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Belowground Resource Exploitation in Semiarid Plants: A Comparative Study Using Two Tussock Grasses That Differ in Competitive Ability

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BELOWGROUND RESOURCE EXPLOITATION IN SEMIARID PLANTS: A COMPARATIVE STUDY USING TWO TUSSOCK GRASSES THAT DIFFER IN COMPETITIVE ABILITY

by

David M. Eissenstat

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

of

DOCTOR OF PHILOSOPHY

in

Range Ecology

Approved:

UTAH STATE UNIVERSITY
Logan, Utah

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ABSTRACT

Belowground Resource Exploitation in Semiarid Plants:
A Comparative Study Using Two Tussock Grasses
That Differ in Competitive Ability

by

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Utah State University, 1986

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The relative competitive abilities of *Agropyron desertorum* and *Agropyron spicatum* were compared using *Artemisia tridentata* transplants as indicator plants. Although these two tussock grasses have similar shoot growth forms and shoot physiological characteristics, they have substantial differences in their competitive abilities. *Artemisia* had lower survival, growth, reproduction, and water potential when transplanted into neighborhoods of *A. desertorum* than in neighborhoods of *A. spicatum*.

Plant attributes associated with the differences in competitive ability were explored. *Agropyron desertorum* and *A. spicatum* have remarkably similar potential growth rates at warm soil temperatures. In a prolonged cold soil temperature treatment in the greenhouse, *A. desertorum* had a 66% greater aboveground relative growth rate than *A. spicatum*. These differences, however, were not apparent for early spring tiller growth rates in the field.

Distinct differences in timing of root growth were found between the two tussock grasses. *Agropyron desertorum* exhibited greater root growth during winter and early spring and invaded disturbed soil space more rapidly than *A. spicatum*, especially if the disturbance occurred soon after the snow had melted. Similarly, *A. desertorum* proliferated its roots in zones of nutrient enrichment created early in the spring sooner than *A. spicatum*. No differences in root growth were found between species in zones of nutrient enrichment that were created later in the growing season.

Despite differences in early spring root growth, water extraction and radiophosphorus acquisition early in the spring were similar for the two grass species. Later in the spring, *A. desertorum* extracted more water and radiophosphorus than *A. spicatum*. Differences in resource extraction between the two species in a specific soil layer occurred weeks before *A. spicatum*, but not *A. desertorum*, had obtained maximum root length. Early root growth probably provides *A. desertorum* an important head start over *A. spicatum* in soil exploration each growing season. Differences in resource extraction, however, do not become apparent between the two species of *Agropyron* until plant demand exceeds soil supply rate to the roots.

(121 pages)

CHAPTER I

OVERVIEW

Plants commonly increase in biomass at the expense of their neighbors. The reasons may be quite obvious, such as a taller plant suppressing a shorter plant in competition for light. However, often the reasons for differences in competitive ability among plants are poorly understood. In a cold-winter, dry-summer steppe environment, plants whose roots explore and occupy favorable soil space or extract resources from that space early in the growing season should be at a competitive advantage over neighbors whose roots develop later. This timing advantage of competitively successful species may be the result of a general plant attribute such as rapid potential growth rates when water and nutrients are abundant. However, more specific plant characteristics, such as more rapid root growth at cold temperatures or more rapid root growth in localized favorable microsites may be involved.

Preliminary evidence indicated that two species of *Agropyron* were ideal subjects for a comparative study of plant attributes associated with competitive ability. Despite remarkably similar shoot characteristics, rooting depths, and patterns of root:shoot biomass allocation, *A. desertorum* appeared to have much greater ability to restrict growth of neighbors than *A. spicatum* (Richards et al. unpubl). In order to confirm these observations, competitive ability of the two grasses was assessed in a lightly grazed rangeland community. Growth and survival of *Artemisia*, transplanted in nearly monospecific stands of the two species of *Agropyron*, were used as indicators of the competitive ability of the grasses. Water extraction rates of the grasses and water potential and nitrogen and phosphorus concentration of the *Artemisia* were also examined in an effort to more completely understand the competitive interactions in these grass stands.

Having established in Chapter II that these grasses are indeed suitable subjects for a study of competitive ability, I examined specific growth characteristics of these grasses that might contribute to their different abilities to compete. Differences in potential growth rate of the two species of *Agropyron* is one possibility (Chapter III). Whole-plant relative growth rates were measured in solution culture where water was not limiting growth and N and P were either optimal or suboptimal. Aboveground growth rates were examined for plants in soil culture at warm and cold soil temperatures. Lastly, growth rates of tillers as well as yearly increases in aboveground biomass of individual tussocks were examined in the field using widely spaced plants, which were essentially free from competition.

Evidence from the potential growth rate investigation suggested that *A. desertorum* grows faster than *A. spicatum* at cold soil temperatures. Therefore, differences in root growth and resource acquisition of monocultures of the two grass species were tested at two times during the growing season (Chapter IV). The amount of new root growth over winter and early spring was first assessed. Then soil was disturbed, either soon after the snow had melted or several weeks later in the spring, and rates of root invasion in the disturbed soil and radiophosphorus and water uptake from the disturbed soil were determined.

In Chapter V, I examine timing of root growth in ferilized microsites. A concentrated liquid fertilizer was injected at two times. In 1985, microsites rich in nutrients were created in early spring, soon after snow melt. In 1984, favorable microsites were created in mid-July.

In the last chapter of this dissertation, I contrast the indicator plant appoach used in Chapter II with other ways that competitive ability can be assessed. I also discuss some characteristics of these plants that might account for their differences in competitive ability. Lastly, I synthesize the information found in this study as well as from other studies to formulate my view of the process by which *A. desertorum* more effectively competes with neighbors than *A. spicatum* in these cold desert communities.

CHAPTER II

COMPETITIVE ABILITY OF TWO TUSSOCK GRASSES: DIFFERENT RATES OF WATER EXTRACTION ARE RELATED TO INDICATOR PLANT PERFORMANCE

Summary

The relative competitive abilities of *Agropyron desertorum* and *Agropyron spicatum* under rangeland conditions were compared using *Artemisia tridentata* ssp. *wyomingensis* transplants as indicator plants. Although *A. desertorum* and *A. spicatum* have similar shoot growth forms and shoot physiological characteristics, these two tussock grasses have substantial differences in their competitive abilities. These differences in competitive ability were manifested by the responses of *Artemisia* shrubs that were transplanted into the location where a tussock grass was removed. The *Artemisia* indicator plants had lower survival, growth, reproduction, and late-season water potential when transplanted into essentially monospecific neighborhoods of *A. desertorum* than into neighborhoods of *A. spicatum*. In similar, essentially monospecific stands, single tussocks were removed and replaced by neutron probe access tubes. Soil moisture measurements with these installations showed that *A. desertorum* extracted water more rapidly from the soil profile than did *A. spicatum*. These differences in extraction rates relate clearly to the differences in *Artemisia* success. Nitrogen and phosphorus concentrations in *Artemisia* suggested these nutrients were not

limiting *Artemisia* growth and survival in the *A. desertorum* plots.

Introduction

Competition for water in arid environments has been indirectly indicated by the improved water status of plants following removal of neighboring plants (e.g., Fonteyn and Mahall 1981, Robberecht et al. 1983, Ehleringer 1984). However, the significance of the timing of water extraction for competitive ability has not been often tested under field conditions (but see Thorgeirsson 1985).

Agropyron spicatum (Pursh) Scribn. and Smith[1] and *Agropyron desertorum* (Fisch. ex Link) Schult. are well suited for an investigation of mechanisms of competition. These grasses have numerous similarities and yet have striking differences in competitive ability (Caldwell and Richards 1986). They are both long-lived grasses with similar tussock architecture and shoot phenological patterns and rooting distributions (Caldwell et al. 1983, Chapter III). Physiologically, these grasses have similar water- and nitrogen-use efficiencies, potential growth rates under various

---

[1] Recent taxonomic revisions have been proposed: *Elytrigia spicata* (Pursh) D.R. Dewey (Dewey 1983) and *Pseudoroegneria spicata* (Pursh) Löve (Löve 1980, Dewey 1984). Although the genomic evidence indicates that this species is not an *Agropyron*, insufficient data are available to clearly finalize its taxonomic position. Therefore, we will use *A. spicatum* in this paper.

nutrient conditions, and seasonal patterns of photosynthesis and leaf water potential (Caldwell et al. 1981, Nowak and Caldwell 1984a, b, 1986, Chapter III).

Despite these similarities in shoot characteristics, Thorgeirsson (1985) demonstrated that soil water depletion in a monoculture of *A. desertorum* occurred earlier and to a greater extent than in an adjacent monoculture of *A. spicatum*. Furthermore, he demonstrated indirectly that the deeper water not used as quickly by *A. spicatum* was heavily used by *Artemisia*.

There are differences in the root systems of these species that are linked with differences in the ability to compete for water and nutrients. Although they have similar root biomass and distribution with depth, *A. desertorum*, by virtue of its thinner roots, has approximately twice the root length of *A. spicatum* (Caldwell and Richards unpubl.). *Agropyron desertorum* also tends to be more heavily infected with mycorrhizae and has greater root growth in winter and early spring than *A. spicatum* (Caldwell et al. 1985, Chapter IV).

The intensive field studies of the comparative physiological ecology of these two grasses cited above were conducted in artificial communities near Logan, Utah. The two-species communities were created by transplanting either *A. spicatum* or *A. desertorum* in a 50:50 mixture with *Artemisia tridentata* ssp. *vaseyana* (Rydb.) Beetle. In the current study we tested the competitive ability of these grasses under rangeland conditions. We used *Artemisia tridentata* ssp. *wyomingensis* (Beetle and Young) transplants, the subspecies native to this site, as an indicator of the competitive ability of *A. desertorum* and *A. spicatum* in an established pasture lightly grazed by cattle. We examined how the transplanted indicator, *Artemisia*, responded to neighboring grasses in terms of survival, growth, water status and concentrations of N and P. Rates of water extraction were also examined from essentially monospecific stands of these two grasses as a potential explanation for observed differences in *Artemisia* success.

Study Area

The study was conducted in Curlew Valley in northwestern Utah near the Raft River Mountains in an *Artemisia tridentata* ssp. *wyomingensis* /*Agropyron spicatum* habitat type (Hironaka et al. 1983) (41° 56' N, 113° 7' W, 1480 m elev.). Soils were sandy loams with alluvial gravels beginning at 40 to 80 cm. Climate of this region, compiled from long-term U.S. Weather Bureau data at Snowville, UT, 40 km east of the study area, is summarized by Caldwell et al. (1977). Precipitation in 1984 was twice the amount in 1985. Precipitation in October through April, a period when evapotranspiration is generally low, was 284 mm in 1983-84 and 134 mm in 1984-85. Precipitation during the active growing season (May to August) was 148 mm in 1984 and 87 mm in 1985, especially where all the vegetation had been removed.

Vegetation in the study area is primarily *Agropyron spicatum*, a complex of the crested wheatgrasses, *Agropyron desertorum* and *A. cristatum* (L.) Gaertn., *Poa sandbergii* Vasey. and scattered *Bromus tectorum* L. (The crested wheatgrass complex will be identified in this study by its most abundant representative in this area, *A.*

desertorum.) The dense interspersed stands of *A. spicatum* and *A. desertorum* found in this area are unusual for the Great Basin region. The mosaic of nearly monospecific stands of these two grasses provided an excellent opportunity to compare their relative competitive abilities under rangeland conditions.

In the 1960's, the stands of *A. spicatum* were interspersed with stands of *Artemisia* at this site. To improve forage production for cattle, the *Artemisia* was sprayed with 2,4-dichlorophenoxy acetic acid in 1968 and 1973. In fall, 1973, the pasture was aerially broadcast seeded with *A. desertorum*. The pasture was grazed by cattle the following winter to tread seeds into the soil to enhance germination and establishment.

This study was initiated in April, 1984. During this study, cattle were brought into the pasture in March and removed in early May. Previously, the pasture had been grazed over winter. In neither year, however, were animals in the pasture late enough in the spring to remove the apical meristems of the tussock grasses. Consequently, defoliation stress was generally light (Richards and Caldwell 1985). Trampling damage of the *Artemisia* indicator plants, however, was quite severe in some plots in 1985.

Methods

Artemisia indicator plants

The transplant experiment was conducted in an area with interspersed, nearly monospecific stands of *A. spicatum* and *A. desertorum*. *Poa sandbergii* and *Bromus tectorum* were the only other species frequently found with the perennial grasses. Neither *Bromus* nor *Poa* contributed appreciably (< 5%) to overall stand biomass. On 5 May, 1984, 30 circular plots, 1.5 m in diameter, were placed in either areas dominated by *A. desertorum* or by *A. spicatum*. There was no evidence to indicate any factors besides the dominant grass species affected the plots; hence, a completely randomized experimental design was assumed. The plots were centered on an *Artemisia* seedling, approximately 10 cm tall, which had been transplanted into the spot where a tussock had been removed. The kind of neighborhood was the primary basis for plot selection. However, no tussock replaced by an *Artemisia* transplant was exceptionally small or large. *Artemisia* transplants were obtained from a recently disturbed area adjacent to the study site. Each *Artemisia* received approximately one liter of water following planting to aid in establishment.

Thirty more plots were added on 25 May where the tussock removed for the *Artemisia* indicator was a different species from the majority of its neighbors (15 for each grass species). In addition, *Artemisia* was transplanted into 14 plots where all the neighbors were removed within a 1-m radius of the transplant (7 plots each in *A. spicatum* and *A. desertorum* stands).

Artemisia survival was tallied in June, August and November, 1984 and May and August, 1985. Total and current year's aboveground biomass was determined by harvesting transplants at ground level on 1 August 1985 and drying at 70°C before weighing. Total N concentration in current year's growth from the August harvest was determined with an ammonia electrode (Orion model 95-12) after Kjeldahl digestion. Total P concentration was determined colorimetrically after ashing at

500 °C (AOAC 1980). Predawn xylem pressure potential of the Artemisia in all plots was determined 11 June and 1 August 1985 with a pressure chamber.

Soil water extraction

Neutron probe access tubes were installed in 18 plots on 8 April 1985 in the place where an individual tussock was removed. In nine plots, a single *A. desertorum* was removed and an access tube installed in its place in an area of predominantly *A. spicatum*. In nine other plots, individual *A. spicatum* were removed for the access tubes in a predominantly *A. desertorum* stand. In each set of nine plots, three were randomly chosen to serve as controls where all the neighbors within 1 m of the tube were removed. Soil water content was monitored weekly by a neutron probe (Campbell Pacific Nuclear model 501DR) until mid-May and then biweekly until mid-June, 1985.

Soil water content during the measurement period was expressed as a percentage of the first measurement of 18 April 1985 for each access tube in Fig 3. The water content on 25 February 1986 was found to be comparable to the 18 April 1985 measurement at 15 and 30 cm. However, at 45 and 60 cm, water content was greater in February than in April, presumably because the water had not fully drained in February from recent heavy rains. Since water is normally extracted from the surface layers first, we believed soil water content on 18 April was a reasonable estimate of field capacity (i.e., water content of the soil after it has fully drained; Hanks and Ashcroft 1980).

Water content was also expressed as a percent of the total water extracted by *A. desertorum* to a depth of 67 cm during the period between 18 April and 13 June (Fig. 4). Soil water content was estimated from the calibration curve provided by Campbell Pacific Nuclear Corp.

Neighborhood analysis

Biomass of neighboring plants in concentric annuli defined by radii of 18, 40, and 75 cm was clipped at ground level for each species after the foliage had senesced. (Annuli were centered on the *Artemisia* transplant.) Annuals (principally *B. tectorum*) in the *A. desertorum* and *A. spicatum* plots were harvested in mid-June, 1985 and perennials (principally *A. desertorum* and *A. spicatum*) were harvested in mid-September. Biomass was weighed in the field and then corrected for differences between fresh and oven-dried biomass using subsamples weighed in the field and then dried at 70°C. To assess the competitive influence of species in the annuli on *Artemisia* performance, we weighted biomass of different species in a manner similar to Weiner's (1982) weighting of number of neighbors:

$$A = \frac{a_1}{d1} + \frac{a2}{d2} + \frac{a3}{d3} \qquad (1)$$

where "A" is the weighted estimate of biomass of a species (or a growth form) around the target individual, "a" is the amount of biomass in annuli 1, 2, and 3, and "d" is the distance of an annulus from the target species (the radius of the circle that divides the annulus into two parts of equal area). The closest distance, d_1, is set equal to 1.0, and the other values of d scaled accordingly. We did not use d2 as did Weiner (1982) because a linear distance (d) produced a fit equally as good or slightly better than d2. Similar results were found subsequently by Weiner (1984).

In the survival analysis of *Artemisia*, plots where at least 80% of the weighted perennial biomass, A, was either *A. desertorum* or *A. spicatum* were designated accordingly. Plots with less than 80% of either species were considered to be a mixture. An 80% criterion was used to define the three kinds of neighborhoods to assure that there were enough *Artemisia* in each category (see Table 1) to permit a robust analysis of the data. For all other analyses, plots designated as either *A. desertorum* or *A. spicatum* had at least 90% of the weighted biomass, A, of that species.

Statistical analysis

Artemisia survival and reproduction were analyzed by log-linear models and significance was determined by the likelihood-ratio chi-square statistic. Model selection was based on methods described by Fienberg (1970). If a significant difference in a treatment was detected, pairwise comparison of individual cells were made using a 2 x 2 chi-squared analysis. *Artemisia* biomass, N and P concentrations, and xylem pressure potentials were analyzed nonparametrically using the Kruskal-Wallis test because of their highly skewed distributions. This test allowed us to determine if a significant difference existed among treatments. Under conditions where a significant difference existed ($P<0.10$; *P*, as used in this dissertation, represents the probability that observed differences in means or medians occurred by chance alone), pairwise comparisons were made of individual treatment medians using the Wilcoxon rank-sum test. Differences in amounts of perennial and annual biomass in the *A. desertorum* and *A. spicatum* plots were also determined by the Wilcoxon rank-sum test. The relationship of neighborhood biomass with *Artemisia* growth was determined by least-squares regression analysis after examination of residuals for normality and independence from X and predicted Y (Framstad et al. 1985). Correlations were tested for significance from zero. Water extraction data were analyzed using a multivariate repeated measures design (Hotelling T2 statistic) which permits correlation among sampling dates (Gurevitch and Chester 1986).

Results

Artemisia indicator plants

Table 1 illustrates the survivorship of *Artemisia* the first summer for the two different planting dates with different neighborhoods. Survivorship was not considered for the later time period from November, 1984 until August, 1985, since only four *Artemisia* died from factors not clearly associated with cattle trampling.

For the *Artemisia* that were transplanted on 5 May, mortality was nearly 8-fold greater with *A. desertorum* neighbors than with *A. spicatum* neighbors during the first growing season. However, when *Artemisia* were transplanted just a few weeks later in the growing season, mortality was less noticeably affected by the species of the neighboring tussock grasses (species x planting date interaction: $P<0.01$). In the later transplanting experiment, there were also plots where all neighbors were removed. In these plots, average mortality

Table 1. Percent mortality of *Artemisia* indicator plants by November, 1984 when planted in either early or late May in different neighborhoods (see text for details; population size in parenthesis). Percentiles followed by a different letter significantly different at $P < 0.05$.

Neighborhood	Planting Date 5 May 1984	 25 May 1984
A. spicatum	5 (22)^{a}	33 (3)^{ab}
Mixture[1]	14 (7)^{ab}	56 (16)^{b}
A. desertorum	40 (30)^{b}	55 (11)^{b}
No neighbors[2]	-	7 (14)^{a}

[1] The neighborhood was a mixture of *A. desertorum* and *A. spicatum* grasses.

[2] Treatment was not imposed on 5 May 1984, so that the percent mortality was only compared among neighborhoods for the 25 May planting date.

