total root biomass is nearly identical.

The two species had essentially parallel root phenology during the depletion phase, with the exception that A. desertorum maintained elongation at 50-110 cm for two weeks longer than A. spicatum. Cessation of water extraction paralleled the cessation of root

elongation. At that point the soil water potentials were very low.

Artemisia tridentata has been shown to have highest rates of root growth in April and May (Fernandez and Caldwell 1975). Resembling the grasses the rate of its root elongation decreased as the soil dried out. Unlike in the grasses, however, Artemisia roots below 50 cm grew throughout the warm season.

Agropyron desertorum seedlings have been shown to have higher rate of root elongation than A. spicatum seedlings at low soil temperatures (Harris and Wilson 1970). Harris (1967) found root growth of A. spicatum to be very limited until May, when the temperature of the soil reached 8 to 12 C. Destructive harvest of plants at our study site showed the root biomass of A. desertorum increasing in March, one month before A. spicatum. (Caldwell et al. 1981).

Continued root elongation is a prerequisite for maintaining water extraction through the depletion phase. The contribution of a root element to the total water uptake of the root system diminishes with the age of that element. This is due to both a decrease in the permeability of the root to water with suberization, and to the depletion of water from the soil immediately surrounding it, resulting in the development of localized rhizospheric resistances (Caldwell 1976). Fernandez and Caldwell (1975) showed a progression of root growth of Artemisia tridentata and two other cold semi-desert shrubs to increasing depth paralleling the depletion of soil water.

Root growth requires maintenance of turgor pressure in the meristematic regions and the zone of elongation of the roots and is thus directly affected by the water potential of the soil immediately surrounding it. Figs. 10 and 11 show the cessation of root elongation

paralleling a decline in soil water potential. Roots can to some extent maintain their turgor by solute accumulation as soil water potential declines by solute accumulation (Osonubi and Davies 1978, Sharp and Davies 1979). The fact that A. desertorum draws the soil water down to lower soil water potentials suggests that it can maintain root growth at lower soil water potentials. Weekly rate of root elongation is, however, not sensitive enough a parameter to describe the response of root elongation to soil water potential at the rate of drying at our study site (approximately 0.05 MPa/d).

Soil temperatures can also become superoptimal for root elongation during the depletion phase. During our observations soil temperatures increased slightly, concurrent with the decline in soil water potential. Compared to temperature responses of tree root elongation, however, soil temperatures were always close to being optimal (Henninger and White 1974, Teskey and Hinckley 1981). By late June, when observations started, soil temperatures ranged from 20.5 C at 20 cm to 16.5 C at 100 cm. The maxima were reached on August 24 when the temperatures reached 25.0 C at 20 cm and 23.3 C at 100 cm. Teskey and Hinckley (1981) showed a linear relationship between root elongation rate of individual roots of white oak and soil water potential when temperature was in the range from 17.0 to 25.0 C. Soil water potential thus seems to be the overriding factor causing the observed cessation of root growth.

Competitive interactions

Competition for belowground resources is more intense in the cold semi-desert environment than competition for light. In these

environments plants have been reported to allocate as much as 70 to 80 % of their annual carbon gain to belowground organs and processes (Caldwell et al. 1977). Some of that is presumably the direct cost of competing for resources, rather than being solely a direct cost of uptake (Caldwell and Richards 1985). Photosynthetic carbon gain in this environment is restricted to few months in the spring and early summer (Caldwell et al. 1977). Low temperatures restrict photosynthesis in late winter (Nowak and Caldwell 1984b), while soil water availability limits it in summer. The fact that the length of the growing season is affected by water availability suggests that water gained by an effective resource acquisition by a plant, or lack of it by its competitors, could extend the growing season for that plant into the summer. Artemisia tridentata elongates reproductive lateral shoots during the warm season and does not mature seed until October. It displays sensitive stomatal control reducing water loss but resulting in curtailment of carbon gain with even moderate water stress (Dina and Klikoff 1973, Deput and Caldwell 1973). More importantly it controls water loss by adjusting leaf area through the shedding of the large ephemeral leaves, only maintaining the small overwintering leaves (Campbell and Harris 1977). Artemisia tridentata ssp. vaseyana is primarily found in the more mesic mountain ranges of the central Rocky Mountains (Beetle and Johnson 1982). It is thus adapted to fairly predictable summer precipitation and can be expected to respond to the additional soil moisture available to it when grown next to A. spicatum. Caldwell (1985) has questioned the significance of the carbon gained during periods of moisture restraints in terms of the annual carbon gain (only 4 to 18 % of the annual carbon gain of two shrub

species in cold semi-desert environment), but suggests that effective depletion of soil moisture could help exclude competitors.

