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The timing and degree of root proliferation in fertile-soil microsites for three cold-desert perennials

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Summary. Root proliferation in nutrient-rich soil patches is an important mechanism facilitating nutrient capture by plants. Although the phenomenon of root proliferation is well documented, the specific timing of this proliferation has not been investigated. We studied the timing and degree of root proliferation for three perennial species common to the Great Basin region of North America: a shrub, *Artemisia tridentata,* a native tussock grass, *Agropyron spicatum,* and an introduced tussock grass, *Agropyron desertorum.* One day after we applied nutrient solution to small soil patches, the mean relative growth rate of *Agropyron desertorum* roots in these soil patches was two to four times greater than for roots of the same plants in soil patches treated with distilled water. Most of the increased root growth came from thin, laterally branching roots within the patches. This rapid and striking root proliferation by *Agropyron desertorum* occurred in response to N-P-K enrichment as well as to P or N enrichment alone. A less competitive bunchgrass, *Agropyron spicatum,* showed no tendency to proliferate roots in enriched soil patches during these two-week experiments. The shrub *Artemisia tridentata* proliferated roots within one day of initial solution injection in the N-enrichment experiment, but root proliferation of this species was more gradual and less consistent in the N-P-K- and P-enrichment experiments, respectively. The ability of *Agropyron desertorum* to proliferate roots rapidly may partly explain both its general competitive success and its superior ability to exploit soil nutrients compared to *Agropyron spicatum* in Great Basin rangelands of North America.

Key words: *Agropyron* – *Artemisia* – Belowground competition – *Pseudoroegneria* – Root proliferation

Nutrient availability in the soil can vary considerably over distances of centimeters (Snaydon 1962). This patchiness in nutrient availability often arises from the localized decomposition of organic matter. In some environments, a significant portion of nutrient uptake by plants can come from temporary patches of nutrient-rich soil (Chapin 1980). Simulation models and sensitivity analyses have shown that in many soil conditions the root property most influencing nutrient uptake is total rooting density (Barber 1984), particularly for the uptake of relatively immobile nutrients like phosphorus (Nye and Tinker 1977). Thus, rapid root proliferation in nutrient-rich soil patches is likely an important mechanism of effective competition for soil nutrients by plants (Tilman 1988).

Numerous studies have demonstrated root proliferation in nutrient-rich environments. Some studies documenting this proliferation used seedlings of crop plants growing in nutrient solutions (Drew and Saker 1975, 1978). Crick and Grime (1987) grew plants in partitioned pots with compartments containing solutions of different nutrient concentrations; roots proliferated in the compartments with the stronger nutrient concentrations. Passioura and Wetselaar (1972) used plexiglass root boxes to show that wheat roots proliferated near banded nitrogen fertilizers. St. John et al. (1983) documented root proliferation in a Brazilian forest using root-bags buried in the soil.

Eissenstat and Caldwell (1988a) used a root periscope (Richards 1984) to observe root proliferation in the field after localized application of nutrient solution for three perennial species common to Great Basin rangelands of North America: a prominent shrub, *Artemisia tridentata* ssp. *vaseyana* (Rydb.) Beetle, a widespread native tussock grass, *Agropyron spicatum* (Pursh) Scribn. and Smith (syn: *Pseudoroegneria spicata* (Pursh) A. Löve ssp. *spicata* (Barkworth and Dewey 1985)), and an introduced Eurasian tussock grass, *Agropyron desertorum* (Fisch. ex Link) Schult. All three species had the ability to proliferate roots within one month of applying nutrient solution to soil patches. Previous research has shown *Agropyron desertorum* to be superior to *Agropyron spicatum* in extraction of soil water (Eissenstat and Caldwell 1988b) and in competition for soil phosphorus (Caldwell et al. 1985).

Although the phenomenon of root proliferation is well documented, the timing of the proliferation has not been investigated. In this study, we examined the timing and degree of root proliferation in enriched soil patches for *Artemisia tridentata, Agropyron spicatum,* and *Agropyron desertorum.* Different patches of soil in the pot of the same plant were treated with low- or high-strength nutrient solutions or distilled water and the roots in those patches were analyzed for differences in mean relative growth rates (RGR). The pattern of root growth was examined for two weeks following application of the solutions that created the patches.

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Materials and methods

This study was conducted with potted plants in the field at a site 4 km northeast of Logan, Utah (41°45′ N, 111°48′ W, 1460 m elev.). Further site description is in Caldwell et al. (1981). Three separate fertilization experiments were performed between June and October, 1988.

Individual plants of each species were transplanted from the field into 6.5-l, 40-cm-tall fiber pots. Four 5-cm square windows were cut in each pot; the top of each window was approximately 10 cm below the surface of the soil. The pots were lined with a transparent Mylar film, allowing root growth to be viewed through the resulting windows. A mixture of equal portions of soil, sand, and fritted clay was used as the growth medium; the same batch was used in all three experiments. The windowed pots were inserted into empty pots to exclude light from the soil patches. Moist sawdust was packed around the pots to maintain a cool soil temperature. The shoots of the plants were exposed to the natural field environment.