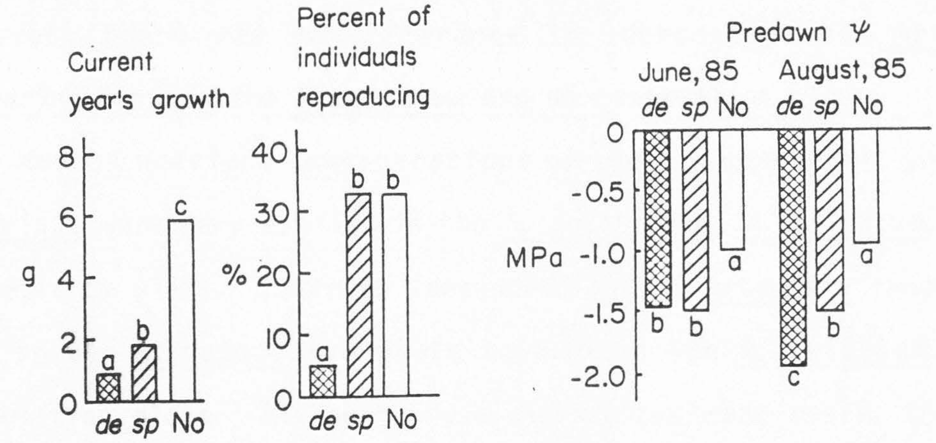

Fig. 1. Current year's aboveground growth, percent of individuals reproducing (with inflorescences), and predawn xylem pressure potentials of *Artemisia* indicator plants that had been transplanted in *A. desertorum* plots (*de*), *A. spicatum* plots (*sp*), or in plots where vegetation had been removed within 1 m of the *Artemisia* (No). Medians denoted by a different letter were significantly different at $P<0.05$ (n=7 to 20).

was only 7%, which was less than mortality in either the mixed plots or the *A. desertorum* plots for the same planting date (*P*<0.01).

Artemisia water status, growth, and reproduction were also affected by the species of *Agropyron* neighbor (Fig. 1). Although there was no difference in predawn for *Artemisia* in the competition plots with the two grass species in June, 1985, by August of that year *Artemisia* in the *A. desertorum* plots was significantly lower than in the *A. spicatum* plots. Several *Artemisia* transplants had predawn , less than -4.0 MPa in the *A. desertorum* plots. *Artemisia* in the no competition plots had greater water potentials than in either the *A. spicatum* or the *A. desertorum* plots.

Growth of *Artemisia* was greatest in the no competition plots, intermediate in the *A. spicatum* plots, and least in the *A. desertorum* plots (Fig. 1). Percent of *Artemisia* individuals with inflorescences was greater in the *A. spicatum* than the *A. desertorum* plots. However, there was no difference in percentage of *Artemisia* flowering between the *A. spicatum* and no competition plots.

Median nutrient concentrations of the current year's growth of *Artemisia* were very similar in the *A. desertorum*, *A. spicatum*, and no competition plots. Nitrogen concentrations of *Artemisia* ranged from 1.9% in the *A. desertorum* plots to 2.1% in the *A. spicatum* and no competition plots. Although these differences were small, they were statistically significant (*P*<0.01). Phosphorus concentrations of *Artemisia* ranged from 0.26% in the *A. spicatum* plots to 0.28% in the *A. desertorum* plots and showed no significant differences among treatments (*P*>0.20). Plants with high nutrient concentrations tended

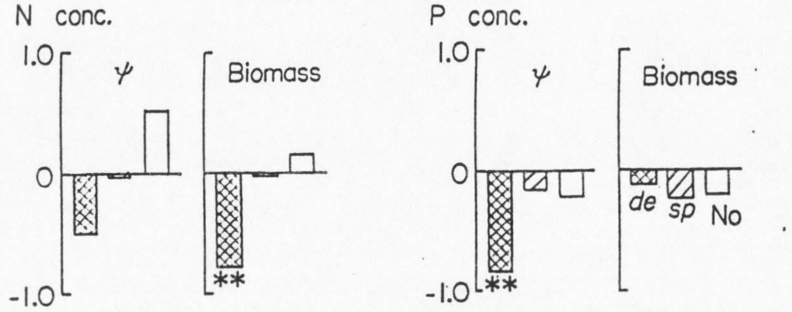

Fig. 2. Correlation coefficients of *Artemisia* N and P concentrations with *Artemisia* predawn xylem pressure potentials and current year's growth. Correlation coefficients were determined for *Artemisia* in *A. desertorum* plots (*de*), *A. spicatum* plots (*sp*) or in plots where vegetation had been removed within 1 m of the *Artemisia* (No) (**= significantly different from zero at $P<0.01$, other coefficients were not significantly different from zero ($P>0.10$); $n=7$ to 11).

to be plants of poorer water status or less current year's growth (Fig. 2). This pattern was especially evident in the *A. desertorum* plots.

Water extraction

Agropyron desertorum extracted water more rapidly than *A. spicatum* from the soil profile to a depth of 45 cm (Fig. 3). Differences appeared sooner closer to the surface than they did deeper in the profile. Differences between species in soil water content after mid-May persisted until the end of the measurement period, indicating *A. desertorum* was able to extract water at rates similar to those of *A. spicatum* even though *A. desertorum* roots were in somewhat drier soil.

The total amount of water extracted by *A. desertorum* to a depth of 67 cm between 18 April and 13 June was approximately 4.7 cm. A

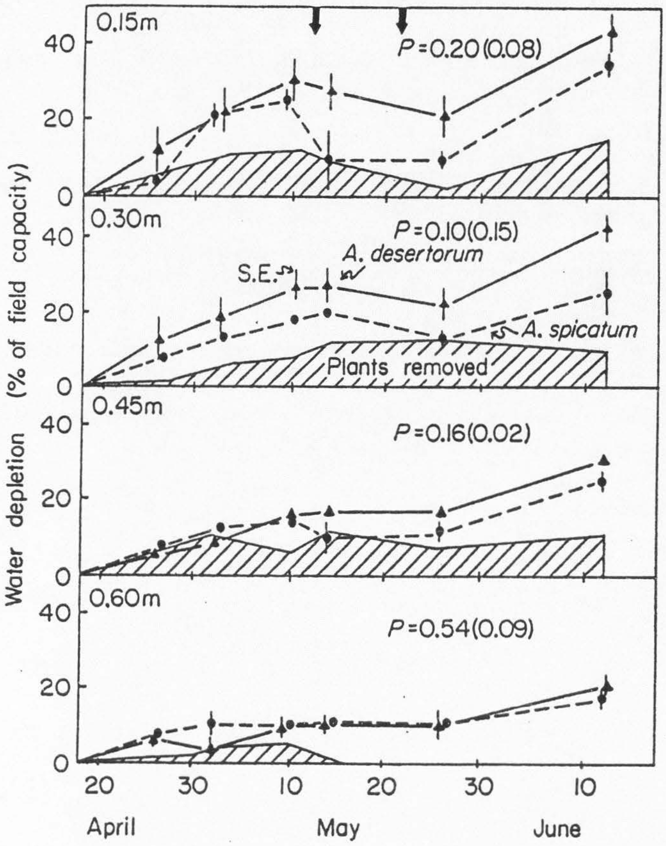

Fig. 3. Soil water depletion in 1985, expressed as a percent of field capacity in *A. desertorum* plots, *A. spicatum* plots, or in plots where vegetation had been removed within 1 m of the neutron access tube. (Field capacity estimated 18 April 1985.) Heavy arrows indicate rainy periods. The probability that the observed difference between *A. desertorum* and *A. spicatum* plots occurred by chance, *P*, is indicated. (The *P*-value for the species x time interaction; i.e., that differences were greater between the two grasses on some sampling dates compared to other sampling dates is shown in parenthesis.)

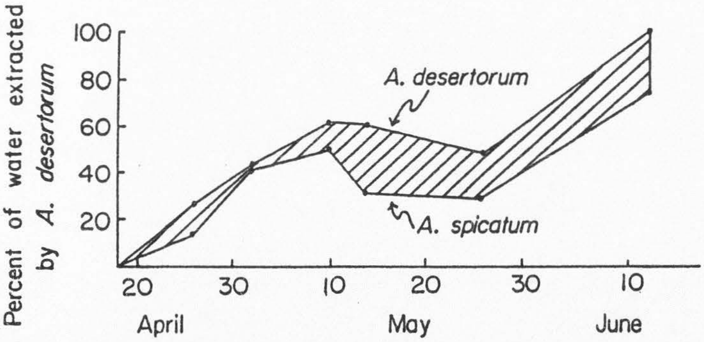

Fig. 4. Soil water depletion in 1985 from 0 to 67 cm in *A. desertorum* and *A. spicatum* plots. Measurements expressed as a percentage of total water extracted by *A. desertorum* during the time period 18 April to 13 June, ca. 4.7 cm. Shaded area indicates average difference in amount of water extracted between plots of the two grass species.

time course for *A. desertorum* and *A. spicatum* water extraction during the spring relative to the total amount extracted by *A. desertorum* for this time period is illustrated in Fig. 4. The amount of water extracted by these two grass species was similar until mid-May. However, after mid-May, *A. desertorum* plots had about 20% less available water than plots of *A. spicatum* (Fig. 4).

Neighborhood analysis

The relationship of aboveground biomass of neighboring perennial grasses, weighted according to their proximity to the *Artemisia*, with current year's growth of *Artemisia* transplants is illustrated in Fig. 5. When analyzed separately, *A. spicatum* plots showed a higher correlation between weighted neighboring perennial grass biomass and *Artemisia* growth ($r^2=0.31$) than did *A. desertorum* plots ($r^2=0.10$, plots with grass biomass = 0 g per plot not included). The significant correlation ($P<0.01$) between weighted *A. spicatum* biomass and *Artemisia* growth was largely due to the presence of four plots with low *A. spicatum* biomass and high *Artemisia* growth (Fig. 5). In other words, once the neighboring perennial grass biomass, A, exceeded 20 g per plot, neighborhood biomass did not relate predictably with *Artemisia* growth for either grass species. Inclusion of *Bromus tectorum* biomass in a multiple regression did not significantly ($P>0.10$) increase the correlation of aboveground neighborhood biomass with *Artemisia* growth.

Median weighted biomass, A, of perennial grasses in *A. desertorum* plots was greater than in *A. spicatum* plots (Fig. 6). Conversely, *B. tectorum* biomass was greater in *A. spicatum* plots although

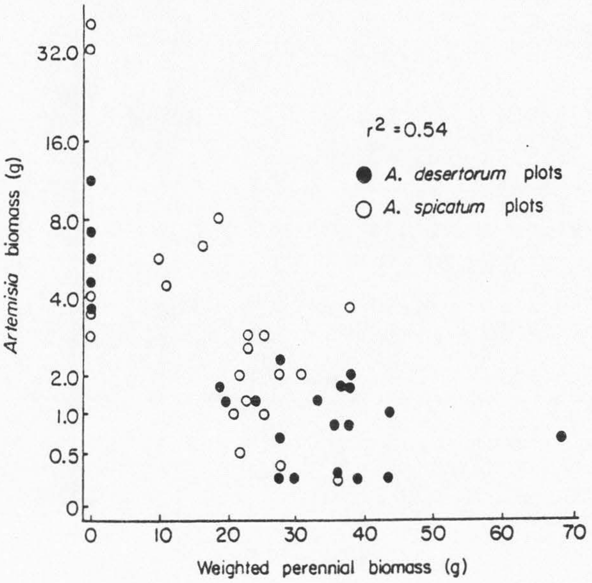

Fig. 5. Relationship of current year's growth of Artemisia indicator plants with weighted biomass of perennial grass neighbors (g per plot), A, around the indicator plant. Plots designated as A. desertorum or A. spicatum had at least 90% of the total weighted biomass, A, of that species. (See Eq. 1 for definition of A.) Agropyron desertorum and A. spicatum plots where all biomass had been removed are also indicated. The negative correlation was significantly different from zero ($P<0.01$).

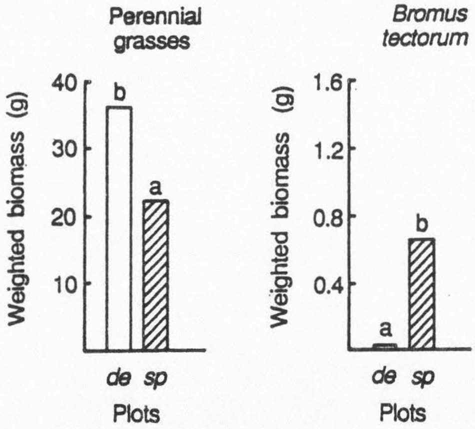

Fig. 6. Weighted perennial grass and Bromus tectorum biomass in A. desertorum and A. spicatum plots. (See Fig. 5 for criteria used in plot designation.) Medians denoted by a different letter were significantly different at $P<0.05$ (n=19 for A. spicatum plots, n=36 for A. desertorum plots).

considerably less than the perennial biomass in those plots.

Discussion

The two tussock grasses we studied exhibited appreciable differences in rate of soil water extraction. The large differences in the performance of the indicator plant, *Artemisia*, in the neighborhoods of the two grass species were likely related to these differences in water extraction. Differences in competitive ability of clipped and unclipped *A. spicatum* and *A. desertorum* were also found in earlier work in common gardens on a different field site (Richards et al. unpubl.)

Artemisia indicator plants

We could only detect large differences in mortality of *Artemisia* between the *A. desertorum* and the *A. spicatum* neighborhoods when the tussock grass was replaced by the *Artemisia* on the earlier planting date (Table 1). In Chapter IV, we show that differences in root invasion by these two grass species is strongly dependent upon the date that a tussock is removed. Extensive root growth over winter and early spring by *A. desertorum* allows it to invade these soil disturbances more rapidly than *A. spicatum*, especially if the disturbance occurs soon after snowmelt rather than later in the spring.

Artemisia reproduction in *A. desertorum* plots was less than in *A. spicatum* plots. However, there was a similarity in percentage of the *Artemisia* flowering (Fig. 1) or in mean weight of inflorescences per individual (data not shown) between the *A. spicatum* and no competition plots. This similarity was probably of only temporary duration. In widely spaced (2 m) plantings on a different field site, *Artemisia* exhibited primarily vegetative growth the second year after transplanting but exhibited approximately 10 times more reproductive growth (inflorescences) than aboveground vegetative growth the third year after transplanting. This magnitude of allocation to reproduction was never observed in more dense plantings (spacing = 0.5 m). Consequently, the *Artemisia* in the plots with the grasses removed probably would have had more reproduction than the *Artemisia* in the *A. spicatum* plots if the experiment had been continued another year.

The influence of *A. desertorum* neighbors on *Artemisia* transplants seemed principally caused by competition for water. A study of nitrogen fertilization of *Artemisia* on a somewhat drier site approximately 40 km southeast of our study area indicated only small increases in shoot length in the first year after fertilization and no increase in either shoot length or shoot weight in the second year (James and Jurinak 1978). Nitrogen concentrations in the shoots, however, were greater for the fertilized than the unfertilized plants in the second year after fertilization. Since even the fertilized plants had approximately 16% lower N concentrations in the shoots than the *Artemisia* in our study, the *Artemisia* in our study may not have been particularly N limited.

The conclusion of the importance of water relative to nutrient competition is further supported by the correlations of nutrient concentration with either plant water potential in August or current growth (Fig. 2). In general, *Artemisia* in *A. desertorum* plots tended to have lower nutrient concentrations when current growth was greater or water status was more favorable. Plants that were severely water stressed and generally had little growth tended to exhibit higher N and P concentrations. The *Artemisia* in the *A. spicatum* and no competition plots, which were under less severe water stress in August (Fig. 1), did not show as strong a negative correlation between nutrient concentration and biomass or water status.

Effect of the species of grass removed

The predominant effect on *Artemisia* performance was likely caused by the species of neighbor, not by the species of grass that was replaced by the *Artemisia*. This view is supported by several lines of evidence. There were no consistent differences in *Artemisia* growth after all neighbors had been removed in areas orginally dominated by either *A. spicatum* or *A. desertorum* (Fig. 5). Secondly, even in the relatively dry year of 1985, soil water content in the *A. spicatum* and *A. desertorum* plots were similar until mid-May (Fig. 6). Yet, differences in *Artemisia* mortality in the relatively wet summer of 1984 was only clearly greater in the *A. desertorum* than the *A. spicatum* plots for those shrubs transplanted 5 May 1984. Furthermore, in those locations where an *A. desertorum* tussock in *A. spicatum* neighborhoods was replaced by a neutron probe access tube, soil water content was greater than in the *A. desertorum* neighborhoods where the species of tussock replaced was *A. spicatum*. Consequently, when the tussock replaced by the *Artemisia* in the 1984 experiments was the same species as its neighbors, the species of tussock removed probably had little impact on the subsequent performance of the *Artemisia*.

Water extraction

Differences in extraction rates of the two grass species may partly reflect differences in shoot biomass. *Agropyron desertorum* plots had a 37% greater mean weighted biomass surrounding the neutron access tubes than *A. spicatum* plots. However, in one *A. spicatum* plot which had greater biomass than any of the *A. desertorum* plots, water extraction was still less than in the *A. desertorum* plots. Furthermore, in garden plots at another field site where average plot biomass of *A. spicatum* exceeded *A. desertorum*, Thorgeirsson (1985) demonstrated and we later also found (Appendix, Chapter IV) that *A. desertorum* in these plots depletes the water in the soil profile sooner than does *A. spicatum*.

Neighborhood analysis

The poor correlation of *Artemisia* growth with aboveground biomass of the tussock grasses may in part be related to the measurement of shoots to infer size and sites of activity of the root system. In another study (Chapter IV), location of active roots of individual tussocks of these two grasses was not closely correlated with size or proximity of shoots. This result was determined by ^{32}P uptake from isotope injected into the soil as a liquid plane and subsequent appearance of radioisotopes in the shoots of neighboring tussocks.

The competitive ability of species can be compared by testing for significant differences in the slopes of the regression lines which relate the amount of shoot biomass of a species in the neighborhood with the performance of the indicator plant (see Goldberg and Werner 1983). However, if correlations of aboveground neighborhood biomass with an indicator plant's success are poor, slopes of regression lines provide little information regarding the relative competitive ability of the neighbors. This problem was avoided in this study because of the existence of interspersed, nearly monospecific stands of the two tussock grasses. This condition permitted an assessment of the relative competitive ability of the two grass species without needing to rely heavily on assumptions that a neighbor's competitive influence on an indicator plant would be a function of location or amount of that neighbor's shoot biomass.

Extension of results beyond the indicator plants

The difference in ability of the two tussock grasses to suppress *Artemisia* transplants has important implications for other neighbors. As a winter annual, *B. tectorum* is largely dependent on stored water for growth and reproduction and would be more limited by neighbors that have early season root growth and extract water rapidly from the soil profile (Harris and Wilson 1970). Thus, the smaller biomass of *B. tectorum* in the *A. desertorum* than in the *A. spicatum* plots (Fig. 6) probably partly reflects differences in competitive ability of these two tussock grasses.

Artemisia tridentata that establishes naturally from seed would probably also be more suppressed by *A. desertorum* than *A. spicatum*. Since *Artemisia* germinates early in the spring (e.g., Young and Evans 1986), differences in survival and subsequent growth of individuals that establish naturally probably would show similar differences as did *Artemisia* transplants to the species of *Agropyron* neighbor (even under conditions where grazing by large herbivores is light).

Conclusion

Agropyron desertorum and *A. spicatum* exhibit marked differences in competitive ability. We demonstrated these differences in rangeland conditions by use of *Artemisia* indicator plants transplanted into interspersed, nearly monospecific stands of the two grass species. Neighborhood analysis, however, was not found useful in the assessment of the relative competitive abilities of these two species of *Agropyron*.

More rapid water extraction by *A. desertorum* than *A. spicatum* is probably a major factor contributing to the differences in *Artemisia* water status, growth, and reproduction in the neighborhoods of the two grass species. Despite the numerous similarities of the shoots of these two grasses, substantial differences in their root systems likely contribute to their different abilities to extract water and compete.