The water acquisition characteristics studied here also apply to nutrients to some extent, since nutrients are taken up as ions from the soil solution. High root density, for example, contributes to competition for nutrients as well as to competition for water. There are other factors, however, that affect competition for nutrients directly. Some of these might contribute to the observed differences in competitive balance between the two grasses and shrubs. Based on this study alone we can not estimate the relative importance of competition for these two resources

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APPENDIX

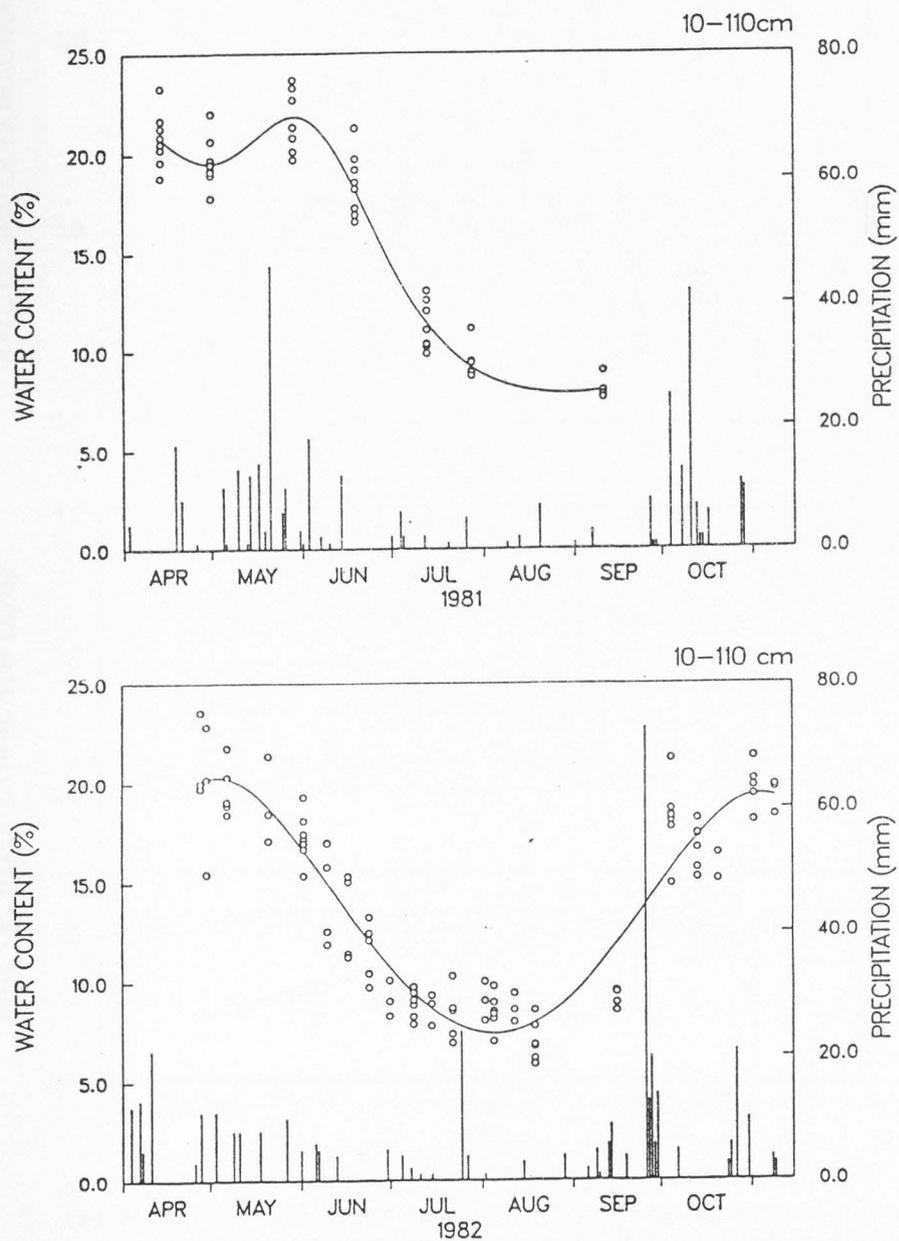


Figure 1. Mean volumetric water content of the top 110 cm of the soil profile measured at 20 cm depth intervals in 1981 and 1982. The circles are values for individual tubes that could be read down to 100 cm (8 in 1981, 6 in 1982). The solid line is a least squares polynomial regression line. Also shown are individual rainfall events (mm) measured at the study site.