Treatments were 20 ml of a high-strength or low-strength nutrient solution or distilled water. To limit the size of the patches created, treatments were administered in 10-ml doses on two consecutive days. The solutions were applied by injection through the center of the Mylar windows using a syringe. Generally the visible area of a created patch was smaller than the 25-cm^2 window. Soil analyses of treated patches showed no evidence of cross-patch contamination. Each plant received all three treatments, but in different, randomly selected windows. One window in each pot was left unused. A window was disqualified from use if it had too few or too many roots apparent when an experiment began. Each experiment was performed on 8 to 10 plants per species and no plant was used for more than one experiment. Plants were well watered throughout the experiments.

The three experiments performed were N-P-K enrichment, P enrichment, and N enrichment. The high-strength N-P-K enrichment was a solution of 8.8 g Miracle-Gro fertilizer (Sterns, Port Washington, NY) per litre of distilled water, with 40 mM $NH_4H_2PO_4$, 25 mM CH_4N_2O, and 14 mM K_2O (plus trace elements). The high-strength P enrichment was an orthophosphoric acid solution (40 mM) with the same total amount of phosphorus as in the N-P-K experiment. The high-strength N enrichment was 45 mM NH_4NO_3, with the same total N as in the N-P-K experiment. The low-strength concentration for each experiment was half of the respective high-strength concentration. Distilled water was the control for the three experiments.

Measurements and analysis

Immediately following the first solution injections, the roots visible through the Mylar windows were mapped on grid transparencies to establish the length of roots apparent in each window prior to any proliferation. Subsequent root growth was traced on the same transparencies. The approximate timing of subsequent mapping was the first day after the initial 10-ml injection and then on days 2, 3, 4, 6, 10, and 14 of an experiment (the exact timing is in the figures). Care was taken to minimize the exposure of roots to light.

The number of intersections of roots with transparency grid lines was used to estimate root length for each window (Newman 1966; Tennant 1975). Root lengths were then converted to relative growth rates ($m \cdot m^{-1}\ day^{-1}$):

$$RGR = (\ln(L_2) - \ln(L_1))/(t_2 - t_1)$$

where L is the root length at either time 1 (t_1) or time 2 (t_2). The RGR values were analyzed by a repeated-measures technique (Gurevitch and Chester 1986) with time as the repeated-measure variable. Specific RGR values from different enrichment experiments were not compared directly because the experiments were performed at different times.

Results

Roots of *Agropyron desertorum* proliferated rapidly and consistently in fertile microsites during the N-P-K experiment. Within one day of the initial solution injection, roots of *A. desertorum* in enriched soil patches had a mean RGR almost four times greater than the mean RGR for roots of the same plants in soil patches treated with distilled water (Fig. 1). *Agropyron desertorum* roots in enriched patches

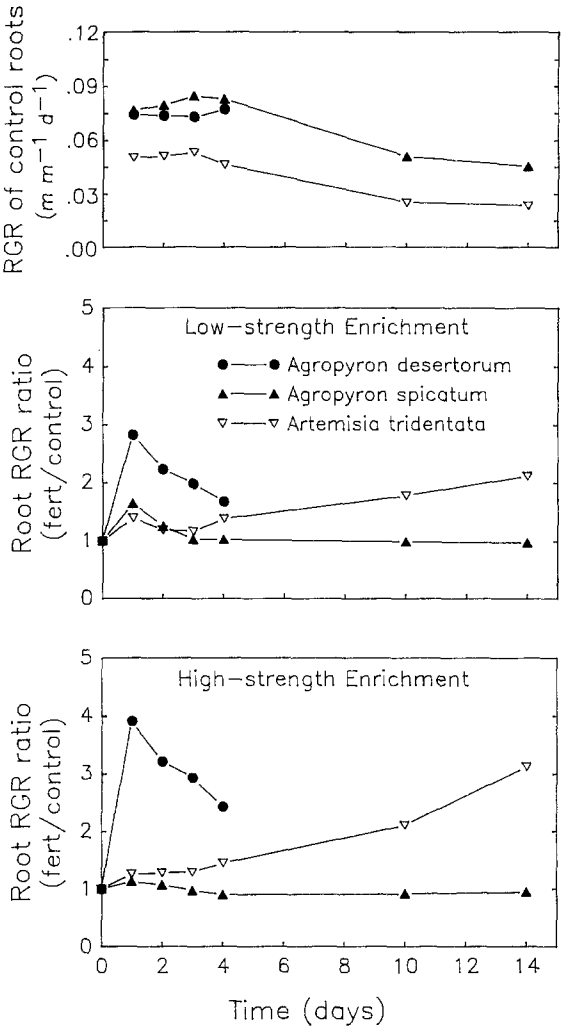

Fig. 1. Mean relative growth rates (RGR) of *Agropyron desertorum*, *Agropyron spicatum*, and *Artemisia tridentata* control roots (*upper graph*) and the ratios of mean RGR for roots in low-enrichment soil patches and control soil patches (*middle graph*) and high-enrichment soil patches and control soil patches (*lower graph*) for each species in the N-P-K-enrichment experiment ($n = 9$ plants per species). A root RGR ratio of 1.0 means that roots in the enriched patches grew no faster than roots of the same plants in control patches treated with distilled water. N-P-K enrichment occurred on day 0 and day 1