CHAPTER III

CHARACTERISTICS OF SUCCESSFUL COMPETITORS: AN EVALUATION OF POTENTIAL GROWTH RATE IN TWO COLD DESERT TUSSOCK GRASSES

Summary

Within the first few weeks after seedling emergence, *Agropyron desertorum*, a more competitive tussock grass, had a much higher mean relative growth rate (RGR) than *Agropyron spicatum*, a very similar, but less competitive species. However, beyond the early seedling stage, the two grasses had a remarkably similar whole-plant RGR in hydroponic culture and aboveground RGR in glasshouse soil, if root temperatures were above approximately 12°C. At soil temperatures between 5 and 12°C, *A. desertorum* exhibited a 66% greater aboveground RGR than *A. spicatum* ($P<0.05$). Both species responded similarly to warming soil temperatures. In the field, however, tiller growth rates were generally similar. Neither species showed marked tiller elongation until a couple weeks after snowmelt, by which time soil temperatures, at least to a depth of 10 cm, were above 12°C for a significant portion of the day. Aboveground biomass accumulation over a three-year period indicated that both grasses have similar potential growth rates whereas *Artemisia tridentata* ssp. *vaseyana*, a common neighbor planted in the same plots, had a much greater potential growth rate. The greater competitive ability of adult *A. desertorum*, as compared to *A. spicatum*, cannot be attributed to appreciable

differences in potential growth rates.

Introduction

Agropyron spicatum (Pursh) Scribn. and Smith, a tussock grass, and *Artemisia tridentata* ssp. *vaseyana* (Rydb.) Beetle, a shrub, are prominent co-occurring species of the Great Basin steppe of North America. *Agropyron desertorum* (Fisch. ex Link) Schult., an introduced tussock grass from Eurasia, has been widely planted in this region. Competition experiments using transplanted mixtures of *Artemisia* with both of these grass species have shown *A. desertorum* to be much more effective in reducing vegetative and reproductive biomass of *A. desertorum* than is *A. spicatum* (Caldwell and Richards 1986). The greatest difference in competitive ability of these two grasses was exhibited two years following transplanting (Richards et al. unpubl). Although these *Agropyron* grasses differ greatly in competitive effectiveness, they have many characteristics in common. They are both long-lived tussock grasses with similar shoot phenological patterns, biomass allocation patterns, water-use and nitrogen-use efficiencies, seasonal patterns of leaf water potential, and light and temperature dependencies of photosynthesis (Caldwell et al. 1981, Nowak and Caldwell 1984a, Nowak and Caldwell 1986).

Competitive advantage can be realized if a plant is able to rapidly occupy space released following disturbance. Preemptive competition in this case is being distinguished from colonization since the leaves or roots of the plants are gaining control instead of new propagules. When new space becomes available, species with greater potential growth rates would be more likely to gain a greater share of the available space and the resources associated with that space and thereby disadvantage the competitive position of their neighbors. Disturbance may simply be the abrupt death of a neighbor or the death of a portion of the neighbor's root or shoot system as could be caused by pathogens, trampling, or burrowing animals.

High growth rates at cold soil temperatures may be particularly beneficial in a steppe environment since most of the soil water recharge comes in the form of melting snow and spring rains with little effective recharge of the soil profile from summer precipitation (Caldwell 1985). Indeed, many species in this environment initiate growth very early. Working in the sagebrush-grass region of southern Idaho, Jensen (1984) found that the date of growth initiation was significantly correlated (correlation coefficient, r=0.82) with the date soil temperatures at 0.5-m depth exceeded 1°C. Most work demonstrating enhanced competitive ability by early spring growth has dealt with seedling establishment (Harris 1967, Larsen and Schubert 1969, Harris and Wilson 1970, Bazzaz 1984). However, adult plants may also gain an advantage over their neighbors in seasonal resource exploitation if they can grow rapidly at cold soil temperatures. In a study of groundlayer species in mesophytic hardwood stands, Rogers (1985) found that the presence of spring-active plants, which generally develop when the soil is still cold, appeared to result in reduced productivity of some summer-active perennials. *Acer saccharum* and *Ulmus rubra* had at least 50% lower cover in locations with a high shoot density of spring-active plants.

We investigated differences in potential growth rates of A. spicatum and A. desertorum under a variety of conditions. We use the term, potential growth rate, to refer to growth rates without either intraspecific or interspecific competition, but constrained only by the genetic potential of the individual, the resource supply, and other abiotic controls (e.g., soil temperature). We wanted to examine the growth responses to very plentiful water and nutrient conditions, as would occur during short-term flushes, as well as to lower nutrient conditions more representative of average conditions. Therefore, we examined mean relative growth rate (RGR) of whole plants in hydroponic culture at saturating and suboptimal N and P concentrations and optimal water conditions. Aboveground growth rates were examined in soil culture under controlled warm and cold soil temperatures. Growth rates of individual tillers were examined in the field using widely spaced individuals in fertilized and unfertilized plots. Annual changes in final standing crop were also examined in the field for the two bunchgrasses as well as their common neighbor, Artemisia tridentata.

Methods

Glasshouse experiments

Glasshouse experiments were conducted from November until March. Air temperatures were approximately 20 to 30°C and photoperiod was held constant at 13 hr using supplemental fluorescent lighting.

Mean relative growth rates (RGR) of whole plants were examined weekly at four levels of phosphorus and two levels of nitrogen in a factorial design with three replicates per treatment. Agropyron desertorum cv. Nordan and Agropyron spicatum cv. Secar were germinated on blotter paper and after 7 d placed in bottles with 900 ml of aerated full-strength nutrient solution (Hoagland and Arnon 1950; modifications: pH 5.5, 50 μM $FeCl_3$, 50 μM of the iron chelate, ethylene di-(o-hydroxy-phenylacetate) (EDDHA). The seedlings were grown for 23 d to reduce the potential benefits derived from differences in the seed, selected for uniformity, and P and N nutrient treatments imposed. Total fresh biomass (± 1 mg) was determined weekly for the following 35 d by blotting roots to a uniform dampness. Mean relative growth rates were calculated over the time interval as follows:

$$RGR = (\ln(W_2) - \ln(W_1)) \times (t_2 - t_1)^{-1}$$

where W = fresh or dry biomass, depending on the experiment, t = time (in days unless stated otherwise) on either the first (1) or second (2) harvest. Mean relative growth rate was expressed on a daily basis for glasshouse experiments to allow for comparison between experiments. The time interval, however, is always noted.

The high-N solution contained saturating N levels typically required of high yielding crop plants (15 mM NO_3^- and 1.5 mM NH_4^+). The moderate-N treatment was 10% of the high N treatment (1.5 mM NO_3^- and 0.15 mM NH_4^+). For the phosphorus treatment, we were interested both in saturating and minimum concentrations for P uptake. Since larger and faster growing plants have a higher nutrient demand, nutrient concentrations in the culture solution which are below saturating levels need to be continuously replenished to accommodate these differences in demand (Ingestad 1982). Phosphorus was therefore added to result in a constant tissue concentration, assuming the relative growth rate remained constant over the subsequent week. The P treatment covered four orders of magnitude. The lowest was lower than the level at which either species could sustain growth, as determined by a pilot experiment, and the highest concentrations saturated uptake (approximate solution concentration range: 0.3 μM to 3 mM).

Plants from the same seed sources as in the hydroponic experiment were grown in soil culture at two ranges of soil temperature and three levels of fertilization. Pots were 50 cm deep and 10 cm in diameter and constructed from plastic pipe with plastic screen attached to the base. Soils ($<$ 6 ppm P, $<$ 0.10% N) were collected from the field site (Caldwell et al. 1981) and mixed in a 1:1 ratio with washed sand to lower the nutrient content and provide a better aerated potting mixture. A small sample of soil from beneath the same species in the field was mixed in the surface layer of the pot to enhance mycorrhizal infection and establishment of soil microbes.

Four seeds per pot were sown and after four weeks, the seedlings were selected for uniform size both within and between species, leaving only one plant per pot. After two additional weeks the cold temperature treatment was initiated. Seedlings were approximately 10 cm in height at this time. Cold soil temperatures were achieved by circulating cooled water through copper tubing surrounding the pots.

Temperatures were monitored with thermocouples at 10- and 40-cm depths. For the first three weeks, temperatures at 10 cm ranged from 13 to 16°C and at 40 cm from 10 to 13°C, after which temperatures were further reduced to 7 to 12°C, and 5 to 6°C, at 10 and 40 cm, respectively. The warm soil treatment ranged from 20 to 26°C throughout its soil volume. After 90 d, all the plants in the warm temperature treatment and 14 of the 28 plants in the cold temperature treatment were harvested. The remaining half in the cold temperature treatment were examined for changes in growth rate by allowing the soil to warm in increments over a 27-d period.

Plants were watered every 3 d as needed and fertilization occurred weekly. The nutrient treatments were full-strength nutrient solution, 1/10-strength solution, and tap water. Ten ml of solution were injected every 10 cm to provide a uniform distribution in the soil.

Aboveground biomass was estimated nondestructively each week by measuring total leaf length and average leaf width of fully expanded leaves. Thirty-two plants were sacrificed 65 d after germination to develop the regression between the product of length and width to dry weight (r^2=0.97; no significant difference between species or treatment) and then tested against final weights of 22 remaining plants (predicted versus observed: r^2=0.97).

Field experiments

The study area is located in a site typical of semiarid North American Great Basin rangelands where *Agropyron spicatum* and *Artemisia tridentata* are native and where *Agropyron desertorum* has been extensively seeded. The study area has been previously described (Caldwell et al 1981); thus, we will describe only the specific plots used to measure potential growth rates. *Agropyron spicatum* var. *inerme*, *A. desertorum*, and *Artemisia tridentata* ssp. *vaseyana* were planted in early June, 1983 in four plots. Competitive interaction was minimized by planting the species in a 2-m spacing. Each individual was surrounded by two plants of the other species. Medium-size tussocks of *A. spicatum* and seedlings approximately 2 yr old ($<$ 10 cm in height) of *A. tridentata* were collected from the surrounding hillsides of the study area. Medium-size tussocks of *A. desertorum* were collected from a pasture sown approximately 30 years earlier about 140 km south of the field site. Two plots were heavily fertilized with 150 kg ha^{-1} $N\text{-}NH_4NO_3$ and 50 kg ha^{-1} $P\text{-}P_2O_5$ in June and September, 1983 and April, 1984. Weeds were controlled with preemergent herbicide (dimethyl tetrachloroterephthalate) sprayed at 8.4 kg ha^{-1} active ingredient each spring and fall and by rototilling between plants no deeper than 10 cm. In 1983, plants were watered to promote establishment. Soil temperatures were monitored in 1984 and 1985 at 10- and 40-cm depths using thermocouples.

Growth rates of ten permanently marked tillers uniformly distributed throughout the tussock for four plants per species per plot were monitored in 1984 using the technique described in the glasshouse soil temperature experiment. A second set of tillers was harvested on 27 May, 1984, weighed, and leaf area determined using a leaf area meter (Licor, Model LI-3000). We found that a simple allometric relationship could not be used to predict tiller biomass in the field, only tiller surface area, since tiller specific area (m^2 kg^{-1}) in the field differed between the species, and varied with time and fertilization ($P<0.05$). In 1985, two tillers per plant from five healthy plants per species per plot were destructively sampled weekly and leaf area and dry biomass were determined.

Final standing crop of the bunchgrasses was determined by clipping the senesced foliage in the fall of each year to a 5-cm height in 1984 and 1985. In 1983, the same year the plants were transplanted, the amount of foliage that had grown after the summer dry period, fall regrowth, was estimated using a reference unit technique (Kirmse and Norton 1985; $r^2=0.95$, n=32). Aboveground biomass of sagebrush was also estimated in 1983 using a log - log relationship of twig biomass to stem diameter ($r^2=0.94$, n=33) and confirmed with 1984 sagebrush seedlings (predicted versus observed: $r^2=0.95$, n=28). In 1984 and 1985, fall biomass was more easily calculated using a correlation between canopy volume and biomass ($r^2=0.98$, n=21) which was checked with 20 sagebrush harvested in 1985 (predicted versus observed: $r^2=0.53$; slope did not differ from 1.0 and intercept did not differ from 0.0, $P>0.20$).

Analysis of field growth rates was complicated by the fact that many *A. spicatum* plants did not undergo transplanting well and many of the tillers in the bunches died by 1984. Since we were interested in potential growth rates, we only compared tiller growth rates and changes in final standing crop of the larger tussock grasses which had established successfully. A minimum oven-dried biomass of 75 g by the

1985 fall harvest was the criterion used to identify the sample populations.

Results

During the first few weeks following germination, *A. desertorum* seedlings had substantially greater RGR than *A. spicatum* in hydroponic culture. These relative growth rates were higher than at any other time during the experiment (Table 2). Similar differences between the species were found in aboveground biomass 51 d after germination in the soil culture experiment. The differences in growth rates of young seedlings of the two species were not related to seed weight.

Table 2. Seed weight, seedling mean relative growth rate (RGR) for the 14- to 21—d interval in full-strength nutrient solution, and aboveground biomass in soil culture 51 d after germination of *A. spicatum* and *A. desertorum* (*** denotes significance at $P<.001$; se=standard error of mean)

	A. spicatum		*A. desertorum*	
	n	mean ± se	n	mean ± se
Seed weight (g/100 seeds)	4	0.321 ± 0.005	4	0.319 ± 0.003
RGR ($g\ g^{-1}\ d^{-1}$)***	27	0.129 ± 0.007	27	0.172 ± 0.005
Aboveground biomass (g)				
soil temperature 20-26 C***	20	0.067 ± 0.008	20	0.127 ± 0.005
soil temperature 5-12 C***	14	0.020 ± 0.001	14	0.034 ± 0.003

After 56 d, *A. spicatum* had very similar whole-plant RGR to *A. desertorum* over a range of nutrient regimes in solution culture ($P=0.67$; Fig. 7). Growth rates were unaffected by the level of N when P was high but were lower at high N than at moderate N when P was low.

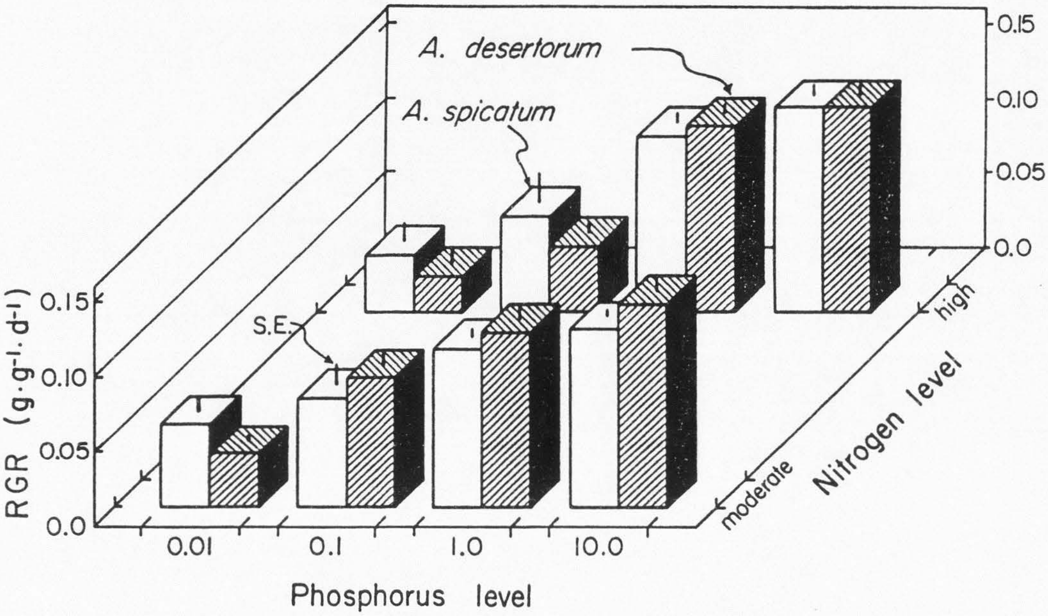

Fig. 7. Whole-plant mean relative growth rates between 49 and 56 d following germination for A. desertorum and A. spicatum plants grown in hydroponic culture ($n = 3$ for each mean) at four levels of phosphorus and two levels of nitrogen. Phosphorus treatment significant at $P<0.001$ and P x N interaction significant at $P=0.07$. No significant differences between species ($P>0.20$).

At the lowest P treatment level, RGR never stabilized but continued to decline to negative values for both species (data not shown).

Plants grown in soil culture in the glasshouse were examined for differential response to soil temperature under various fertilization regimes. Plants tended to have an exponential rate increase of aboveground biomass at warm temperatures, especially with high fertilization, but increased only linearly at cold temperatures (time course not shown). Mean relative aboveground growth rates from 51 to 66 d at soil temperatures between 20 and 26 C also did not differ between species ($P>0.20$; Fig. 8). Fertilization did increase RGR ($P<0.01$) at these temperatures. At soil temperatures between 5 and 12 °C, RGR from 51 to 90 d was 66% greater for A. desertorum ($P=0.04$) and fertilization had an inconsistent effect ($P=0.20$). We also examined absolute growth rates for the same time interval for the cold temperature treatment. Agropyron desertorum had nearly a four-fold greater median growth rate (1.29 versus 0.346 mg d^{-1}) than A. spicatum during this period (Wilcoxon Sum Rank Test; $P<0.01$), and fertilization did not affect the absolute growth rate of either species (Kruskal-Wallis Test; $P>0.20$).

Plants were also examined for differential ability to respond to a change in soil temperature (Fig. 9). Neither species exhibited an substantial lag in growth acceleration as soil temperatures increased, and their RGR values never differed from one another ($P>0.20$). Fertilization did not affect plant growth rates during the warming period.

Although there was a distinct difference in RGR of the two species as a result of a prolonged cold soil temperature treatment in the glasshouse, this was not generally apparent in the field. Field absolute growth rates of tillers from widely spaced plants in the spring did not show any appreciable differences (Fig. 10). Snow melted approximately 22 d before the first measurement in 1984 and 9 d before the first measurement in 1985. Soil temperatures beneath the snow were 1 °C at 10 cm and 2 °C at 40 cm in March, 1985. As would be expected, soil layers closer to the surface exhibited a much greater

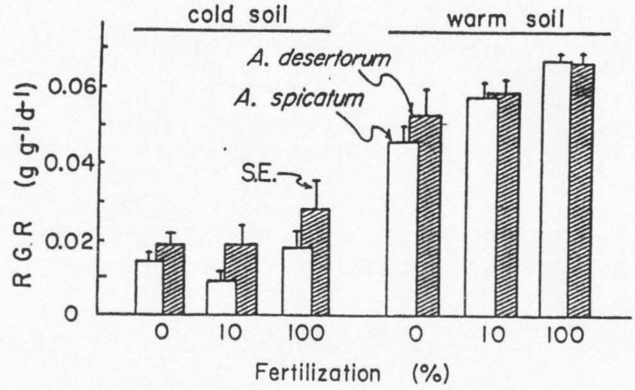

Fig. 8. Aboveground relative growth rates of A. desertorum and A. spicatum from 51 to 66 d for the warm soil treatment (20 to 26°C; n= 6 to 7) and from 51 to 90 d for the cold temperature treatment (5 to 12 °C; n=4 to 6). Fertilization represents 0, 10 and 100% of modified Hoagland's solution (see text for details). For the cold temperature treatment, species differences were significant (P=0.04) but increased fertilization did not consistently increase RGR (P=0.20). For the warm temperature treatment, there were no significant differences between species (P>0.20), but fertilization was significant (P=0.002).

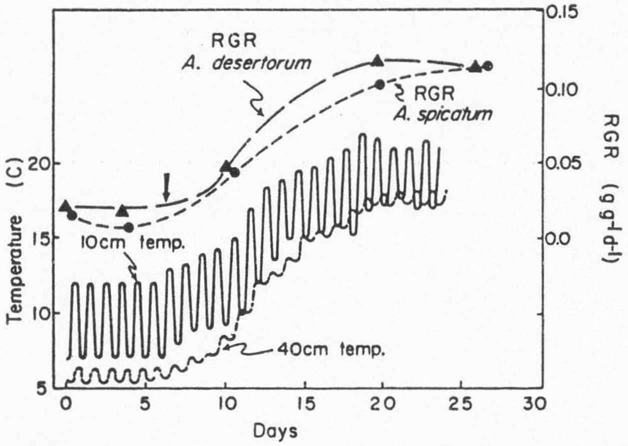

Fig. 9. Mean relative growth rates (RGR) of aboveground biomass of A. desertorum and A. spicatum and corresponding soil temperature at 10- and 40-cm depths in the glasshouse. Relative growth rate at day=0 calculated over a 39-d time interval, and the remaining means plotted at the end of the time interval for which they were calculated (e.g., RGR at day=4 had a time interval of 4 d). Relative growth rates of fertilized and unfertilized did not differ significantly and were pooled (P>0.20). Arrow indicates the day on which soil was allowed to warm. No significant differences were found in RGR between species (P>0.20).

diurnal range (Fig 10). In 1985, soil in the surface layers began to experience periods of the day above 15 degrees within a week after snowmelt. At the 40-cm depth, temperatures fluctuated less and took several weeks or longer to warm above 12°C, depending on the year.