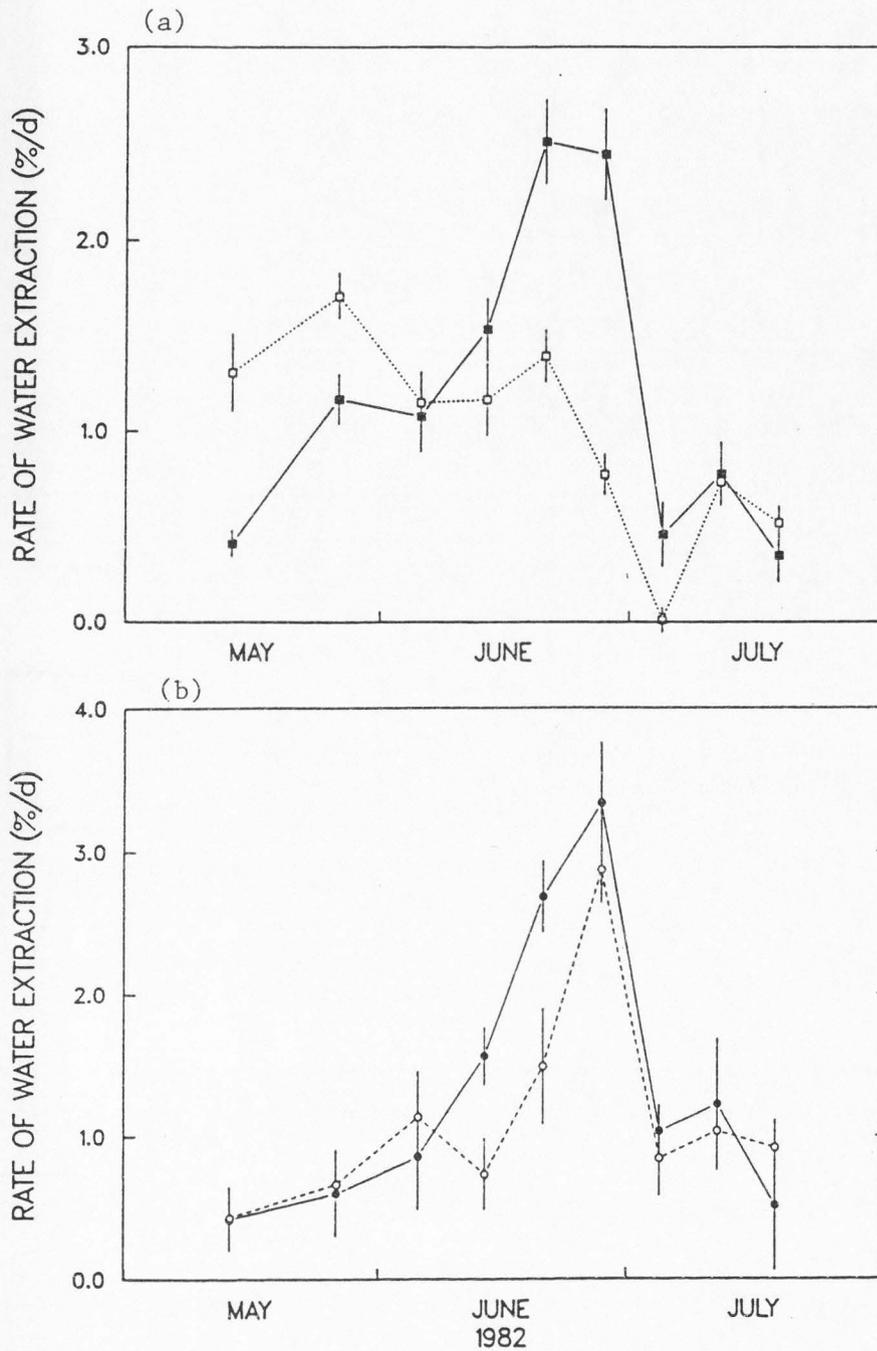


Figure 2. (a) Rate of water extraction (% of reserves/day) from 10-30 cm (open squares, dotted line) and 70-90 cm (filled squares, solid line) of the soil profile during the depletion phase (May 7-July 22) in 1982. Each data point is a mean \pm 1 S.E. of both monocultures and all mixtures ($n=16$). (b) Rate of water extraction (% of reserves/day) by monocultures of *A. desertorum* (dots, solid lines) and *A. spicatum* (circles, broken lines) from 50-90 cm of the profile during the depletion phase (May 7 -July 22) in 1982. The values are a mean \pm 1 S.E. of rates calculated from two access tubes each.

