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## Characteristics of successful competitors: an evaluation of potential growth rate in two cold desert tussock grasses

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**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 of 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 had 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.

**Key words:** *Agropyron* – *Artemisia* – Relative growth rate – Competition – Tussock grass

*Agropyron spicatum* (Pursh) Scribn. and Smith<sup>1</sup>, 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* (Cald-

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

well and Richards 1986). The greatest difference in competitive ability of these two grasses was exhibited two years following transplanting (Eissenstat and Caldwell 1984). 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 h 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<sub>3</sub>, 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 ( $\pm 1$  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:

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

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<sub>3</sub><sup>-</sup> and 1.5 mM NH<sub>4</sub><sup>+</sup>). The moderate-N treatment was 10% of the high-N treatment (1.5 mM NO<sub>3</sub><sup>-</sup> and 0.15 mM NH<sub>4</sub><sup>+</sup>). 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 a normal complement 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. *inermis*, *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

**Table 1.** 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*

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

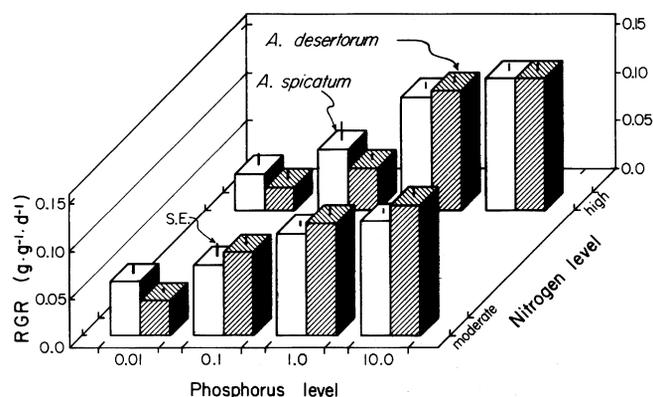
\*\*\* denotes significance at  $P < 0.001$ ; se = standard error of mean

*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 200 km south of the field site. Two plots were heavily fertilized with  $150 \text{ kg ha}^{-1} \text{N} - \text{NH}_4\text{NO}_3$  and  $50 \text{ kg ha}^{-1} \text{P} - \text{P}_2\text{O}_5$  in June and September, 1983 and April, 1984. Weeds were controlled with preemergent herbicide (dimethyl tetrachloroterephthalate) sprayed at  $8.4 \text{ kg active ingredient ha}^{-1}$  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 ( $\text{m}^2 \text{kg}^{-1}$ ) 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 tolerate transplanting well and many of the tillers in the bunches died



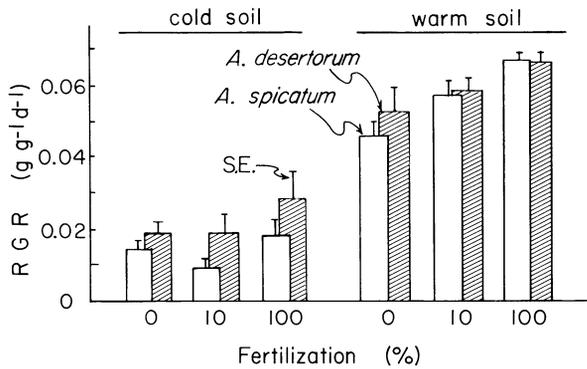
**Fig. 1.** Whole-plant mean relative growth rates between 49 and 56 d following germination for *A. desertorum* and *A. spicatum* plants grown in hydroponic culture ( $n = 3$  for each mean) at four levels of phosphorus and two levels of nitrogen. Phosphorus treatment significant at  $P < 0.001$  and  $P \times N$  interaction significant at  $P = 0.07$ . No significant differences between species ( $P > 0.20$ )

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.

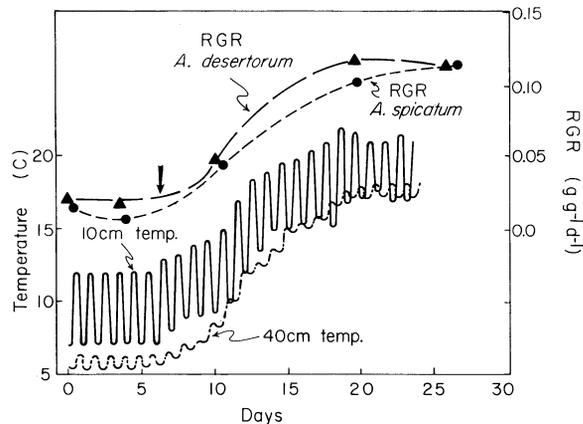
## Results

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 1). 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.