In 1984, biomass was estimated by a single destructive harvest (data not shown) on 30 May. On this date, tiller biomass of *A. spicatum* was greater than biomass of *A. desertorum* ($P<0.05$), presumably since tiller height of *A. spicatum* is usually greater than that of *A. desertorum* at full extension. In 1985, very early spring tiller biomass was generally similar for the two species. On 23 April, however, following a week of cold weather and cold soil temperatures, *A. desertorum* did exhibit greater tiller biomass than *A. spicatum* ($P=0.02$), but these differences disappeared by the following week. Until the end of May in 1984, and after the first measurement in 1985, green surface area of tillers of the two grasses showed differences in magnitude ($P<0.05$), but no difference in slope (i.e., absolute rate of increase). Fertilization had inconsistent results on green surface area between the two fertilized and two unfertilized plots ($P>0.20$). Relative growth rates of green foliage surface area were also similar for the two grasses (data not shown). Since *A. desertorum* tends to have greater specific foliage area (Fig10, 1985 data; see also Caldwell et al. 1981, Nowak and Caldwell 1984b), the greater green surface area of *A. desertorum* in 1984, does not reflect appreciable differences in tiller biomass.

Total aboveground biomass measured in the fall of each year with minimal competition was quite different for *A. tridentata*,

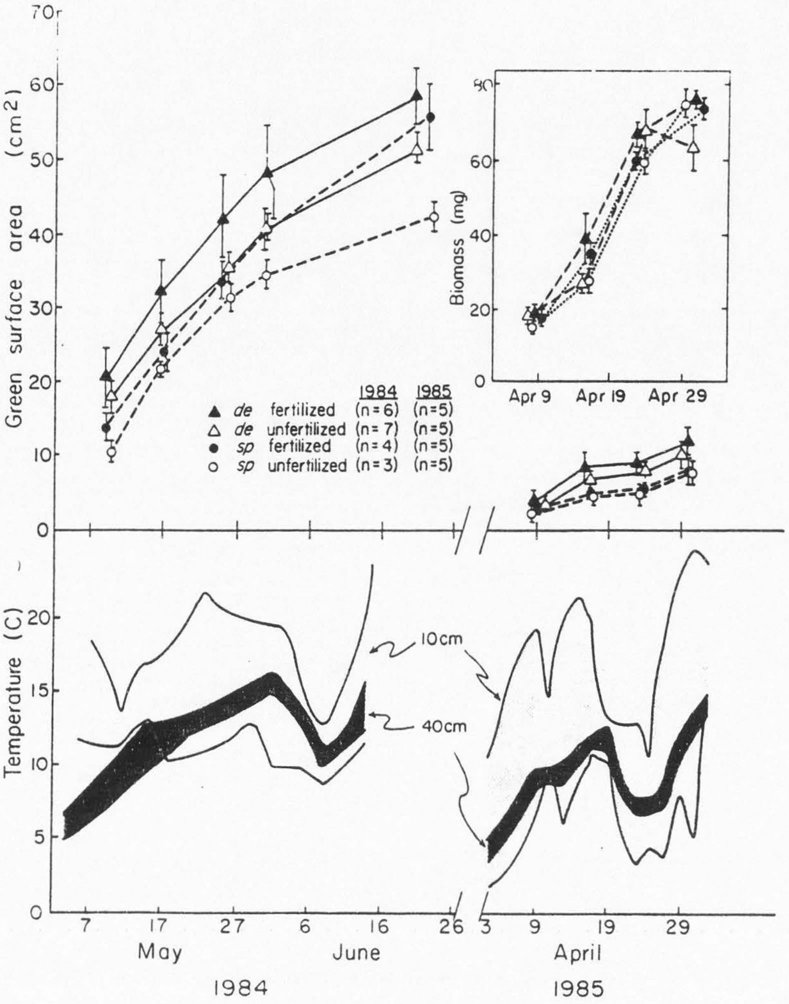

Fig. 10. Green surface area per tiller in 1984 and 1985 from *A. desertorum* (*de*) and *A. spicatum* (*sp*) planted in the field in a 2-m spacing and corresponding diurnal soil temperature range at 10- and 40-cm depths. Means of green surface area differed significantly between species until end of May 1984 and after first measurement in 1985 ($P<0.05$), but absolute growth rate did not differ significantly ($P>0.20$). Inset: aboveground biomass accumulation of 1985 tillers. Biomass in 1985 was only significantly different between species on one sampling date, which immediately followed a period of cold soil temperatures (23 April, $P=0.02$). Vertical bars represents ±1 standard error of individual plants in fertilized and unfertilized plots; not the error associated with the fertilization treatment (n=2). Each plant (3 to 7 plants per mean) represents the average of 5 to 10 tillers in 1984 and 2 tillers in 1985. Fertilization did not significantly affect either green surface area or biomass ($P>0.20$).

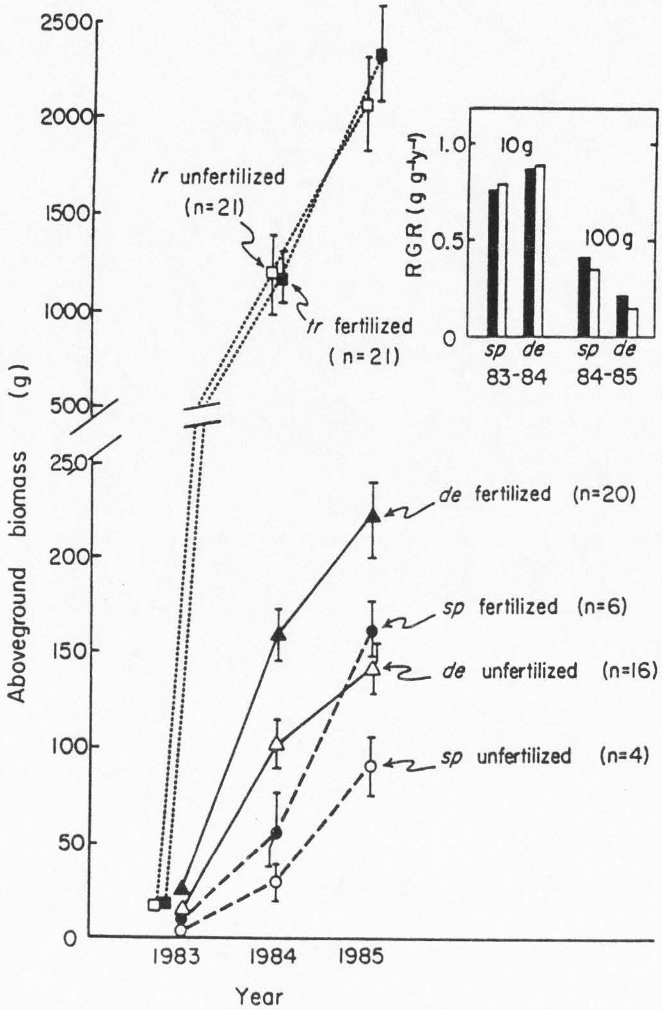

Fig.11. Aboveground biomass accumulation of A. desertorum (de), A. spicatum (sp), and Artemisia tridentata (tr) planted in early June, 1983 in a 2-m spacing in fertilized and unfertilized plots. Biomass measured in fall of each year. Vertical bars unless covered by symbol represents ±1 standard error of the mean of plants in the fertilized and unfertilized plots; not the error associated with the fertilization treatment (n=2). The fertilization treatment only affected 1983 grass biomass ($P=0.013$), and neither absolute nor relative growth rates. Note change in scale of ordinate axis. Inset: Annual mean relative growth rate of aboveground biomass of A. desertorum and A. spicatum for a 10- and 100-g initial biomass for the time intervals from 1983 to 1984, and from 1984 to 1985, respectively (calculated from a linear model used in an analysis of covariance). Initial weights of 10 and 100 g represent the magnitude of initial biomass in 1983 and 1984, respectively. Solid bar = fertilized plots, open bar = unfertilized plots. Mean relative growth rates using an analysis of covariance (initial biomass used as the covariate) were slightly greater for A. desertorum between 1983 and 1984 ($P=0.07$) and much greater for A. spicatum from 1984 to 1985 ($P<0.001$).

A. spicatum, and *A. desertorum* (Fig. 11). *Agropyron desertorum* withstood transplantation better than *A. spicatum* and had greater fall regrowth in 1983 ($P<0.01$). Fall regrowth in 1983 was also affected by fertilization ($P=0.01$). This initial advantage in recovery from transplantation was the major reason for the large differences in biomass between the two tussock grasses in 1984 and 1985. The slopes of the lines through time represent absolute growth rates. From 1983 to 1984, absolute growth rates of *A. desertorum* were similar to those of *A. spicatum* from 1984 to 1985 (Fig.11). Since mean relative growth rates declined as biomass increased, initial weight was used as a covariate of RGR to determine differences between species and response to fertilization. *Agropyron desertorum* had a slightly greater RGR between 1983 and 1984 ($P=0.07$), while *A. spicatum* had a much greater RGR between 1984 and 1985 ($P<0.01$; Fig 11 inset). Fertilization did not affect RGR in either period ($P>0.20$).

The shrub, *Artemisia tridentata*, had much higher aboveground growth rates than either grass species. Inflorescence mass alone of *A. tridentata* in 1985 was more than four times the biomass of the grasses.

Discussion

Several studies that have examined reasons for differences in competitive ability among established plants have emphasized differences in growth form and morphological development (Pavlik 1983c, Grace 1985, Kuppers 1985), differences in shoot phenological patterns (Rice and Menke 1985), shoot:root allocation patterns (Baan

Hofman and Ennik 1982, Pavlik 1983b), and nitrogen-use efficiency (Pavlik 1983a). None of these morphological or physiological characteristics clearly explain the differences in competitive ability of these two Agropyron species. Indeed, these grasses are very similar in a wide array of morphological and physiological traits (Caldwell et al. 1981, Caldwell et al. 1983, Nowak and Caldwell 1984a, 1984b, 1986). Only two factors have thus far been identified that differ between these species that may contribute to greater competitive ability. Agropyron desertorum has greater root length per unit root biomass (Caldwell and Richards 1986) and a greater number of penetrations by mycorrhizal hyphae per unit length of root infected with mycorrhizal arbuscules (Caldwell et al. 1985).

In this study, we wished to determine if there were differences in potential growth rate of these grass species as established plants, especially in early spring, that might place A. desertorum at some advantange in competition with neighbors. Hydroponic culture, though obviously a very artificial medium, provided the opportunity to assess whole-plant growth rates under optimal and suboptimal nutrient conditions and optimal water status. The glasshouse soil culture experiment provided a controlled examination of the influence of soil temperature on aboveground RGR while the field experiments permitted an assessment of aboveground growth rates with minimal competition in the natural environment.

The principal difference between the grass species emerging from these experiments was a greater tiller growth rate of A. desertorum in the glasshouse, cold-soil experiment. This difference was not apparent in the field tiller growth studies even in cold spring periods. Only once, following a week of cold weather and soil temperatures in late April, 1985, did *A. desertorum* exhibit greater tiller biomass. Nowak (unpubl.) also indicated greater leaf biomass of *A. desertorum* on some winter and spring sampling dates in 1981 and 1982. Both in the earlier studies (Nowak and Caldwell 1984b, Nowak unpubl.) and in the present study, *A. desertorum* exhibited greater surface area of tillers in the early spring. However, as with tiller biomass, the grass species increased in surface area during the spring at similar rates.

The lack of appreciable differences in tiller growth rates in the early spring cautions against extrapolating from controlled glasshouse or growth chamber experiments to conditions found in the natural environment. One reason for the discrepancy between the cold temperature glasshouse experiment and what was observed in the field might be that in the field, there was only a short period of time between snowmelt and warming of the surface soil. More importantly though, belowground we have found considerable early spring root growth in *A. desertorum* compared with *A. spicatum* (Chapter IV, Thorgeirsson and Richards 1983).

The growth rates of both grasses pale by comparison, however, when compared to the growth rates of *Artemisia tridentata* (Fig. 11). *Artemisia tridentata* is indeed an effective competitior with both *Agropyron desertorum* and *A. spicatum* (e.g., Cook and Lewis 1963). Yet, the differences in competitive ability among these three species are definitely not proportional to their potential growth rates.

The importance of high potential growth rates as a general attribute of competitive ability is well documented in comparisons of species from different environments (Grime 1977, Bazzaz 1979). However, a high potential growth rate as a general characteristic of competitively successful plants is probably not sufficient to explain specific differences among plants in similar environments. Similiar to the results obtained in this study, there is often little relationship between growth in monocultures and competitive ability in mixtures (e.g., Eagles 1983).

Fertilization in the field had a weaker effect than expected, possibly due to increased mineralization of nutrients during site preparation. Thus the 'control' plots probably had more available nutrients than what would be normally expected in established pastures in this area. The fertilization treatments show, however, that nutrients were not a limiting factor in testing the potential growth rates of these species.

This study has concentrated on potential growth rates of plants which are beyond the very early seedling stage, because of the striking difference between these grass species in their ability as older plants to suppress biomass production of their neighbors. In the first few weeks following germination, potential growth rates of A. desertorum in this study were much greater than that of A. spicatum, regardless of soil temperature. This difference in the early seedling stage probably contributes to the greater competitive ability of A. desertorum in mixtures with winter annual species

(Harris and Wilson 1970) and in mixed seedings with other perennials (Schuman et al. 1982). Obviously, rapid growth in the very early seedling stage will probably result in accrued benefits later even if subsequent growth rates are the same as those of competitors. However, a favorable competitive position achieved in the seedling stage may not be retained as an adult. For example, Grace (1985) found that competitive differences of *Typha* species as seedlings were not always apparent in later growth stages.

These two *Agropyron* species are so similar in many respects that their striking difference in competitive ability is not easily ascribed to particular traits. The difference in potential growth rate in the very early seedling stage is not so apparent in later growth stages. Competitive advantage of the older, more established plants is due to other characteristics such as root morphology, root symbiotic associates and timing of root growth.

CHAPTER IV

EARLY SEASON INVASIVE ROOT GROWTH AND ITS SIGNIFICANCE FOR RESOURCE COMPETITION: A COMPARISON OF TWO TUSSOCK GRASSES

Summary

Agropyron desertorum, a more competitive tussock grass than *Agropyron spicatum*, exhibited greater root growth during the winter and early spring than *A. spicatum*. Furthermore, when new soil space was made available by removing a neighboring tussock, the rate of root invasion into this space was more rapid for *A. desertorum* than for *A. spicatum*. This difference between species was more pronounced when the removals were conducted soon after the snow melted in early spring than when the removals were conducted 24 d later. Despite the large difference in root invasion in the first removal experiment, acquisition of ^{32}phosphorus placed in the soil where the tussocks had been removed was similar for the two grass species. In the second removal experiment, *A. desertorum* did acquire considerably more ^{32}P from the disturbed soil than did *A. spicatum*. In both removal experiments, the greater invasive root growth of *A. desertorum* was reflected in slightly faster soil moisture extraction. Rapid root growth in the early spring can allow a plant to occupy a greater soil volume or soil microsites richer in resources. However, greater resource acquisition due to this rapid, early-season root growth may not become apparent until resources become limiting which often does

not occur until later in the spring.

Introduction

Difference in competitive ability between species of similar life form and physiological characteristics may be determined by subtle traits. In temperate environments, early season root growth may be important in competition for limited resources, not only for seedlings (Harris 1967, Larsen and Schubert 1969), but also for established perennial plants.

Agropyron spicatum (Pursh) Scribn. and Smith, a tussock grass, and *Artemisia tridentata* ssp. *vaseyana* (Rydb.) Beetle, a shrub, are prominent co-occurring species of the Great Basin steppe of North America. *Agropyron desertorum* (Fisch. ex Link) Schult., an introduced tussock grass from Eurasia, has been widely planted in this region. Competition experiments using transplanted mixtures of *Artemisia* with both of these grass species have shown *A. desertorum* to be much more effective in reducing vegetative and reproductive biomass of *A. tridentata* than is *A. spicatum* (Caldwell and Richards 1986). Although these *Agropyron* grasses differ greatly in competitive effectiveness, they have many characterisitics in common. They are both long-lived tussock grasses with similar shoot phenological pattern, biomass allocation, water- and nitrogen-use efficiencies, and seasonal course of leaf water potential. Seasonal photosynthetic rates and photosynthetic responses to temperature and light are also very similar (Caldwell et al. 1981, Caldwell et al. 1983, Nowak and Caldwell 1984a, b, 1986). However, *A. spicatum* generally has slightly greater yield in monocultures than *A. desertorum* (Eissenstat unpubl.).

Rapid root growth at cold soil temperatures may be particularly beneficial in a cold-winter, dry-summer steppe environment since most of the soil water recharge comes in the form of melting snow and spring rains with little effective recharge of the soil profile from any subsequent summer precipitation (Caldwell 1985). Most work demonstrating enhanced competitive ability by early spring root growth has dealt with seedling establishment (Harris 1967, Larsen and Schubert 1969, Harris and Wilson 1970). However, adult plants may also gain an advantage over their neighbors in seasonal resource exploitation if their roots grow rapidly at cold soil temperatures.

In a controlled greenhouse experiment, *A. desertorum* had similar relative growth rates (RGR) at warm soil temperatures (20-26 °C) compared to *A. spicatum*, but at cold soil temperatures (5-12°C), *A. desertorum* exhibited greater RGR (Chapter III). In the field, aboveground growth rates of these two grasses early in the spring were very similar (Chapter III). Preliminary evidence, however, has indicated that *A. desertorum* exhibits more root growth at low temperatures (Thorgeirsson 1985, Thorgeirsson and Richards 1983). They found greater adventitious root initiation from the base of tillers in fall and winter for *A. desertorum* than for *A. spicatum*.

Earlier root growth may provide a competitive advantage by allowing a plant to invade unoccupied soil space sooner and thereby limit use of the resources in that volume by neighbors. Small-scale disturbance, such as livestock trampling, burrowing animals, harvester ants or pathogens, are some of the more obvious ways soil space may become free of roots in cold desert communities. Even without disturbance, some soil space becomes available due to high annual root system turnover in most plant communities (Caldwell 1986). The advantages of earlier seasonal root growth should be further enhanced if soil space becomes available over winter rather than later in the spring after the soils have warmed.

In Chapter II, we demonstrated that the survival of _Artemisia_ indicator plants, when transplanted soon after the snow melted, was strongly dependent on whether its neighbors were _A. desertorum_ or _A. spicatum_. When the indicator plants were transplanted later in the spring, there were no apparent differences in _Artemisia_ survival between _A. desertorum_ and _A. spicatum_ neighborhoods. We also showed that essentially monospecific stands of _A. desertorum_ extracted water sooner than did stands of _A. spicatum_ under rangeland conditions. These phenomena suggest that there were early-season differences in root growth of these grass species.

The objectives of this study were: (1) to determine whether _A. desertorum_ has greater root growth than _A. spicatum_ during the winter and early spring, (2) to determine whether _A. desertorum_ has greater ability to extend roots into disturbed soil space and extract water and phosphorus from that space, and (3) to determine whether root invasion and resource acquistion of the two grass species respond differently to time of disturbance. The experiment was conducted in replicated monocultures of each grass species.

Methods

The study area is located on a site typical of semiarid North American Great Basin rangelands where Agropyron spicatum and Artemisia tridentata are native and where Agropyron desertorum has been extensively seeded. The study area has been previously described (Caldwell et. al 1981); thus, we will describe only the specific plots used in this investigation. Two monocultures of each grass species were planted in late spring, 1983, and sprinkle irrigated in the first summer to facilitate establishment. Tussocks of A. spicatum were collected from the hillsides surrounding the study area. Similar-sized tussocks of A. desertorum were collected from a pasture sown approximately 30 years earlier about 200 km south of the study area.