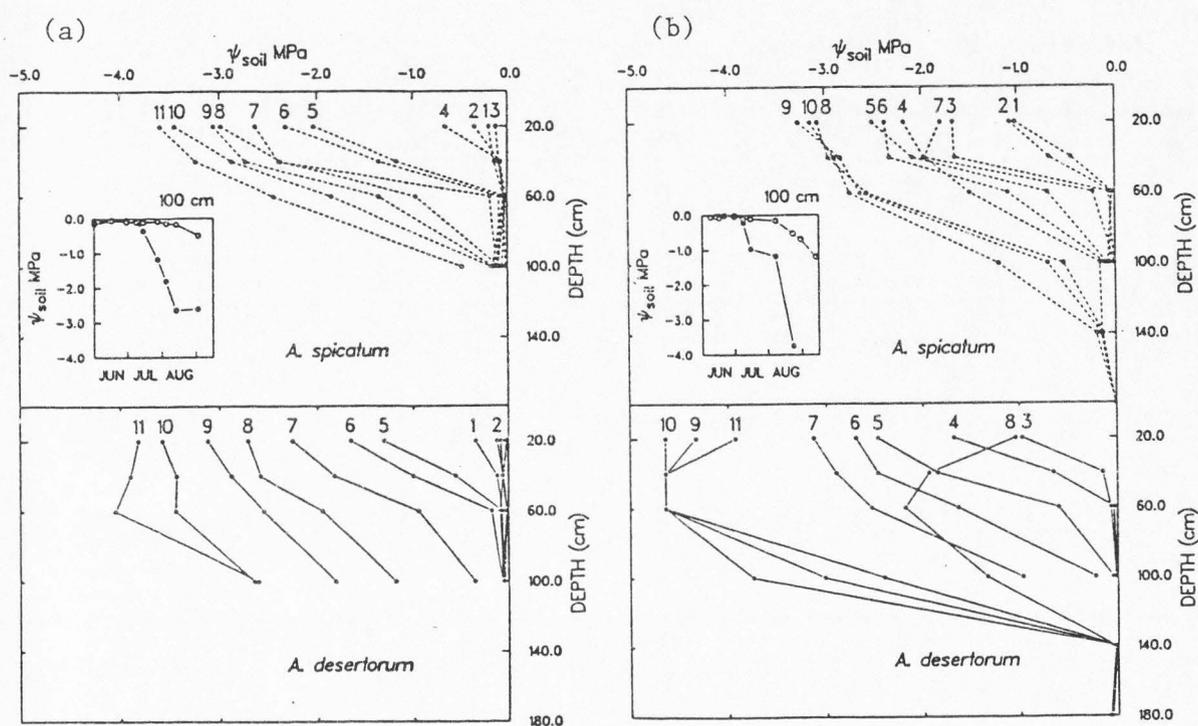


Figure 3. Soil water potential (MPa) at various depths under monocultures of *A. spicatum* and *A. desertorum* in 1981 (a) and 1982 (b). Duplicate determinations (at 50 % of the sampling points), were always within 10 % of each other. Each line represents values measured on following dates in 1981: (1)May 3, (2)May 29, (3)June 1, (4)June 17, (5)June 30, (6)July 9, (7)July 15, (8)July 28, (9)August 5, (10)August 14, (11)September 3; and in 1982: (1)June 9, (2)June 14, (3)June 17, (4)June 22, (5)July 1, (6)July 9, (7)July 16, (8)August 8, (9)August 24, (10)August 31, (11)September 14. The inserts show soil water potential at 100 cm under *A. spicatum* (circles, dashed lines) and *A. desertorum* (dots, solid lines) for the same periods.