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

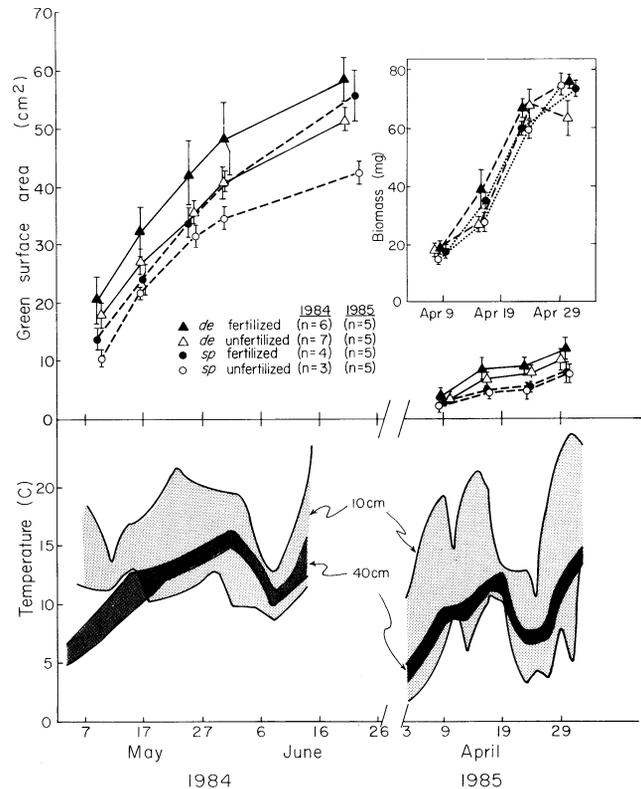


**Fig. 2.** Aboveground relative growth rates of *A. desertorum* and *A. spicatum* from 51 to 66d for the warm soil treatment (20 to 26°C;  $n=6$  to 7) and from 51 to 90 d for the cold temperature treatment (5 to 12°C;  $n=4$  to 6). Fertilization represents 0, 10 and 100% of modified Hoagland's solution (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. 3.** 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 4d). Relative growth rates of fertilized and unfertilized plants 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 ( $P>0.20$ )

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. 2). 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 ab-

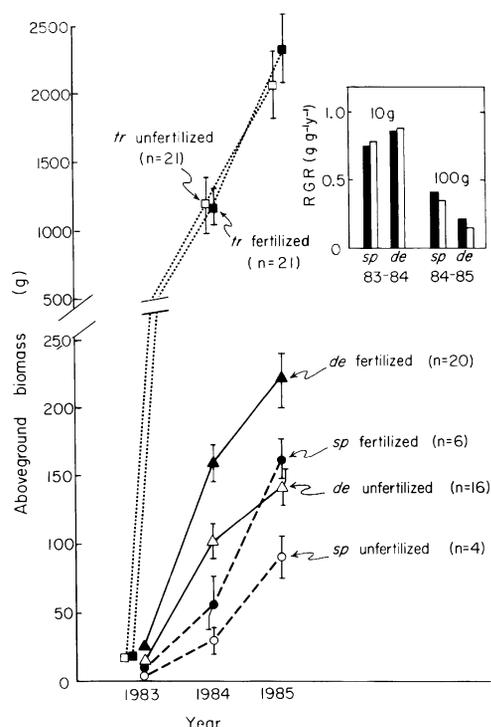


**Fig. 4.** Green surface area per tiller in 1984 and 1985 from *A. desertorum* (*de*) and *A. spicatum* (*sp*) planted in the field in a 2-m spacing and corresponding diurnal soil temperature range at 10- and 40-cm depths. Means of green surface area differed significantly between species until end 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  $\pm 1$  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 ( $P>0.20$ )

solute 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  $\text{mg d}^{-1}$ ) 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. 3). Neither species exhibited a 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. 4). Snow melted approximately 22 d be-



**Fig. 5.** 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 a symbol, represent  $\pm 1$  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 ( $P<0.001$ )

fore the first measurement in 1984 and 9 d before the first measurement in 1985. Soil temperatures beneath the snow were  $1^{\circ}\text{C}$  at 10 cm and  $2^{\circ}\text{C}$  at 40 cm in March, 1985. As would be expected, soil layers closer to the surface exhibited a much greater diurnal range (Fig. 4). 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  $12^{\circ}\text{C}$ , 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 those 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 tempera-

tures, *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 (Fig. 4, 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*, *A. spicatum*, and *A. desertorum* (Fig. 5). *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. 5). 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. 5 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, Küppers 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 estab-

lished plants, especially in early spring, that might place *A. desertorum* at some advantage 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* (Eissenstat and Caldwell unpublished work, Thorgeirsson and Richards 1983).

The growth rates of both grasses pale by comparison, however, when compared to the growth rates of *Artemisia tridentata* (Fig. 5). *Artemisia tridentata* is indeed an effective competitor 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. Similar 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 normally would be 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.

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