Soils in the four plots were analyzed by the Utah State University Soil Testing Service for texture, available P (Olsen's bicarbonate - 0.5 M $NaHCO_3$ extractable), and total Kjeldahl N. Soil was collected at depths of 0 to 0.2 and 0.2 to 0.4 m on 10 and 17 June, 1985. A portion of the soil was dried to calculate gravimetric water content. Bulk densities were determined from single samples in each of the North and South Plots (Fig. 12) to allow comparison to neutron probe volumetric water content data. (Soil water content was expressed on a mass basis (θ_m) rather than a volume basis in Table 4 because soil bulk density was not determined for each soil sample.) The relationship between soil water content and soil water potential was developed from a comparison of neutron probe and soil psychrometer measurements at this field site. Soil temperature at 0.1- and 0.4-m depths and precipitation were continuously monitored within

50 m of the study plots.

Soil free of living roots was created by removing a single tussock and its associated soil volume in subplots at two times in the spring. Preceding these removals, glass plates were installed November, 1984 to separate the plant root systems and to provide an estimate of overwinter root activity prior to the disturbance. Two glass plates, 0.5 m wide and 0.4 m deep, were installed on both sides of the plant to be removed, 0.3 m from the center of the neighboring plants, and perpendicular to an imaginary line connecting the center of the removal plant and its neighbor (Fig. 12). The plates were placed into the frozen soil, by first digging a trench with a pick, approximately 8 cm wide and then backfilling with the same soil after removing the rocks. Consequently, for a distance of approximately 4 cm next to the plate, the soil was free of living roots after installation. The configuration of the experimental manipulations and root observation devices is illustrated in Figure 12.

Different subplots were disturbed either on 12 April 1985 (Time 1), or on 6 May 1985 (Time 2). (The snow had melted by March 31.) The central plant was removed and a 0.08-m^3 volume of soil was excavated. Roots against the glass plates were then traced and their total length against the plates was determined (Newman 1966, Tennant 1975). The plates were then removed and the soil was replaced at similar depths and densities from which it was removed. Soil settlement was minimal. Minirhizotrons (Richards 1984), 38 mm in diameter and 0.5 m in length, were installed in a row of three and inclined 30 degrees from normal to the surface (Fig. 12). (Vertical tubes tend to result in roots growing down along the tube-soil interface which causes an overestimation of root length at deeper depths; Bragg et al. 1983.)

On 23 April, 25 ml of orthophosphoric-^{32}P acid (carrier-free in 0.02 N HCl) were injected with a syringe into each of 10, 0.30-m deep holes spaced 25 mm apart so as to form a plane of isotope solution. Each plane had a total of 18.5 MBq (500 μCi), injected at 74 kBq ml^{-1}. Two planes of ^{32}P were injected, 0.35 m on either side of center of the removed plant (Fig. 12).

Approximately every 10 d, six to ten tillers were harvested from the two plants directly adjacent to the injection plane in each subplot. Tillers closest to the injection planes, tillers in the middle of the tussock, and tillers on the side of the tussock remote to the injection plane were harvested so as to obtain an average amount for the entire tussock. Tillers were dried at 70 °C, weighed, and ashed at 500 °C in borosilicate vials. The ash was then suspended in 6 N HCl and brought to dryness twice and then resuspended in 0.1 N HCl. An aliquot was then placed in scintillation cocktail and counted. Counts were corrected for decay, quench, and counting efficiency and then expressed as original Bq of activity.

After nearly a month, we still found only very low levels of radiophosphorus in individual tillers (on the average, less than 0.5 counts s^{-1} g^{-1} tiller above background). Most tillers had no detectable activity. Therefore, we reinjected subplots of Time 1 with ^{32}P on 23 May.

Aboveground foliage of all nine plants that surrounded the

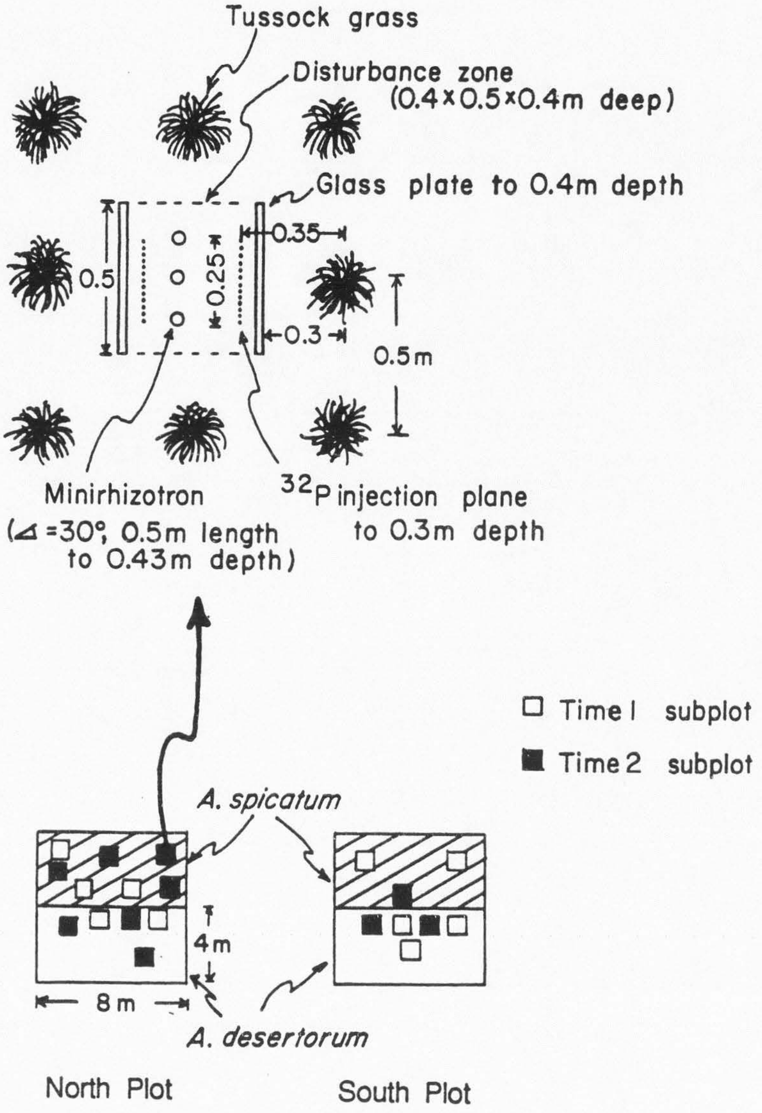

Fig. 12. Design of Timing Experiment. Bottom: Scaled diagram of replicated monocultures of *Agropyron spicatum* and *A. desertorum* with locations of Time-1 and Time-2 subplots indicated. Top: Scaled diagram of a subplot, which included nine tussock grasses of either *A. desertorum* or *A. spicatum* in a 0.5-m spacing. The center plant and associated soil (as defined by disturbance zone) were removed on either 12 April, 1985 (Time-1 subplots, 13 d after the snow melted) or 6 May, 1985 (Time-2 subplots, 37 d after the snow melted). Roots growing against glass plates were then traced, the plates were removed, the soil was replaced, and the minirhizotron glass tubes were installed. ^{32}Phosphorus was then injected as liquid planes (see text for details).

disturbance area (Fig. 12) was harvested on 13 June, and oven-dried biomass was determined. Since ^{32}P is an energetic beta emitter, radioactive plants could be readily determined by a Geiger-Muller (G-M) surface scanner. Tillers of each radioactive plant were cut into fine pieces, mixed, and total ^{32}P activity in aboveground foliage was determined. Entire crown tissue and roots in the upper 50 mm of soil were also harvested from the radioactive plants. These were dried, weighed, and ashed in their entirety. Preparation was the same as for the aboveground tissues, except the acidified ash was decolorized using activated charcoal to reduce quenching.

On 30 May, Time-2 subplots were injected with two, 18.5-MBq planes of ^{32}P as previously described. The aboveground foliage of the nine plants surrounding the disturbance area was harvested on 20 June and analyzed for total radioactivity. Crowns were scanned with the G-M scanner and radioactivity calculated from a regression (after adjusting for decay) of G-M counts to actual radioactive emission developed from the Time-1 crowns ($r^2 = 0.63$, n=17).

Only three of the five Time-1 and Time-2 subplots were injected with P radioisotopes using the liquid injection technique. The other two subplots were labeled with gelatin capsules (Jacobs et al. 1970). This technique proved unsatisfactory in our highly buffered semiarid soils (Caldwell et al. 1985) because of very low P uptake, which was more than two orders of magnitude less than that obtained using the liquid injection technique. Analysis of P acquisition, therefore, only includes the liquid injection subplots.

Analysis of variance was used to test for differences between species and between times of disturbance (a subplot was randomly assigned to be disturbed either at Time 1 or Time 2). The basic model was:

$$Y = \text{plot} + \text{species} + \text{time} + (\text{species} \times \text{time}) + \text{error}$$

with 3 degrees of freedom (df) for estimation of error. The model was simplified (thereby increasing the df for estimating error) when the plot or interaction term explained very little of the total variance ($\underline{P}>0.40$). A square root transformation was required for the phosphorus data to satisfy the assumption of equal variance among treatments. A repeated measures component was added to the model for the minirhizotron measurements using a Geisser-Greenhouse adjustment of degress of freedom to control correlation among measurements (Gurevitch and Chester 1986).

Results

Soils

Soil texture of the study plots was approximately 33% sand, 51% silt, and 17% clay to a depth of 0.4 m and relatively uniform throughout the study plots. Available P was less in the South Plot and decreased with depth in both plots (Table 3). Judging from the low concentrations measured, available P may have limited plant growth in these soils (e.g., Hays et al. 1982). Neither total soil N nor available P were different between the two grass monocultures in either the North or South Plots.

Soil temperatures were near 0 °C beneath the snow in March. After

Table 3. Nutrient content of air-dried soil from replicated monoculture plots of _Agropyron desertorum_ and _Agrypyron spicatum_.

	Available P[a]		Total N[b]	
Soil Depth (m)	0 - 0.2	0.2 - 0.4	0 - 0.2	0.2 - 0.4
North Plot				
A. desertorum	5.2	3.8	0.93	0.90
A. spicatum	6.0	3.9	0.85	0.85
South Plot				
A. desertorum	3.0	1.7	0.93	0.83
A. spicatum	3.8	1.9	0.95	0.80
LSD (0.10)	1.5	0.8	0.17	0.09

[a] 0.5 M $NaHCO_3$ extractable P (Olsen's P) ($\mu g\ g^{-1}$)
[b] Kjeldahl N ($mg\ g^{-1}$)

the snow melted, the soil tended to warm rather quickly near the surface but took considerably longer to warm at greater depths. A week before the Time-1 disturbance, soil temperatures were approximately 5°C at 0.4-m depth and ranged from 3 to 12°C at 0.1 m. On the day the Time 1 disturbance was initiated, soil temperatures at 0.1 m had reached daily maxima between 18 and 22 C. At 0.4 m however, soil temperatures were generally below 10 to 12°C until the end of April. Soil temperatures at the initiation of the Time-2 disturbance were above 15°C to a depth of 40 cm; temperatures at which the two grasses have been shown to have similar growth responses in greenhouse experiments (Chapter III).

Root growth

Root growth over winter and during the 13 d after the snow melted (Time 1) was estimated by tracing roots that had grown against the glass plates. _Agropyron desertorum_ had nearly 3.4 times the root

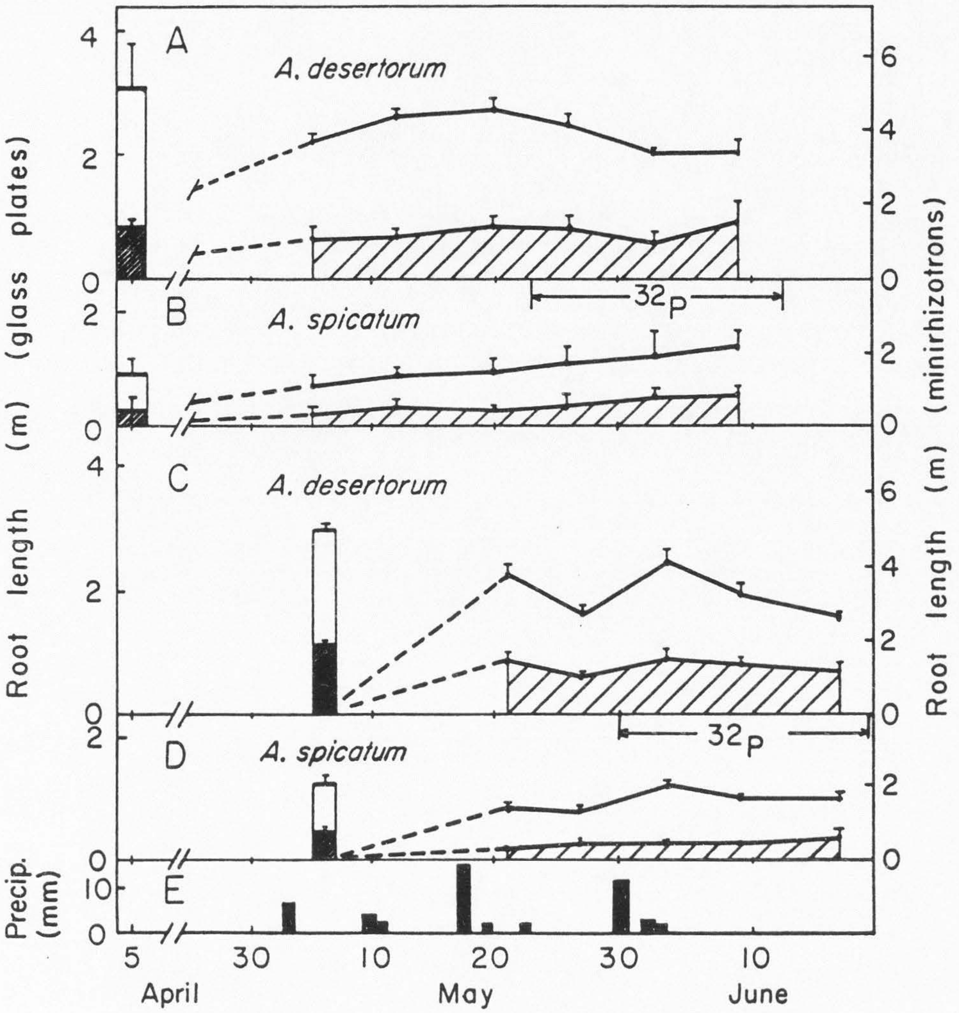

Fig. 13. Mean root length against glass plates (bar graphs) of Agropyron desertorum and A. spicatum subplots (averaged for the two monocultures; + S.E.=standard error) just prior to disturbance at 13 d after the snow melted (A and B; Time-1 subplots) and 37 d after the snow melted (C and D; Time-2 subplots). Hatched portion of bar represents root length at 0.2-to-0.4-m depth; open portion of bar represents root length at 0.0-to-0.2-m depth. Mean root length of A. desertorum and A. spicatum subplots (averaged for the two monocultures; + S.E.) against minirhizotron glass tubes measured nondestructively through May and early June, 1985 at 0.22 to 0.43-m depth (hatched portion) and 0.0- to-0.22-m depth (open portion). Slopes of dashed lines represent approximate rate of growth from time of disturbance (at which time there were no roots) to the time of first measurement. Both glass plate and minirhizotron data are presented as root length m^{-2} of glass. Note break of time axis in April. Precipitation on site (E) and period of ^{32}P acquisition are also noted.

length of by *A. spicatum* against the glass at this time as represented by the bars in Figs. 13A and 13B ($P<0.01$). After the plates were removed and the soil replaced, the length of roots which grew into the disturbed zone as determined by the minirhizotrons was also considerably greater for *A. desertorum* than for *A. spicatum* ($P<0.01$). When disturbance occurred in early May (Time 2), root growth into the released soil space was much more rapid (Figs. 13C and 13D). *Agropyron desertorum* also had considerably greater root length than *A. spicatum*, both prior to disturbance (glass plate data, 2.2-fold greater than *A. spicatum*) and in the disturbed soil volume (minirhizotron data).

Root growth of *A. desertorum* exhibited somewhat more fluctuation through time than root growth of *A. spicatum* in the shallower layers. *Agropyron desertorum* also showed a greater proportional increase in root growth in the deeper (0.22 - 0.43 m) soil layers earlier in the growing season (Fig 13). When the soil disturbance occurred early in the spring (Time 1), root length of *A. desertorum* in the shallow soil layers reached a maximum by about 20 May and then subsequently declined. Root length in the deeper soil layers remained more or less constant. *Agropyron spicatum* on the other hand, exhibited a steady increase in root length at both depths throughout the measurement period. For the Time-2 disturbance, root growth was apparently enhanced by the rainfall at the end of May and in early June, but the increases were greater for *A. desertorum* than for *A. spicatum*. (The probability that the two grasses had different seasonal patterns of root growth by chance was 0.006 and 0.06 for the 0-to-0.22-m and 0.22-

to-0.43-m depths, respectively.)

The percentage of total root length in the deeper soil layers for the two grass species is illustrated in Fig. 14. In order to contrast different periods of root growth activity, the minirhizotron data only include the first three measurements of Time 1, when the soil was quite moist and root length was increasing for both species, and the last three measurements of Time 2 when root length of both species was declining. The percentage of total root length that was in the deeper soil layers tended to be fairly constant for A. spicatum for either

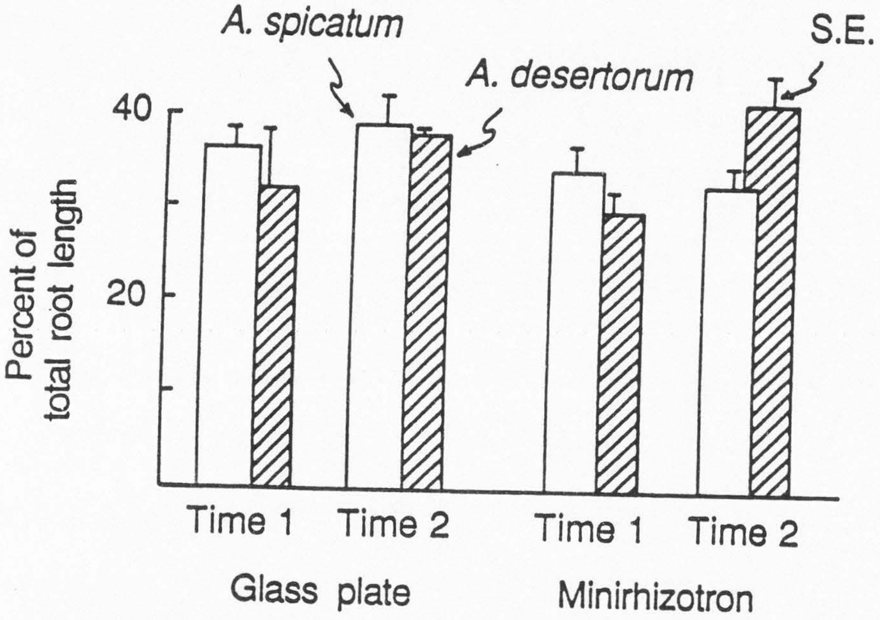

Fig. 14. Percentage of total root length in the deeper soil layers (0.2 to 0.4 m for glass plates and 0.22 to 0.43 m for minirhizotrons) for Agropyron spicatum and A. desertorum subplots (averaged for the two monocultures). For minirhizotron data, Time 1 represents the period when both grasses had increasing total root length (first three measurements) and Time 2 represents the period when both grasses had decreasing root length (last three measurements, see Fig. 13). See text for statistical significance of various treatments.

the glass plate or minirhizotron measurements. *Agropyron desertorum*, however, had proportionately greater root length in the deeper (0.22 - 0.43 m) soil layers for Time 2 than Time 1 for the minirhizotron data (species x time interaction: glass plate, *P*=0.66; minirhizotron, *P*=0.04).

Soil water extraction patterns reflected the greater proportional root growth of *A. desertorum* compared to *A. spicatum* in the lower soil depths in June. Soil water content in the *A. desertorum* plots at the 0.2-to-0.4-m depth on 10 and 17 June was slightly lower than in the *A. spicatum* plots. Since the soil was quite dry, the differences in soil

Table 4. Gravimetric soil water content (θ_m) at two soil depths in Time-1 subplots (sampled 10 June) and Time-2 subplots(sampled 17 June) (soil bulk density = 1600 kg m^{-3}). Means represent average of North and South monoculture Plots (see Fig. 12; standard error in parenthesis). The South Plots tended to be drier than the North Plots. Significance of factors in the analysis of variance model are noted (MSE=mean square error; *P* = probability that observed difference occurred by chance).