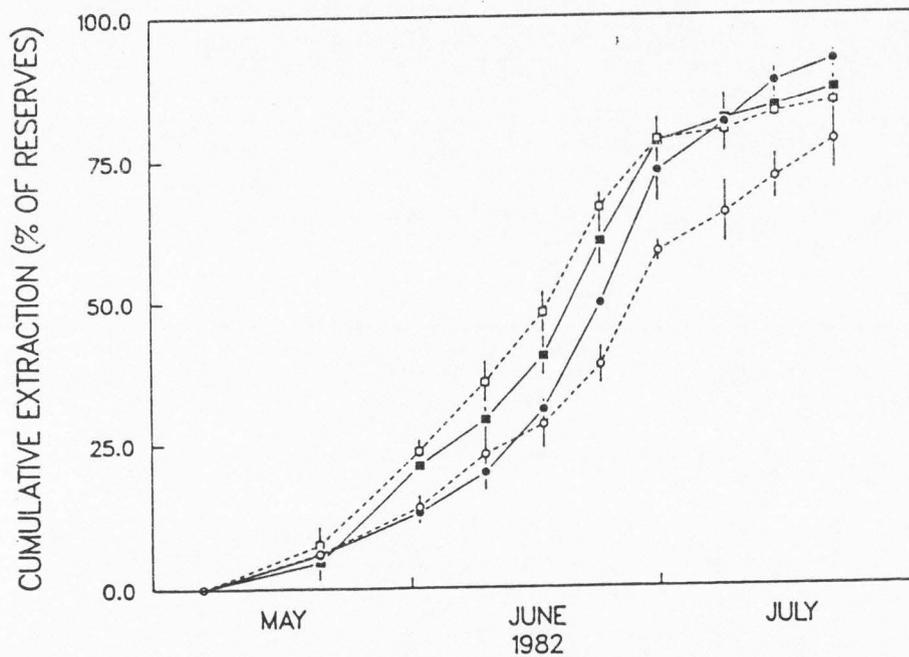


Figure 4. Mean \pm 1 S.E. cumulative water extraction (% of reserves) by monocultures (n=2) (dots and circles) and mixtures (open and filled squares) of *A. spicatum* (n=7) (broken lines) and *A. desertorum* (n=5) (solid lines) with *Artemisia tridentata*, from 50-90 cm of the soil profile during the depletion phase (May 7 - July 22) in 1982.