		θm (%)			
		0 - 0.2m		0.2 - 0.4m	
Time 1					
A. desertorum		11.2	(0.5)	10.6	(0.7)
A. spicatum		11.0	(0.8)	11.4	(0.02)
Time 2					
A. desertorum		8.8	(1.3)	9.3	(0.3)
A. spicatum		9.9	(0.3)	10.2	(0.8)
	df	MSE	*P*	MSE	*P*
Species	1	0.52	0.47	1.34	0.07
Time	1	6.07	0.05	3.31	0.02
Plot	1	2.70	0.14	1.65	0.05
Error	4	0.82		0.21	

water potential were proportionately larger. A range of 8.8 to 11.4% in θ_m at this field site corresponds to differences in soil water potential at these soil water contents of approximately -3.0 to -0.5 MPa.

Agropyron desertorum roots consistently proliferated in the disturbance zone more rapidly than those of A. spicatum. Figure 15A illustrates the rate of root growth from the time of disturbance to the first minirhizotron measurement for each species at Time 1 and Time 2. At either time of disturbance, A. desertorum root extension rates were considerably greater than those of A. spicatum; the differences were more pronounced at Time 2 when the roots were

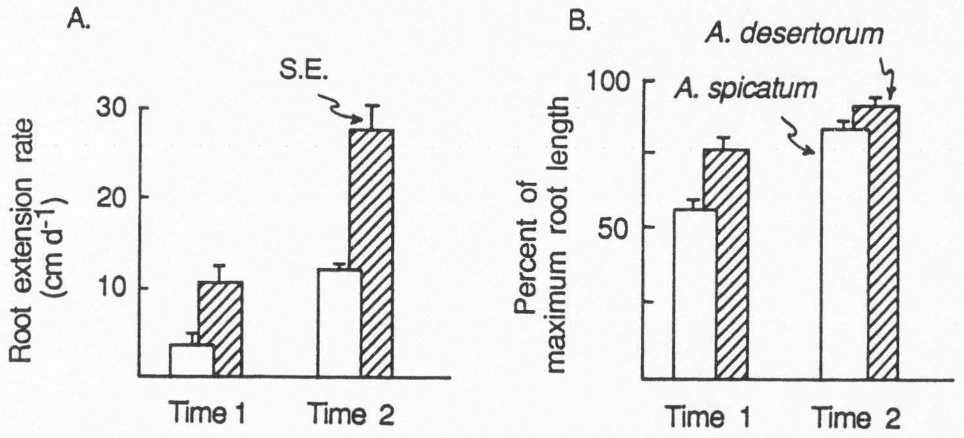

Fig. 15. The effect of time of disturbance on root extension rates of Agropyron desertorum and A. spicatum in subplots (averaged for the two monocultures). A. Rate of root extension from time of disturbance to the first minirhizotron measurement (35 d after disturbance) for Time 1 and for Time 2 (14 d after disturbance). (Root length data calculated m^{-2} of glass.) B. Percent of maximum root length achieved by the time of the first minirhizotron measurement for Time 1 and Time 2. See text for statistical significance of various treatments.

growing faster (species x time interaction: *P*=0.04). However, the proportional difference in root extension rates between the species was greater at Time 1 than at Time 2 (3.1- and 2.3-fold difference between the species at Time 1 and Time 2, respectively). If root length as observed with the minirhizotrons is expressed as a percentage of the maximum root length achieved during the measurement period in each subplot (Fig 15B), *A. desertorum* in either time period had a greater proportion of its maximum root length in the disturbance zone sooner than *A. spicatum* (species main effect: *P*=0.06). This difference was more apparent in Time 1 than in Time 2 (species x time interaction: *P*=0.17). (The maximum root length achieved during the measurement period for either species was very similar in Time 1 and Time 2, *P*>0.50.)

Phosphorus acquisition

Phosphorus acquisition by the grasses in the disturbed subplots was extremely variable. Figure 16 represents distributions of ^{32}P acquired by the final harvest among the nine plants surrounding the disturbance zone in a subplot. ^{32}Phosphorus acquisition was clearly not correlated with plant size. Plants in the corners tended to be less radioactive than plants directly adjacent to the injection planes. However, ^{32}P acquisition differed by orders of magnitude among individual tussocks whose shoots were equally distant from the injection planes.

Total P acquisition by the nine grasses surrounding the disturbance zone did not differ between species for Time 1 (Table 5). For Time 2, *A. desertorum* extracted more ^{32}P, but the variability was

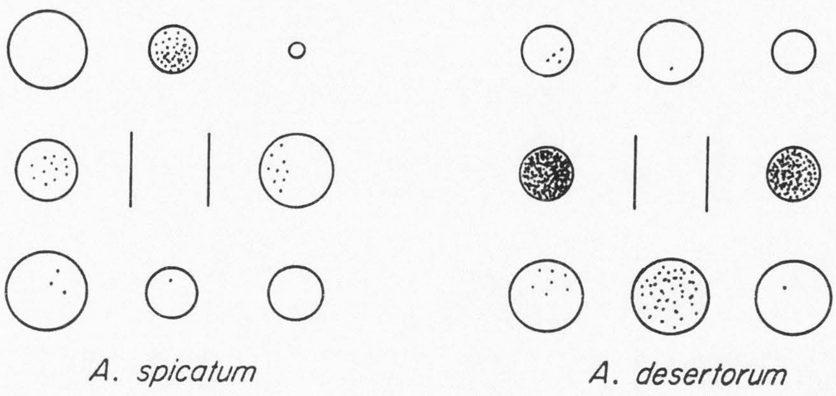

Fig. 16. Distribution of ^{32}P among tussocks in subplots of A. desertorum and A. spicatum. Each dot represents 1 kBq. The area of the circles are proportional to aboveground biomass of tussock. Lines indicate location of the ^{32}P injection plane.

Table 5. Total ^{32}P acquisition in aboveground biomass of the nine grasses in the 6 suplots (3 subplots per species) of Time 1 and of Time 2 (see Fig. 12). Data required a square root transformation to maintain homogeneity of variance. Retransformed means and 90% confidence intervals (LC = lower confidence limit, UC = upper confidence limit) are presented. Significance of factors used in analysis of variance are noted (MSE = mean square error; P = probability that observed difference occurred by chance).

	^{32}P in aboveground biomass (kBq)	
	Mean	(LC, UC)
Time 1		
A. desertorum	94	(17, 235)
A. spicatum	84	(12, 219)
Time 2		
A. desertorum	271	(118, 489)
A. spicatum	15	(0, 90)

	df	MSE	P
Species	1	5216	0.07
Time	1	63	0.80
Species x Time	1	4369	0.08
Error	4	838	

very large between monoculture plots, as indicated by the broad 90% confidence limits (Table 5). The differences in aboveground ^{32}P pools between the two species in either time period could not be related to differences in aboveground biomass of the nine plants surrounding the disturbance zone nor to differences in allocation of P to the crown tissue (Table 6).

The time course of ^{32}P uptake also indicated very little difference in rates of ^{32}P acquisition by the two grass species (Fig. 17A). (A time course of ^{32}P acquisition was only done for the Time-1

Table 6. Mean aboveground biomass of nine grasses in subplots of Time 1 and Time 2 (see Fig. 12) and proportion of ^{32}P in foliage relative to crowns. Means represent average of North and South monoculture Plots (Standard errors in parenthesis). (The South Plots tended to have lower biomass than the North Plots.) Significance of factors used in analysis of variance are noted (MSE = mean square error; *P* = Probability that observed difference occurred by chance).

	Aboveground biomass (g)		$\frac{\text{foliage } ^{32}P}{\text{crown } ^{32}P}$[a]	
Time 1				
A. desertorum	448	(56)	3.9	(0.1)
A. spicatum	633	(3)	4.1	(1.1)
Time 2				
A. desertorum	498	(17)	4.7	(1.5)
A. spicatum	571	(29)	2.9	(2.2)

	df	MSE	*P*	MSE	*P*
Species	1	70688	0.01	1.26	0.63
Time	1	166	0.81	0.09	0.89
Plot	1	11573	0.12	3.80	0.42
Species x Time	1	13103	0.11	2.13	0.53
Error	3	2380		4.36	

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[a] If a simplified model was used in analysis of variance, there would havebeen no effect on significance of Species or Time effects (see Methods).

disturbance.) These data were collected from the two tussocks on either side of the injection plane in each of the three subplots (Fig. 12 and 15). The first three sampling dates indicated that very little of the ^{32}P injected on 23 April (11 d after disturbance) was taken up by the plants. Generally, fewer than half of the plants sampled showed detectable activity despite their proximity to the injection plane. On one sampling date, A. desertorum appeared to have greater uptake than A. spicatum, but this was the result of single very radioactive tillers in two of the replicate plants. (Six tillers per plant were sampled.) On the following sampling date, when 10 tillers were sampled from each plant, mean radioactivity of A. desertorum plants was very similar to that of A. spicatum plants. By the time ^{32}P was injected a second time in the Time-1 subplots, a profuse root system had developed (Fig. 17B). In this case, ^{32}P uptake was rapid and most plants exhibited radioactivity. Within 20 d, average radioactivity per mass of plant tissue had increased three orders of magnitude. Surprisingly, there were still no differences in ^{32}P acquistion between the two grass species despite the large differences in root length of the two species in the disturbance zone.

Discussion

The two tussock grass species we studied exhibited large differences in their root growth during the winter and in the early spring when soil temperatures were cold, although the timing of shoot growth does not differ between these species (Chapter III). In this study, we examined the importance of timing of root growth and

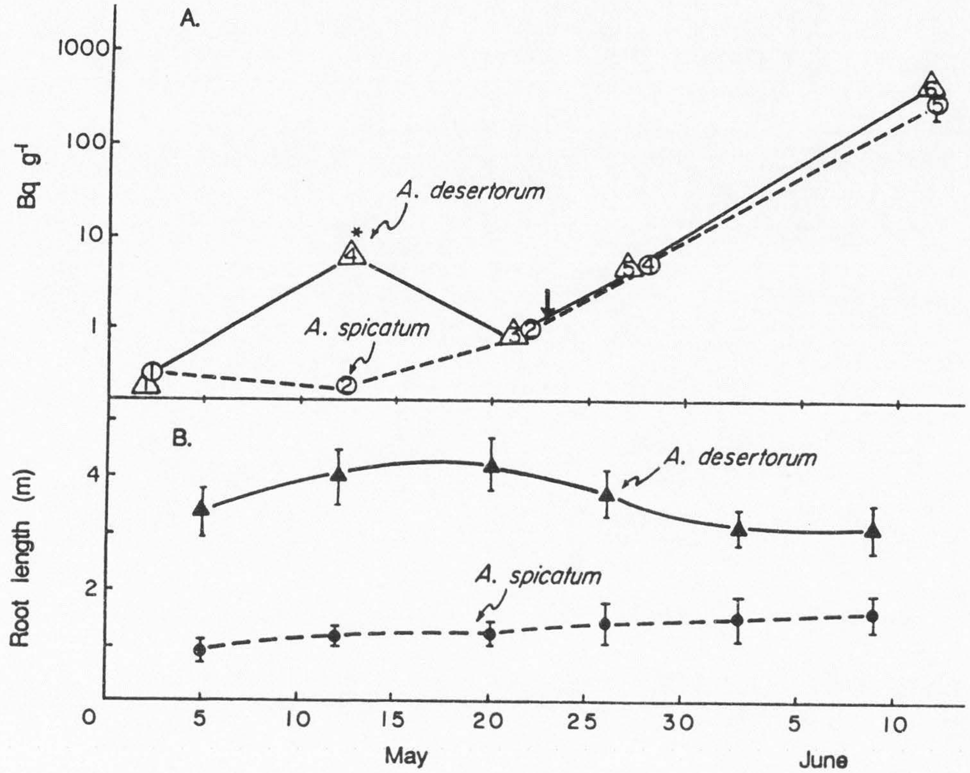

Fig 17. Time course of ^{32}P acquisition for Time-1 subplots. A. Average concentration of ^{32}P in tillers of *A. desertorum* and *A. spicatum* for tussocks adjacent to planes of ^{32}P injection (2 tussocks per subplot; see Fig. 16). Numbers inside symbols represent the number of tussocks (of the 6 sampled) with measurable radioactivity. The *A. desertorum* measurement denoted by an asterisk was the result of single very radioactive tillers in two of the replicate plants. Six to 10 tillers representing a cross-section of the tussock were used on the first four sampling dates. For the final harvest, all the tillers of a tussock were cut into small pieces, pooled, and subsampled. Heavy arrow indicates time of second ^{32}P injection for Time 1 (see text for details). Final measurement represents means and standard error (S.E.) (unless covered by symbol) for monocultures of each grass species (n=2). B. Mean root length (m^{-2} of glass) in the 0.0-to-0.30-m depth interval (same depth as for ^{32}P injection) in *A. desertorum* and *A. spicatum* subplots (averaged for the two monocultures; +/- S.E.).

resource acquisition, by removing single plants in uniform monoculture plots at two times, the first soon after the snow melted and the second when the soil was still moist, but considerably warmer. The ability to rapidly extend roots into available soil space and extract resources from that space is considered an important attribute of competitive ability for these semiarid grasses.

In our experiments, we used disturbance to create soil space unoccupied by roots. However, the soil already occupied by perennial plant roots is continually reexplored as roots senesce and new roots grow (Caldwell 1976). A large proportion of the root system of plants turn over each year (Caldwell 1986); thus, even without disturbance, soil space is continually becoming unoccupied. Plants with actively growing roots which can explore and occupy this space before their neighbors should be at a competitive advantage.

Root growth

The timing of invasion of the new space differed markedly between the two grasses. At either time of disturbance, *A. desertorum* had much greater extension rates into the zone of disturbance compared to *A. spicatum*. This is in part due to the greater rooting density of *A. desertorum*. *Agropyron desertorum* has thinner roots and, thus, greater root length for the same investment in root biomass (Caldwell and Richards 1986). In addition, *A. desertorum* had developed a greater proportion of its root length in the disturbance zone earlier than *A. spicatum* (Fig. 15B).

Similar differences between the two grass species were found at this study site in rates of root invasion into small fertilized microsites (Chapter V). When liquid fertilizer was injected into the soil in the early spring near minirhizotrons, roots of A. desertorum began to proliferate in the favorable microsites without delay. Agropyron spicatum and also Artemisia tridentata, however, did not begin extensive root growth in either the fertilized or unfertilized soil until about two weeks later. When fertilized microsites were created in July, they were rapidly occupied by all three species in a similar fashion.

The glass plates and minirhizotrons provide only a relative measure of root length and not absolute root density in the soil (Böhm 1979). However, for a measure of relative root length in our experiments, we feel these techniques provided a valid comparison of these two species. Extensive destructive harvest of roots in sagebrush-grass mixtures in this area in July indicated that A. desertorum has approximately twice the rooting density of A. spicatum regardless of soil depth (Caldwell and Richards, unpubl.). Since both the minirhizotrons and the glass plates at Time 2 also showed about a two-fold greater root length for A. desertorum, we feel these approaches adequately represented the differences in root length of these two species.

Competition and neighborhood analysis

Many investigators have attempted to evaluate a neighboring plant's influence on a target plant by the neighbor's size, proximity, and the degree to which its roots can directly interact with a target plant without having to go around another neighbor (i.e., "angular dispersion", Mack and Harper 1977). For individual tussocks neighboring a removed plant in our study, these attributes corresponded only weakly with the location of active roots as indicated by ^{32}P uptake (Fig. 16). Unfortunately, easily measured shoot attributes of a neighbor and a target species may still shed little light on the intensity of root interactions.

Phosphorous acquisition

Although the root length data clearly support the hypothesis that *A. desertorum* invades more rapidly into the newly available soil space early in the spring, this is not reflected in greater ^{32}P acquisition at Time 1. The results of Time 1 were surprising since *A. desertorum* not only has much greater root length than *A. spicatum* during this period (Fig. 17), but *A. desertorum* also has been found, at least in late summer, to have a greater number of mycorrhizal hyphal penetrations per unit root length with arbuscules, the transfer organ of the fungus (Caldwell et al. 1985).

The appearance of ^{32}P in the shoots of these grasses is a reflection of both shoot demand for P and the ability of the roots to supply P to meet shoot demand. ^{32}Phosphorus acquisition by the two grasses may have been similar for Time 1 because demand did not exceed the supply rate. Phosphorus, therefore, may not have been limiting plant growth at this time of year when the grasses were still in an early stage of shoot growth. Earlier studies (Mazurski unpubl.) indicated that early season P fertilization did not result in any observable effects either in tissue P concentrations nor increased biomass of either grass species.

The differential phosphorus acquisition by the two species in late spring (Time 2) probably was a result of larger plants creating greater shoot demand and restricted ^{32}P supply to the roots due to reduced soil moisture (Table 4). Soil moisture influences P availability in many diverse ways. Reduced soil water content directly reduces the rate at which P can diffuse to the root (Olsen et al. 1965). At reduced soil water contents, water depletion zones around the roots are more likely to develop. Low soil water content should affect P acquisition of *A. spicatum* more than of *A. desertorum*. Since *A. spicatum* has less root length, water uptake rates per unit length of root would be greater for this species than for *A. desertorum* for the same transpiration rate. Greater demand for water per unit root length would contribute to greater development of water depletion zones around individual roots (Passioura 1982). Greater water depletion zones, of course, would contribute to reduced P diffusion to *A. spicatum* roots. Further interactions between soil water content and nutrient acquisition are discussed by Nye and Tinker (1977).

Consequently, the greater root absorbing surface of *A. desertorum* may principally be an advantage for P acquisition later in the season when soil moisture is less abundant or under other conditions where plant demand exceeds the soil supply rate. Caldwell et al. (1985) showed directly that *A. desertorum* was more effective than *A. spicatum* in acquiring labeled P and limiting uptake of P by neighboring *Artemisia* later in the season on this study site.

Early season root growth may also contribute to more effective acquisition of P later in the season. A plant with earlier root development may restrict root growth of neighbors in soil abundant in P even before plant demand exceeds the supply rate. Depletion of resources other than P, such as water, would limit invasion of that soil volume by roots of neighbors. Therefore, each time the soil moisture is recharged, plants with roots occupying the most favorable soil volumes would acquire more P. Although difficult to demonstrate, exudation of toxic compounds is another way by which root exclusion may occur.

Water extraction

Differences in rate of root invasion of the two grass species into available soil space apparently contribute to differences in ability to extract water. The greater soil water extraction in June at 0.2-to-0.4-m depth (Table 4) corresponds with the earlier increase in the proportion of roots at these depths by *A. desertorum* (Fig. 14). In other undisturbed planted monocultures at this site, similar differences between these two species in rates of water extraction have also been demonstrated (Thorgeirsson and Richards 1983, Thorgeirsson 1985, Appendix). We also demonstrated these differences in soil moisture extraction rates for a rangeland site (Chapter II).

As with P, appreciable differences in water extraction between the two grass species may occur after the period of greatest difference in root extension rate. Very early in the spring, these grasses have similar rates of water extraction (Chapter II, Appendix).

However, as the spring progresses, plant demand quickly exceeds soil water supply.

Even though differences in resource extraction between *A. spicatum* and *A. desertorum* only become apparent later in the spring, early-season root growth is probably an important factor contributing to the greater competitive ability of *A. desertorum*. The head start provided by early root growth allows *A. desertorum* to have proportionately more root length in soil space richest in resources than species whose roots develop later (Fig. 15B; also see Chapter V) When plant demand for water begins to exceed supply (ca. mid-May for 1985), a greater rate of water extraction by *A. desertorum* compared to *A. spicatum* is likely to be a result of the earlier root growth as well as the finer root morphology of *A. desertorum*. Greater P acquisition by *A. desertorum* compared to *A. spicatum* in later spring may further enhance differences in water extraction potential (e.g., Radin and Eidenbock 1984). Therefore, preemption of the water resource by *A. desertorum* would disadvantage competing species such as *A. spicatum* or *A. tridentata*, whose root growth is somewhat delayed.