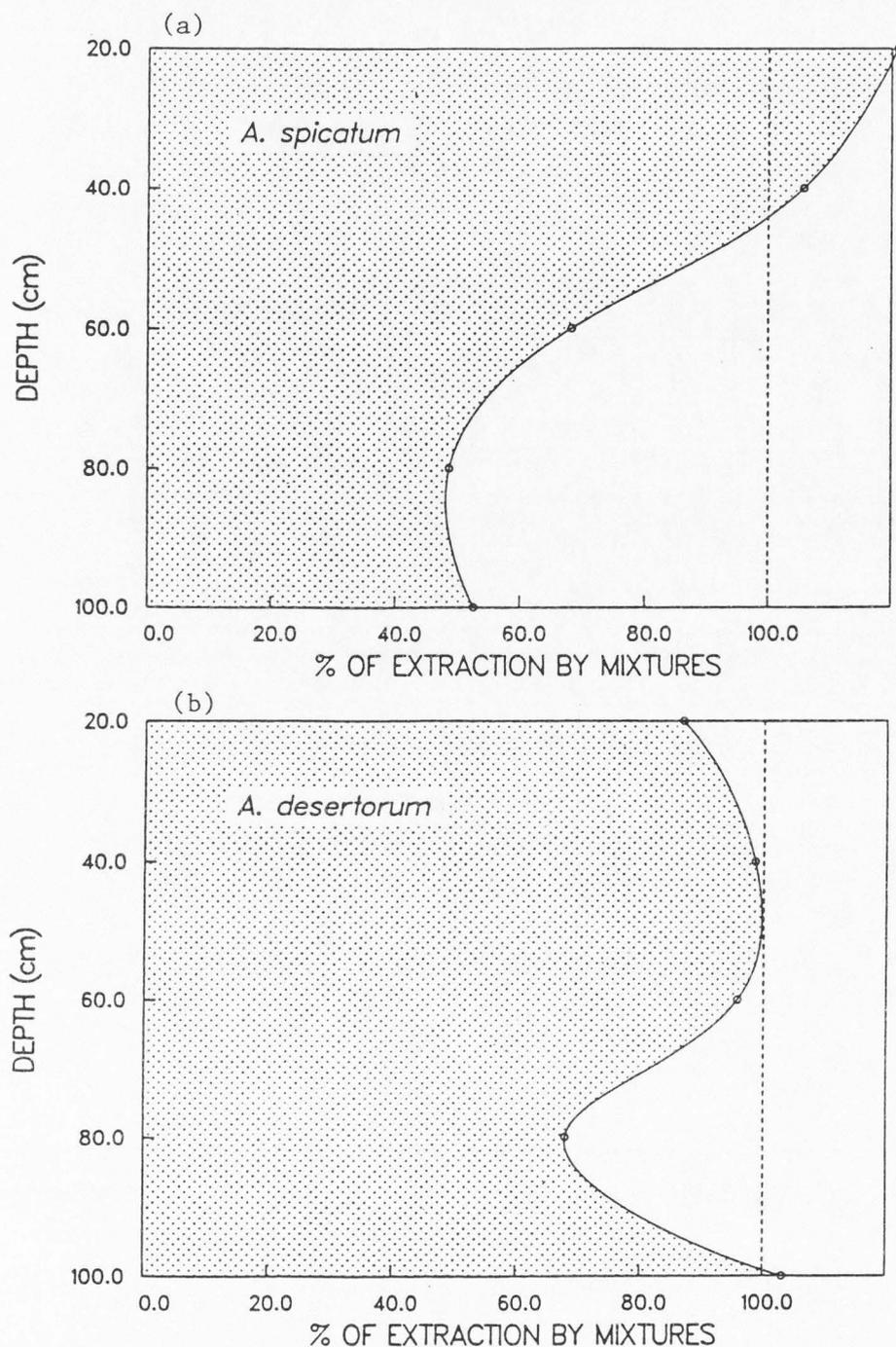


Figure 5. Water extraction by monocultures of *A. spicatum* (a) and *A. desertorum* (b) from 10-110 cm of the profile during the early part of the depletion phase (May 7 - June 24) in 1982, expressed as a percentage of water extraction by two-way (50:50) mixtures of these species with *Artemisia tridentata*. The circles indicate the depths measured. The 20 cm through 80 cm values are based on two monoculture tubes and five mixture tubes, while the 100 cm value is based on one and two, respectively. The line connecting the points was interpolated using a spline function. The broken line indicating 100 % is where extraction by the monoculture equals that of the mixture. The white area between the broken line and the solid line represents soil moisture resource used exclusively by *Artemisia*.

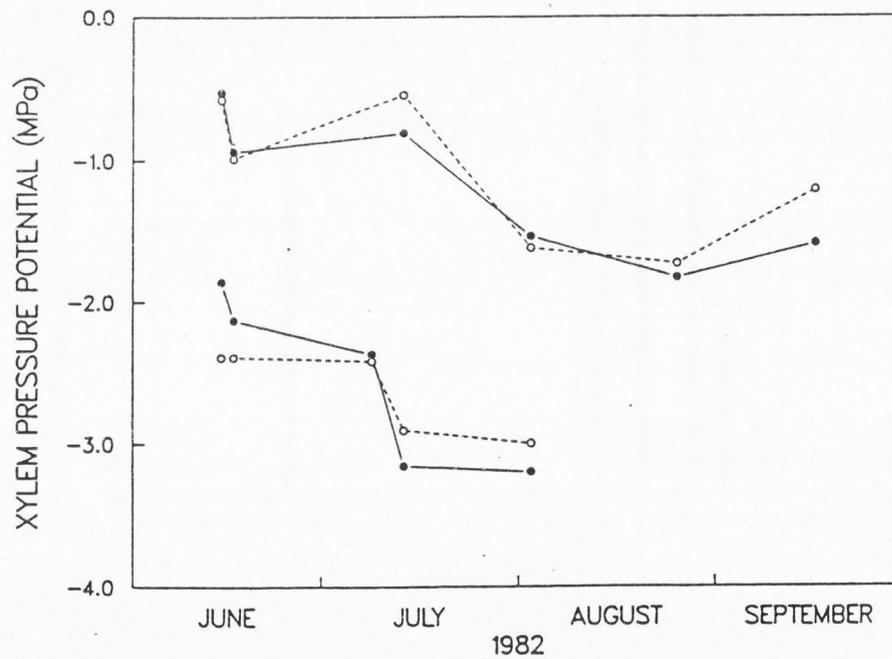


Figure 6. Predawn and midday xylem pressure potentials (MPa) of *A. spicatum* (circles, broken lines) and *A. desertorum* (dots, solid lines) in monocultures from June until September in 1982.