Conclusions

Early root growth initiation and rapid invasion of roots into newly available soil space is an attribute of *A. desertorum* which probably contributes to the greater competitive effectiveness of this species when compared with *A. spicatum*. However, this ability to rapidly occupy resource-rich soil space with roots did not cause immediate differences in water or P acquisition. The benefits of early root growth may be delayed until resources become more limiting which may not occur until later in the growing season.

CHAPTER V

CHARACTERISTICS OF SUCCESSFUL COMPETITORS: TIMING OF ROOT GROWTH IN FAVORABLE MICROSITES

Summary

Agropyron desertorum is more successful in competition with *Artemisia tridentata* ssp. *vaseyana* than is *Agropyron spicatum* (Chapter II). Root growth in favorable microsites was compared for *A. desertorum*, *A. spicatum*, and *Artemisia*. Favorable soil microsites were created by the injection of concentrated nutrient solution at two times, once soon after snow melt in mid-April, 1985 and the other in mid-July, 1984. For either time, all three species showed similar levels of enhanced root growth in the favorable microsites relative to unfertilized controls. However, since *A. desertorum* had more root growth in unfertilized soil early in the spring than the other two species, this competitively successful species occupied the favorable microsites created in early April weeks sooner than either *A. spicatum* or *Artemisia*. No such differences between species were found for the July fertilization. The consequences of early occupancy of favorable microsites on competition are discussed.

Introduction

The heterogeneous nature of soil is well known. Over short distances, a soil may vary considerably in nutrient and water availability, physical impedance, toxic ion concentration, and numerous other factors that affect plant growth and function.

Localized root growth in small soil volumes with favorable chemical and physical characteristics is well documented (Fitter and Hay 1981, St. John et al. 1983, Wang et al. 1986). Such responses are generally considered to be mechanisms by which plants compensate for the generally unfavorable conditions of the bulk soil (e.g., St. John et al. 1983).

Aggregations of roots in favorable microsites may limit use of those microsites by roots of plants that arrive later. Restriction may occur in the small soil volumes by temporary depletion of water, nutrients, or in some other way preempting resources important to neighboring plants (e.g., occupancy of soil channels, Wang et al. 1986). Thus, rapid occupancy of a limited number of favorable soil microsites may be an important attribute of a plant's ability to compete.

Studies on intrinsic differences among species in rates of root development in favorable microsites are scarce. In a split-root solution-culture experiment, Robinson and Rorison (1983) examined root growth of a low- and high-nutrient-adapted grass which also differ in their ability to compete (Grime 1979). A cultivated grass species was also included in the study. The high-nutrient-adapted grass had greater root growth rates than the low-nutrient-adapted grass in the uniformly available-N control; a result commonly reported in the literature (Chapin 1980). The high-nutrient-adapted grass also had greater root growth rates in the high-nutrient compartment of the split-root treatment than the low-nutrient-adapted species. However, the low- and high-nutrient-adapted grasses as well as the cultivated grass exhibited similar root growth enhancement in the high-N compartment of the split-root treatment relative to the uniformly available-N control.

In this study, we compare rates of root proliferation in favorable microsites of two *Agropyron* species and their frequent *Artemisia tridentata* ssp. *vaseyana* (Rydb.) Beetle neighbor. These two *Agropyron* tussock grasses differ strikingly in their ability to compete with *A. tridentata*. The grass of greater competitive ability, *Agropyron desertorum* (Fisch. ex Link) Schult., is introduced from Eurasia and widely planted in the Great Basin steppe of North America. *Agropyron spicatum* (Pursh) Scribn. and Smith, a native codominant with *A. tridentata*, has experienced a decline in abundance since the coming of European settlers, presumably due to excessive livestock grazing and fire suppression (Tisdale and Hironaka 1981).

Material and Methods

The study area is located on a site typical of semiarid North American Great Basin rangelands where *Agropyron spicatum* and *Artemisia tridentata* are native and where *Agropyron desertorum* has been extensively seeded. The study area has been previously described (Caldwell et al. 1981); thus, we will describe only the specific plots used to measure root growth. Root measurements in 1984 were made in two-species grass-shrub mixtures planted in a 0.5-m spacing in spring, 1979. Mixtures had a 50:50 ratio with each species surrounded on all four sides by plants of the other species. Although older roots of the shrub are readily distinguishable from roots of the two grass species (Richards 1984), very young roots of the shrub and grasses are very similar in appearance. Therefore, 1985 root measurements were made in plots containing all three species that had been transplanted in a 2-m spacing in order to minimize overlap of the root systems. Plants were transplanted June, 1983. Each individual was surrounded by two plants of the other species.

For both plots, medium-size tussocks of A. spicatum and seedlings approximately 2 yr old (<10 cm in height) of A. tridentata were collected from hillsides surrounding the study area. Similar-sized tussocks of A. desertorum were collected from a pasture sown approximately 30 years earlier, 200 km south of the study area.

For the 1984 experiment, glass tubes, 38 mm in diameter and 50 cm in length, were installed approximately 10 cm from the north edge of the tussock grass and inclined 30 degrees from normal to the soil surface. Glass tubes were installed in a similar manner in the plots used for the 1985 experiment, except additional tubes were placed 20 cm from the base of the Artemisia shrub. Glass tubes were installed in August, 1983 and March, 1985 for the 1984 and 1985 experiments, respectively.

Root length against the glass tubes was measured with a root periscope (Richards 1984). A collar that fixed the azimuth angle of the periscope to the glass tube was added to the instrument. The collar permitted us to count root intersections down the glass tube, which was more rapid than counting intersections circumferentially as described by Richards (1984). Since the azimuth angle as well as depth of individual roots were known, a map of root length against the glass tube could be produced (Fig. 19). Six passes in 60 degree intervals were made around each tube with root length mapped in 5-cm intervals (vertical depth = 4.3 cm) down the tube.

Liquid fertilizer was applied using plastic tubing (2-mm outside diameter) that was attached to the glass tubes at depths of 8.7 and 34.6 cm. Fifty ml of fertilizer were injected at each depth and then repeated 24 h later. In this way, drainage down the glass tube was minimized. Commercially available fertilizer was used to make the nutrient solution (49 mM NH_4-N, 59 mM $CO(N_2H_2)_2$-N, 42 mM P, 16 mM K) Fertilizer was injected 17 July 1984 and 22 April 1985 for the 1984 and the 1985 experiments, respectively.

The *A. desertorum* and *A. spicatum* plants used for the 1984 experiments were located in parallel rows in adjacent plots. Since plots were not replicated and the plants of the two species were not interspersed, species differences could not be analyzed statistically. Plants were randomly assigned to receive fertilization; thus, the effect of fertilization was replicated. Root length just prior to fertilization was used as a covariate to test for subsequent differences in root length between plots and between fertilized and unfertilized plants using a repeated-measures design.

The 1985 measurements of root growth were located in plots where all three species were interspersed. Thus, a completely randomized, repeated-measures design was used. The algorithm developed by Gurevitch and Chester (1986) was used to test for differences in shape of the root growth response curves. We used Robson's (1959) procedure to derive the orthogonal polynomials for the unequally-spaced sampling dates.

Results

Figure 18 provides a time course of root growth against the glass tubes in the 1984 and 1985 experiments. Since the data are plotted on a natural log scale, the slopes of the lines correspond to relative growth rates of the roots (m m^{-1} d^{-1}).

Agropyron desertorum had rapid root growth around the glass tubes in late April and early May (Fig. 18A). *Agropyron spicatum* and *Artemisia* on the other hand, did not initiate rapid root growth until the latter half of May (cubic or S-shaped pattern differed between species, P=0.01). Although fertilization clearly increased root growth (P=0.01), the increase in root growth relative to unfertilized controls was generally similar for the three species (fertilizer x species interaction: P>0.20). The enhanced relative growth rates of roots in April and May due to fertilization may have been the reason why growth rates for the fertilized plants diminished earlier in the growing season than growth rates for the unfertilized plants (quadratic or U-shaped pattern affected by fertilization, P=0.03).

There were no differences in root growth patterns in July and August in the *A. desertorum* and *A. spicatum* plots (P>0.20, Fig. 18B). Fertilization in July caused similar increases in root growth relative to the controls in the two plots (fertilizer effect: P<0.01).

For the glass tubes where fertilizer was injected, root growth

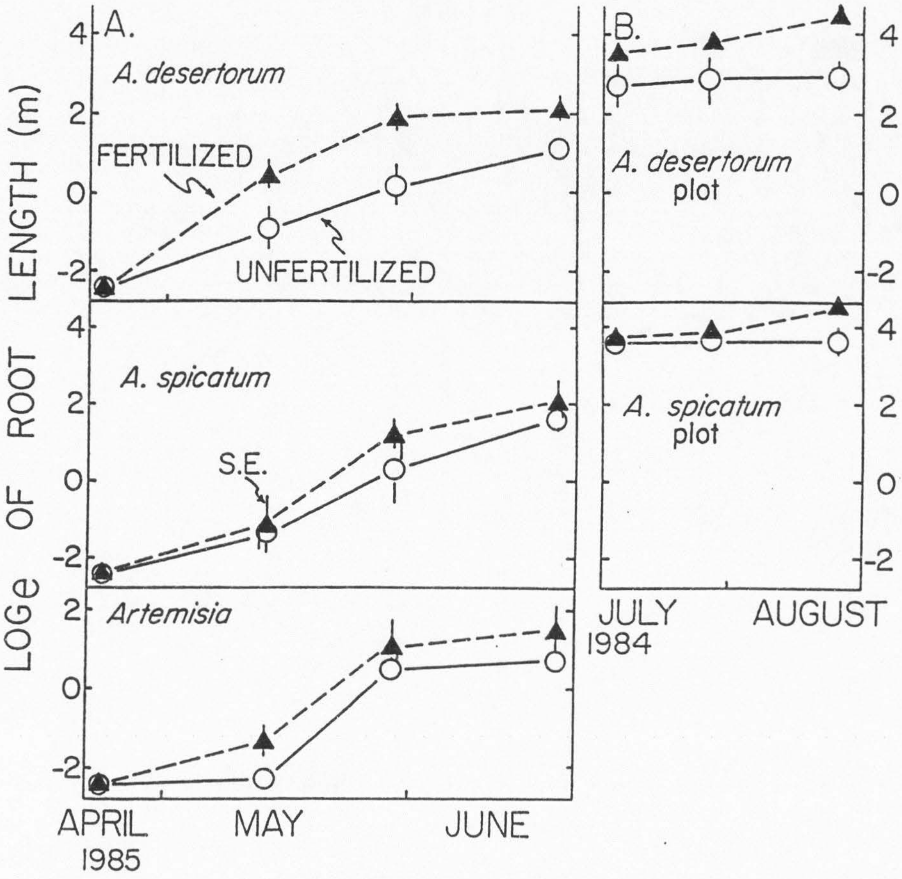

Fig. 18. Visible root length against glass tubes (m^{-2} of glass surface) from depths of 0 to 43 cm for fertilized and unfertilized plants. Fertilization achieved by injecting 50 ml of nutrient solution in the soil adjacent to the glass tube at depths of 8.7 and 34.6 cm and then reapplied 24 hr later. A. Agropyron desertorum, Agropyron spicatum, and Artemisia tridentata planted in a 2-m spacing in the same plot. Fertilization occurred 22 April 1985 after the first measurement (n=4 or 5; see text for statistical comparisons). B. Agropyron desertorum and A. spicatum, each planted with Artemisia in separate but adjacent plots in a uniform matrix in a 0.5-m spacing. Glass tubes were installed next to the tussock grass. Fertilization occurred 17 July 1984 after first measurement (n=2 for unfertilized, n=6 for fertilized; see text for statistical comparisons).

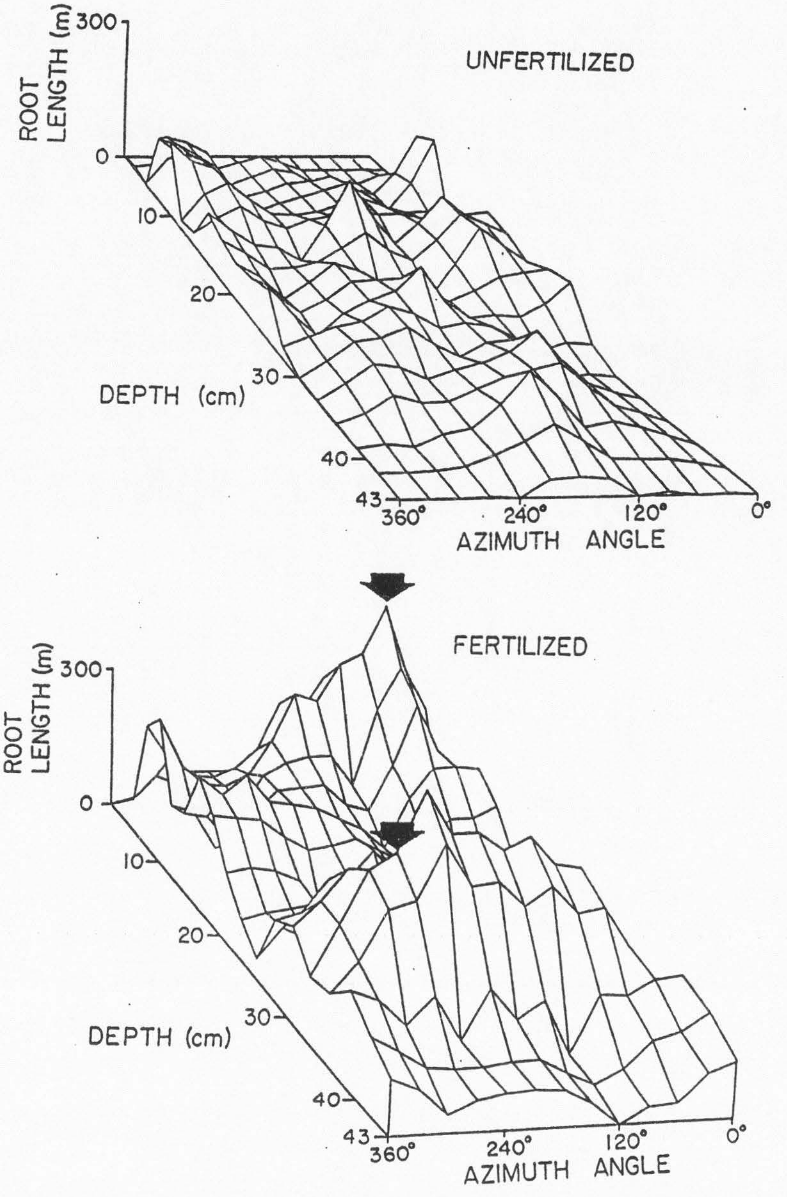

Fig. 19. Pattern of root length against glass tubes in the *A. desertorum* plot for a fertilized and a unfertilized plant 28 d after fertilization. The tubes chosen were representative of the general response to fertilization, which was also exhibited by *A. spicatum* and *Artemisia*. Fertilizer was injected 17 July 1984 at 8.7 and 34.6 cm (indicated by heavy arrows), at which time root length was nearly identical around the two tubes. The amount of root length is calculated for each 10 cm2 of glass surface area and is expressed as m of root length m-2 of surface area.

was primarily restricted to the microsites that received the liquid fertilizer (Fig. 19). Elsewhere on the tube, root length was comparable to root length on tubes where no fertilizer was applied.

Discussion

The ability of roots to proliferate in favorable microsites was vividly demonstrated by this experiment. Furthermore, absolute differences in early spring root growth of these species allowed *A. desertorum* to invade and occupy favorable microsites weeks earlier than either *A. spicatum* or *Artemisia*. However, despite the different root growth forms of the grasses compared to the shrub and the different competitive abilities of the two grasses, we found no differences among the three species in relative root response to fertilization (Fig. 18).

Evidence for earlier growth of *A. desertorum* compared to *A. spicatum* also has been illustrated under other environmental conditions. Under controlled, constant-cold soil temperatures, *A. desertorum* has greater aboveground relative growth rates than *A. spicatum*, even though the relative growth rates of the two species are very similar at warm soil temperatures. *Agropyron desertorum* has more root growth than *A. spicatum* during the winter and in the early spring (Chapter IV). Consequently, *A. desertorum* invades areas of soil disturbance more rapidly than *A. spicatum*, especially when disturbances occur early in the spring (Chapter IV).

Further evidence that once the soil warms, differences in root growth behavior between species diminish is provided by the 1984 experiment. These data indicated no differences in root growth pattern in July and August in the A. desertorum and A. spicatum plots. Although we could not tell if fine roots belonged to a tussock grass or to Artemisia, previous soil coring and root profile wall studies in similar plots (Caldwell and Richards unpubl.) suggest that roots this close to the tussock grass and at soil depths less than 50 cm should be primarily grass roots.

Our field experiments corroborate earlier work in solution culture (Robinson and Rorison 1983). The amount of root growth enhancement in fertilized microsites relative to growth in unfertilized soil may be quite similar for genetically and ecologically diverse species. However, absolute growth in these microsites may differ markedly among species, depending on the time of year and their genetic potential for rapid root growth.

Early occupancy of favorable microsites is probably an important way a plant can gain a competitive advantage over its neighbors. Available resources in favorable microsites normally should decline as occupants of the microsites use the resources for their growth processes. The reduced availability of resources would tend to restrict efficient root growth and resource acquisition of roots of species which arrive later.

The patterns of root growth of the species used in this study suggest that such competitive dominance of favorable early-season microsites likely occurs. By the end of May, total A. desertorum root length around the glass tubes where fertilizer was applied averaged nearly 7.4 m m^{-2} of glass surface (Fig. 18A). Root length of A.

spicatum and *Artemisia* at this time was only about 3 m m^{-2}. The lack of additional root growth by *A. desertorum* in June suggests that resources like water in the fertilized microsites no longer could sustain further root growth. The conditions that caused this lack of root growth in June for *A. desertorum* probably would also hamper root invasion of *A. spicatum* and *Artemisia* into the fertilized microsites occupied by *A. desertorum*. However, when these species did not have to compete with *A. desertorum*, their root growth in June was substantial (Fig. 18A, recall that data are plotted on a log scale).

In a greenhouse experiment, Fitter (1976) provides direct evidence that utilization of favorable microsites by *Lolium perenne* can be restricted by neighbors. He grew *Lolium perenne* in an experimental system containing a row of five compartments in which roots could grow freely into adjacent compartments. *Lolium* was planted in the second compartment. Root and shoot growth of *Lolium* was strongly enhanced if the third soil compartment was fertilized. However, if *Plantago lanceolata* was planted in the fourth compartment, root growth of *Lolium* in the fertilized third compartment was inhibited, and concomitantly, overall shoot and root production of *Lolium* was reduced. In conclusion, early occupancy of soil volumes most favorable for plant growth is probably an important factor contributing to the competitive success of *A. desertorum*.

CHAPTER VI

SYNTHESIS

Assessment of Competitive Ability

The major focus of this study was to identify plant characteristics that might account for the differences in competitive ability between *A. desertorum* and *A. spicatum*. However, the basis for this comparative analysis, i.e., that *A. desertorum* did indeed have greater competitive ability than *A. spicatum*, was a result of investigations in garden plots near Logan, Utah. In Chapter II, I described results from an indicator-plant approach conducted in a rangeland community that support the garden-plot evidence that *A. desertorum* is generally more competitive than *A. spicatum*. Assessment of competitive ability, however, is at best an inexact process. Several studies have indicated that a species that is more competitive than another species under one set of conditions may be less competitive if environmental conditions are changed (see Harper 1977). Conversely, other studies have indicated that a plant may be a superior competitor than a number of species under a range of conditions (e.g., Welbank 1963). In this section, I will briefly review the major techniques for determining the relative competitive ability of a species, discuss their strengths and weaknesses, and compare them with the indicator-plant approach chosen for this study.

Pot experiments

Pot and cultivated-garden approaches to the analysis of competitive ability have undergone intensive examination and review.