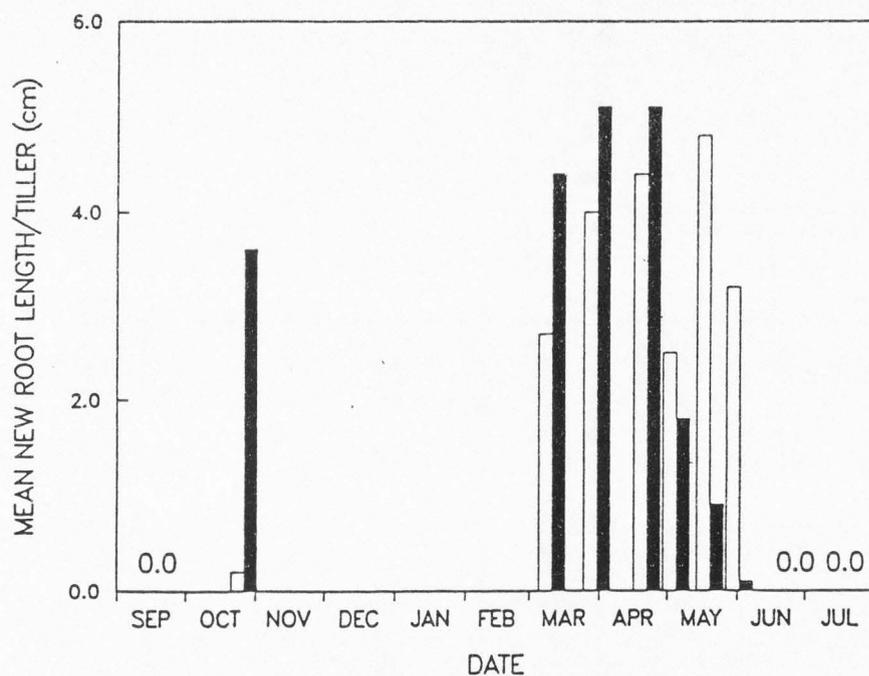


Figure 7. Mean length (cm) of new adventitious roots per tiller of *A. spicatum* (open bars) and *A. desertorum* (solid bars). Data compiled from destructive harvest of tillers from the fall of 1980 to the fall of 1981. Three bunches (with 121-331 tillers per bunch) of each species were sampled on each date.

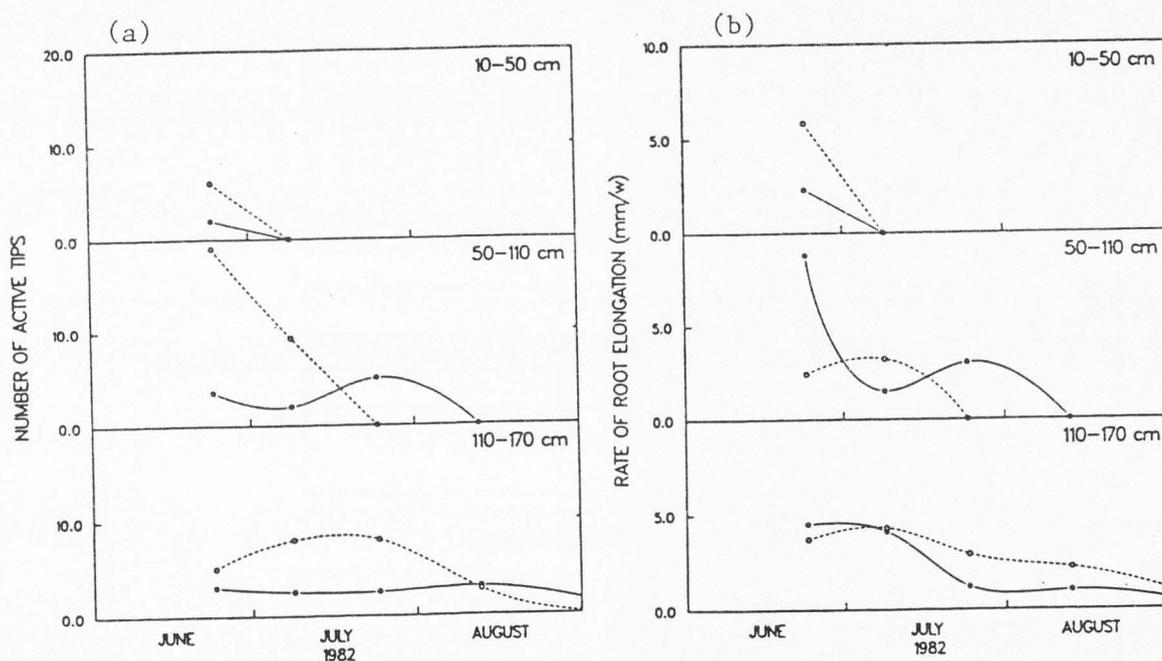


Figure 8. Number of active tips (a) and rate of root elongation (mm/week) of active tips (b) located in 1982 within 10 x 30 cm sampling areas on the glass viewing panels of a root observation chamber facing monocultures of *A. spicatum* (circles, broken lines) and *A. desertorum* (dots, solid lines).