Probably the most common way competitive ability is determined is by the use of the substitutive or replacement-series design (de Wit 1960). This design involves comparing two species, i and j, at various proportions in mixture with total density kept constant. Competitive ability of the two species is usually compared by calculation of the relative crowding coefficient, k_{ij} (de Wit 1960):

$$k_{ij} = \frac{z_j y_{ij} / z_i y_{ji}}{y_{ii} / y_{jj}}$$

where y_{ij} and y_{ii} are the dry weight or number of seeds per pot of a strain i in mixed or pure stands, and z_i and z_j are the relative seed frequencies of strains i and j, respectively ($z_i + z_j = 1$). If species i has proportionately greater yield in mixture than in monoculture compared to species j, then k_{ij} will be greater than one. Although uncommon, a replacement-series design can be used in a natural community by removing individuals to achieve a desired density and frequency (e.g., Berendse 1983).

A diallel approach is very similar to a replacement-series approach except only a single frequency ($z_i = z_j = 0.5$) is used and the competitive ability involves calculation on a per plant basis. Commonly, the increment or decrement of the performance of strain i due to the effect of strain j, h_{ij}, is calculated using the natural logarithm of individual plant performance:

$$h_{ij} = \ln Y_{ij} - \ln Y_{ii}$$

where Y_{ij} is the average individual plant performance of strain i in association with strain j, and Y_{ii} is the average individual plant performance in monoculture (Sano et al. 1984). Similarly, the effect of species i on its associate, j, is given by $-h_{ji} = \ln Y_{jj} - \ln Y_{ji}$. The value of h_{ij} represents the "resistance" of i to the effects of j, and $-h_{ji}$, the "aggressiveness" of i on j. One can consider average "resistance" of target i measured in a diallel experiment as the mean effect of all species acting on the target plant (Wilson and Keddy 1986). A species with high resistance generally grows better with other species than with itself. The average "aggressiveness" of target plant, i, is a measure of the average response of different species when i is their neighbor. Commonly, a plant that is resistant to the effects of competitors is also quite aggressive, but not always (e.g., Sano et al. 1984).

The overall "competitive effect" in a diallel experiment represents the sum of the measures of resistance and aggressiveness $(h_{ij} - h_{ji})$. Sano et al. (1984) demonstrate that the competitive effect represents the natural log of the relative crowding coefficient, k_{ij}, when k_{ij} is calculated on a per plant basis.

An important benefit of the substitutive design, especially when analyzed with a diallel approach, is that the resistance component of competitive ability and the aggressiveness component can be analyzed separately. Furthermore, a diallel approach is often used to compare the relative competitive abilities of several species by planting the species in all pair-wise comparisons. Such an approach is not possible with designs that have numerous densities or frequencies for each pair-wise comparison. Apart from an analysis of competitive ability, another advantage of the substitutive design is its ability to provide information regarding the relative yield of mixtures vs. monocultures (i.e., relative yield total, see Harper 1977). However, there are also some major shortcomings of the substitutive design.

In recent years, the substitutive design has received criticism for its many theoretical and statistical pitfalls (e.g., Inouye and Schaffer 1981, Firbank and Watkinson 1985, Connolly 1986). One major problem is that density is held constant. Such a restriction is very artificial, since one of the important traits of competition is that density changes during the course of an experiment. Also, the density chosen is arbitrary. A number of studies have demonstrated that the relative competitive abilities of two species can be affected by a change in density (e.g., Bazzaz et al. 1982). Another problem of substitutive designs concerns the use of monoculture production as a baseline measure of species' performance. Species can differ in the intensity by which they compete intraspecifically. In addition, the intensity of intraspecific competition is density dependent (Jolliffe et al. 1984). Lastly, the statistics commonly calculated in substitutive designs (e.g., relative crowding coefficient) can be widely unstable (Connolly 1986).

A common alternative to the substitutive design is the additive design. Additive experiments involve planting individuals at different densities around a constant number of target individuals. Plots of target plant performance as a function of neighborhood density are then compared for different species of neighbor. Commonly, the target is an important crop species and the neighbors are specific densities of weedy species (e.g., Welbank 1963).

Earlier workers generally felt that competition experiments based on a substitutive design were easier to interpret than additive experiments, where density and frequency are typically confounded. However, more recent studies have demonstrated that two-species mixtures that change both density and frequency can be analyzed by simple mathematical models using a reciprocal equation (Watkinson 1985). For the two species condition,

$$Y_1 = Y_{m1}(1 + a_1(N_1 + b_{12}N_2))^{-c_1}$$

$$Y_2 = Y_{m2}(1 + a_2(N_2 + b_{21}N_1))^{-c_2}$$

where Y is the mean yield per plant of species 1 and species 2, Y_m is the yield with no density stress, 1/a is the density of plants at which mutual interference between individuals becomes appreciable, and -c describes the efficiency of resource utilization (Watkinson 1981). The competition coefficients, b_{12} and b_{21}, determine the equivalence between the two species. This "recent" theory, has brought plant competition models into agreement with other well known models, including the self-thinning rule (Yoda et al. 1963) and the Lotka-Volterra equations (see Watkinson 1985).

Designs which vary both frequency and density avoid many of the problems that are associated with the basic substitutive experiment. However, designs which do not hold density constant still have many problems. The number of species which can be effectively compared for differences in competitive ability is reduced because of the number of pots or plots required to examine the two species at a range of densities and frequencies. Systems which examine a range of frequencies and densities in a single planting may successfully circumvent this problem (Antonovics and Fowler 1985). However, serious statistical problems associated with these fan-type designs still need to be resolved.

Another problem with use of the negative reciprocal equation is the assumption that the competition coefficients, b_{12} and b_{21}, are constant. Competitive ability may be a function of many factors, including population density, plant age, and resource supply.

Lastly, a basic problem common to all the experimental designs discussed so far is the difficulty of extending the results to conditions that actually occur in nature. Various attempts to invoke more realism, such as placing pots outdoors or use of garden plots, reduce, but do not eliminate this problem. For instance, the greatest response of a target plant to changes in neighborhood density occurs at very low densities; densities which may be very uncommon for natural conditions (Chapter II, also see Harper 1977). Consequently, the parameters that define the reciprocal equations may be strongly influenced by very unnatural conditions and, therefore, may have little correspondence to potential differences in competitive ability commonly occurring in the field.

Natural communities

Few studies have attempted to contrast competitive ability of different species in natural communities. Generally, workers have restricted themselves to a simple assessment of the importance of competition relative to other environmental factors, such as resource supply, disturbance, and predation (del Moral 1983, Cook and Ratcliff 1985, Rabinowitz and Rapp 1985, Parker and Salzman 1985).

Fowler (1981, 1984) demonstrated the difficulty of analyzing competitive ability in the field. In a North Carolina grassland, she removed individuals singly or in groups and then measured the response of companion species. She found interactions among species to be generally nonreciprocal (i.e., removal of species i affected species j, but not the reverse). Often, competition appeared diffuse in that several neighboring plants were affecting an individual. Lastly, she detected no clear competitive dominant in these communities and felt that higher-order interactions may be present (e.g., a third species affects the intensity of competition between two other species).

Goldberg and Werner (1983) describe in detail a method for the assessment of competitive ability in the field, although a review of the literature has not revealed any published studies that have used their technique. The method utilizes an indicator plant or "phytometer" (sensu Clements and Goldsmith 1924) to measure the aggressiveness of neighbors. The influence of neighbors on the indicator plant is characterized using neighborhood models (e.g., Weiner 1982). Neighborhood models typically assign a single value to the overall influence of the neighborhood on the target individual by summing the separate effects of each neighbor. A neighbor's influence on the target individual is determined by various formulations of the neighbor's shoot biomass, distance from the target species, and ability to directly influence the target species without another neighbor interferring.

In the Goldberg-Werner experimental design, individual indicator plants are transplanted into stands dominated by a specific species of neighbor. All other species in the neighborhood are removed and the desired species of neighbor is then thinned to a specific density or degree of influence as determined by neighborhood analysis (simply referred to by Goldberg and Werner as neighborhood "amount"). By creating a range of neighborhoods, indicator-plant performance as a function of neighborhood amount can be calculated by regression. Slopes of the regression lines for various species of neighbor can then be compared for equivalence of competitive ability on the target species.

Despite the problems encountered in Fowler's work, the methodology described by Goldberg and Werner avoids many of the problems encountered in the designs ascribed to pot or garden experiments. For instance, they express competitive effects of neighbors on a "per-amount" or "per-unit biomass" basis, which relates much more to resource use, than a "per-individual" or "density" basis. This use of amounts also avoids the restrictions of even-aged populations with monocultures used as the base-line for competitive ability.

The methodology used in Chapter II was in many ways similar to the approach described by Goldberg and Werner (1983). The major differences were that I did not manipulate the amount or frequency of grasses in the plots and I did not use the slopes of the regression lines to contrast competitive ability of A. spicatum with A.

desertorum. Goldberg and Werner (1983) warn that if one does not artificially create a range of neighborhood amounts, microsite differences may be confounded with neighborhood effects. Since *A. desertorum* was seeded following sagebrush removal and was highly interspersed among the *A. spicatum*, it seemed unlikely that strong microsite differences were correlated with the distribution of the two grasses. I further tested for this possibility by examining the performance of indicator plants where all the grasses removed within 1 m of the indicator plant was either principally *A. desertorum* or principally *A. spicatum*.

Manipulation of neighborhood shoot amounts may cause unexpected changes below ground. For instance, the amount of decomposing roots and available soil space might only weakly reflect shoot manipulations. In Chapter IV, I demonstrated that available soil space created by the removal of a plant may be explored more rapidly by one grass species than another. Thus, thinning shoots to a specific density may benefit individuals of one species more than another, so that general competitive ability is confounded with the ability to respond to disturbance.

I chose not to assess competitive ability of the two bunchgrass species by contrasting slopes of the regression lines because of the poor correlation of amount of neighbor with indicator-plant performance at densities typical of field situations. Relatively high correlations with sharply negative slopes are not uncommon when neighbor amount is low. However, as the amount of neighbors increases, often the variance around the regression line increases and the slope approaches zero. These problems greatly complicate the use of a regression approach at naturally occurring neighborhood densities.

Fowler (1981, 1984) also found that the noise in a natural community may make modelling of neighborhood effects difficult. A neighborhood approach is probably better than a density approach but still may describe only a small amount of the variance in indicator-plant performance. Diffuse competition, higher-order interactions, variability of microsites and genotypes, and differences in transplantation shock among indicator species are just some of the reasons why the poor correlations exist. An additional reason concerns the difficulty of predicting the influence of a neighbor's roots by the amount and location of its shoots (Chapter IV).

In this study, I used average indicator-plant response in natural neighborhoods of the two grass species to assess competitive ability. Nearly monospecific stands of the grasses permitted such an analysis. An important assumption of an indicator-plant approach is that the response of the indicator plant reflects general competitive ability. Harper (1977) and Newman (1983) discuss experiments where the ranking of competitive ability among species tends to be fairly constant for different indicator species. Whether this is true for the two species of Agropyron would require further study.

In summary, there is no measurement of competitive ability which does not have problems. Pot and garden methods provide more detailed information, but extrapolation to natural communities is tenuous.

Field methods may be unable to detect important differences in competitive ability in natural communities with so many uncontrolled factors possibly affecting the experiments. Although the methods I chose for this study worked remarkably well, they are poorly suited for more diverse communities.

Characterisitics of Successful Competitors

Competitive ability is a complex process and may be related to many traits. Often a trait associated with physiological vigor such as high photosynthetic rates of a plant would also provide for greater competitive ability. However, plants in a cold-winter, dry-summer steppe environment must also tolerate other selection pressures, including herbivory, drought, salinity, fire, and pathogens. Often selection for a general trait such as competitive ability involves a tradeoff in tolerance to some other stress (Grime 1977). A remarkable aspect of these two grass species is that compared to _A. spicatum_, _A. desertorum_ does not seem to have less tolerance of environmental extremes despite its great competitive ability.

Root length per unit root biomass

An obvious reason for the greater competitive ability of _A. desertorum_ compared to _A. spicatum_ is differences in their root morphology. _Agropyron desertorum_ obtains much more root length for a similar investment in root biomass (Caldwell and Richards 1986). This more efficient allocation of biomass for production of length and surface area has far-reaching implications in terms of rapid rates of exploration of unoccupied resource-rich soil and water and nutrient uptake when plant demand is high and soil supply rate is low (Chapter IV). Another possible advantage is that fine roots should grow faster through small pores because they encounter less resistance than coarse roots (Whiteley and Dexter 1983). However, this advantage may be offset by the ability of coarse roots to displace soil aggregates normally more easily than fine roots (Whiteley and Dexter 1984).

Amounts of mycorrhizal infection

In late summer, *Agropyron desertorum* had a greater number of hyphal penetrations per unit root length with arbuscules than *A. spicatum* (Caldwell et al. 1985). Mycorrhizae have been shown to enhance acquisition of several nutrients and also may aid in water uptake (Auge et al. 1986). However, the amount of root length infected by mycorrhizae can be influenced by many factors, including herbivory, soil aeration, and soil fertility (Mosse et al. 1981). Thus, the degree to which mycorrhizae benefit *A. desertorum* significantly more than *A. spicatum* during the growing season and under various environmental stresses is not clear.

Root growth at cold soil temperatures

This study provides strong evidence that part of the competitive success of *A. desertorum* compared to *A. spicatum* is due to its greater root growth at cold soil temperatures. This trait, as well as the traits mentioned above, allow *A. desertorum* to occupy resource-rich sites in the spring sooner than *A. spicatum*. Early occupancy provides future advantages in resource acquisition as discussed in Chapters IV and V.

Other traits

I did not find appreciable differences between the two grasses in potential growth rates or responsiveness of roots to fertilized microsites. The list of other traits that might potentially influence competitive ability is only limited by one's imagination. I emphasized traits that would allow a plant to rapidly occupy space because soil space must be reexplored each year and preemption of soil space is most clearly associated with belowground competition.

The main resource that limits growth in these systems is water. Rates of water extraction are influenced by the plant's potential transpiration rate and the ability of the roots to supply water to the shoot. Soil depletion rates in early spring did not appear to differ between species, but variability at this time of year was high and more data should be collected. Data on whole-bunch transpiration rates in early spring would also be useful. The greater leaf area of *A. desertorum* than *A. spicatum* early in the spring suggests it may have a higher transpiration rate and, thus, may use stored water more rapidly. Similar differences in leaf area of the two grasses in the fall may also cause differences in water extraction.

Later in the spring, potential rates of shoot transpiration exceed the rate that roots can supply the shoots with water. The ability of roots to supply water is a function of their length and surface area, their hydraulic conductivity, and their spatial distribution. The differences in root length have already been discussed. Proportionately, *A. desertorum* and *A. spicatum* have quite similar root distributions with soil depth (Caldwell and Richards

1986), although A. desertorum may have greater ability for continued root growth at low soil matric potentials (Thorgeirsson 1985). Almost no information exists on the root hydraulic conductivity of these two grass species and the various characteristics associated with it, including: percent suberization, root hair length and density, axial resistance, radial resistance, tendency to maintain good soil-root contact in dry soil, and resistance to xylem vessel cavitation. Consequently, more detailed information on the rates water can be absorbed per unit length of root would be of considerable interest in order to better understand the water-extraction capabilities of these two grasses.

Another direction which might lead to a better understanding of competitive ability is the development of a mechanistic water-uptake model of these two grass species and probably also Artemisia. The Bunchgrass Project has considerable root length data, water extraction data, and shoot demand data over the growing season. This information is essential for meaningful model development. With good soil and root hydraulic conductivity data, the beginnings of a mechanistic model should be attempted. A modelling approach would help focus efforts aimed at understanding processes of water extraction for perennial shrubs and grasses in steppe environments as well as efforts to identify plant characteristics associated with competitive ability.

An important question is whether the traits which confer competitive success for A. desertorum can be extended to other competitively successful species. Preliminary evidence suggest that shrubs may gain a competitive advantange in ways very different from grasses. *Artemisia*, for instance, is very competitive even though it has considerably less root length, rates of mycorrhizal infection, and early-season root growth than *A. desertorum*. The competitive success of *Artemisia* may be partly due to its high potential growth rate and large stature. *Artemisia* may also have the ability to produce allelopathic compounds. Clearly, more work on the relative competitive abilities within and between life forms needs to be conducted before generalizations can be made.

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APPENDIX

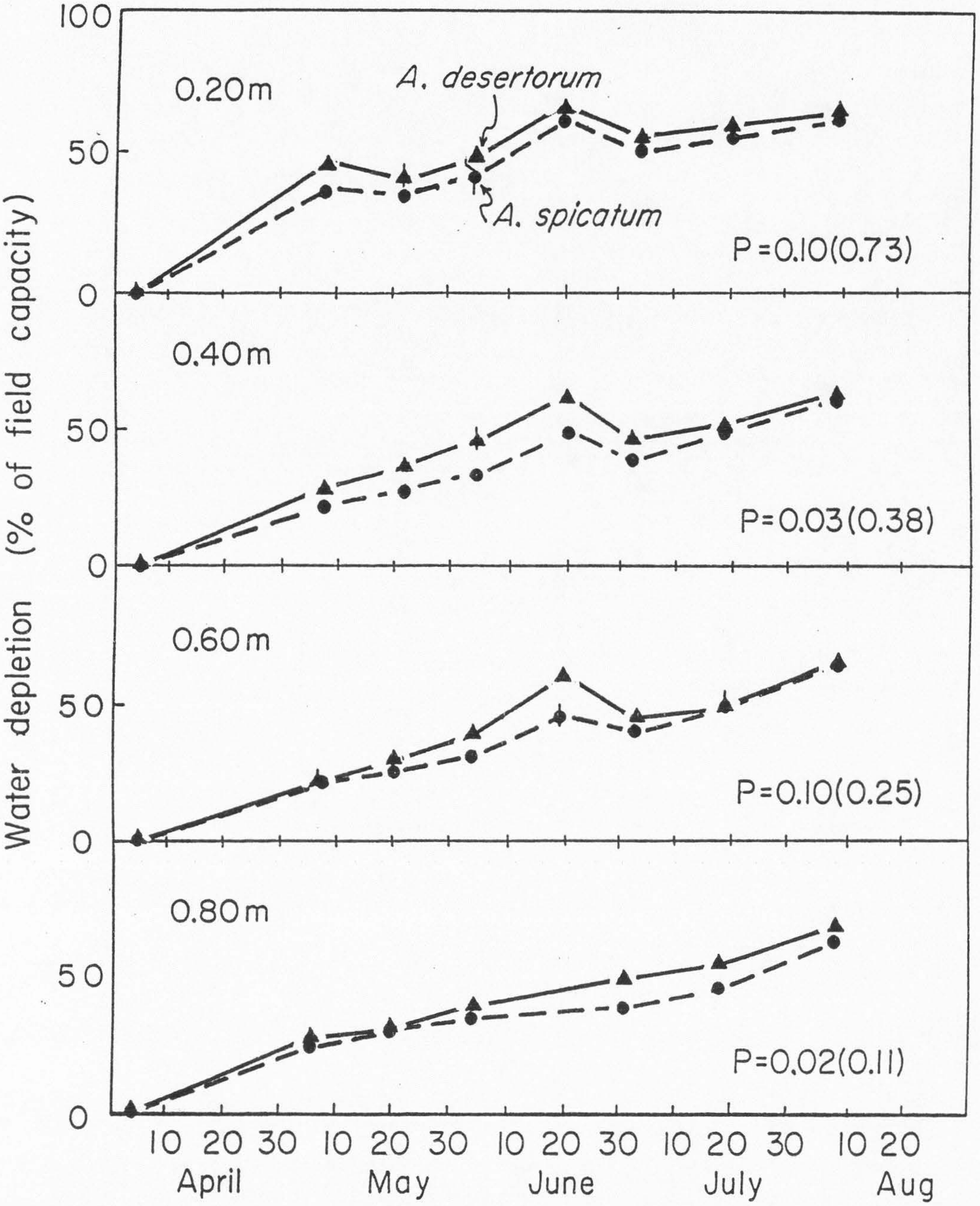

Fig. 20. Soil water depletion in 1985 in adjacent monocultures of *A. desertorum* and *A. spicatum* (established in 1978). Data are expressed as the percent of field capacity. The probability that the observed difference in water extraction occurred by chance, *P*, is indicated. (The *P*-value for the species x time interaction; i.e., that differences were greater between the two grasses on some sampling dates than on other sampling dates is shown in parenthesis.)

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