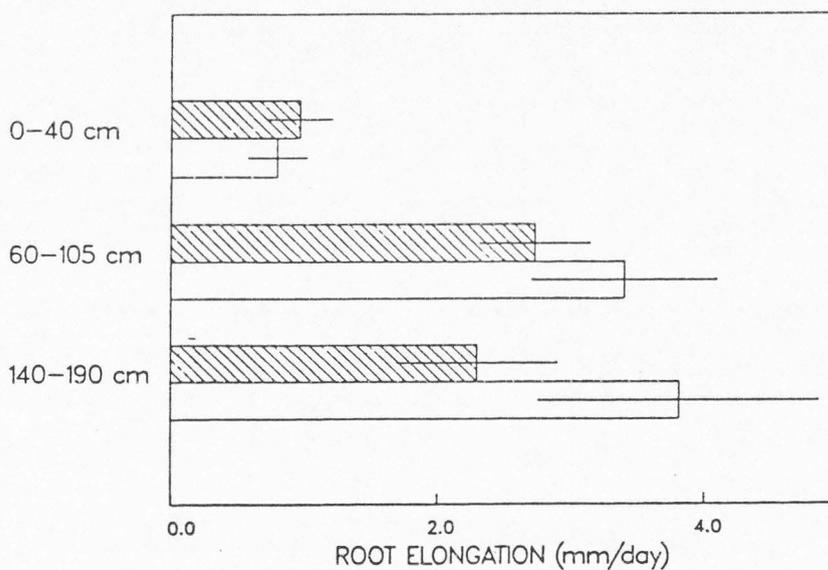


Figure 9. Mean daily elongation rates \pm 1 S.E. for *A. spicatum* (open bars) and *A. desertorum* (lined bars) root tips at various depths in mid-July 1981. Sample sizes were 5, 9 at 0-40 cm, 25, 30 at 60-105 cm, and 32, 16 at 140-190 cm for *A. spicatum* and *A. desertorum*, respectively.

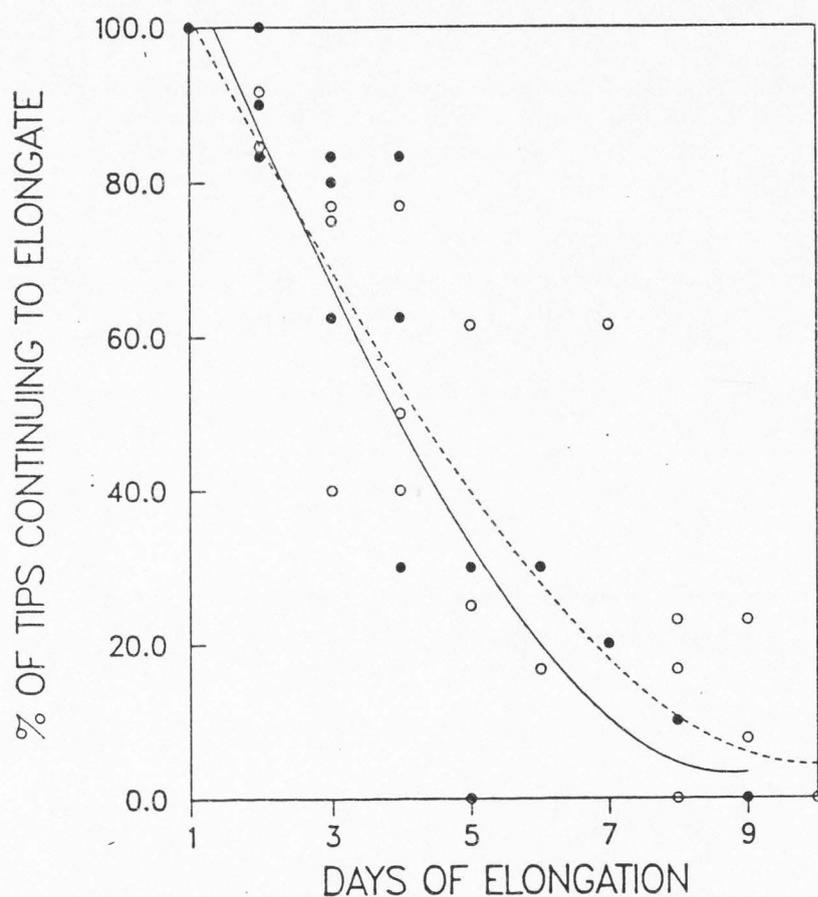


Figure 10. Survivorship patterns for elongation of lateral root tips of *A. desertorum* (dots, solid line) and *A. spicatum* (circles, broke line) at all depths in 1982. Survival is in this case defined as continued elongation, even though the laterals certainly live for some time after elongation ceases. The two regression lines are not significantly different.