Table 1. Repeated-measures analysis of variance for relative growth rate data from the N-P-K-, P-, and N-enrichment experiments ($n=9$ plants per species for the N-P-K and N experiments; $n=8$ plants per species for the P experiment). The data were analyzed through day 4, day 14, and day 10 for the N-P-K, P, and N experiments respectively. The numbers in parentheses refer to the appropriate error-term number

Source	N-P-K experiment			P experiment			N experiment		
	DF	MS	Fcalc	DF	MS	Fcalc	DF	MS	Fcalc
Species (1)	2	0.264	20.6***	2	0.0390	1.05	2	0.128	14.6***
Error 1	24	0.0128		21	0.0372		24	0.00875	
Fertilizer (2)	2	0.0950	19.6***	2	0.0573	19.8***	1	0.207	23.0***
Spec × Fert (2)	4	0.0674	13.9***	4	0.0142	4.90**	2	0.0884	9.83***
Error 2	48	0.00485		42	0.00289		24	0.00900	
Date (3)	3	0.00996	16.5***	5	0.0489	27.3***	5	0.00534	12.2***
Error 3	24	0.000603		35	0.00179		40	0.000439	
Spec × Date (4)	6	0.00478	10.7***	10	0.00233	3.02**	10	0.000833	1.36
Fert × Date (4)	6	0.00316	7.11***	10	0.00452	5.87***	5	0.000180	0.293
Spec × Fert × Date (4)	12	0.00159	3.58***	20	0.00319	4.14***	10	0.000924	1.51
Error 4	192	0.000449		280	0.000771		200	0.000613	

*** Significant at $P<0.001$; ** significant at $P<0.01$

branched profusely and tended to be thinner than roots of this grass in unenriched patches. Roots of *Agropyron spicatum* did not proliferate in the enriched soil patches during the 2-week experiment. Fertilized roots of the shrub *Artemisia tridentata* proliferated considerably, but the response was more gradual than for *Agropyron desertorum*. Proliferated roots of *Artemisia* were highly branched and thinner than roots of this species in control patches. *Agropyron desertorum* and *Artemisia* roots in soil patches enriched with the low-strength solution also exhibited proliferation relative to roots in control patches. The timing of this proliferation was the same as in the high-strength patches but the magnitude was less. Control roots of both *Agropyron* species had similar mean RGR, but *Artemisia* control roots had a mean RGR approximately half that of the grasses (Fig. 1).

Because the fertilized *Agropyron desertorum* roots proliferated so rapidly in this first experiment, accurate mapping of roots for the species was no longer possible after the fourth day. Therefore, the N-P-K-enrichment RGR analysis in Table 1 is only for the initial four days of the experiment for all three species. Roots of *Agropyron spicatum* and *Artemisia* were mapped for 14 days.

Fertilized roots of *Agropyron desertorum* in the P- and N-enrichment experiments also proliferated within one day of the initial solution injection (Figs. 2, 3). Root proliferation of *A. desertorum* in the P-enrichment experiment slowed after 4 days whereas it persisted at about the same rate for at least 10 days in the N-enrichment experiment. Proliferation of *A. desertorum* roots in the low-strength patches of the P-enrichment experiment mirrored proliferation in the high-strength patches; the timing of the proliferation was similar but the magnitude was less. *Agropyron spicatum* exhibited no root proliferation in fertilized patches of any experiment. In contrast to the N-P-K experiment, *Artemisia* root proliferation in the P-enrichment experiment was minimal. In the N-enrichment experiment, however, fertilized *Artemisia* roots proliferated within one day of initial solution injection (Fig. 3) and continued to proliferate for the entire two-week experiment. The pattern of control-root RGR for all three species was similar for the P- and N-enrichment experiments, but the RGR of *Artemisia* control roots were generally less than for control roots of either tussock grass.

The analysis of the P-enrichment RGR data was for the entire two-week experiment (Table 1). Relative growth rates from the N-enrichment experiment were analyzed only through day 10 (Table 1); *Agropyron desertorum* roots in N-enriched patches proliferated so rapidly that accurate mapping of roots of this species was no longer possible after that time. Data from the low-enrichment patches of the N experiment were not included in the analysis because of inadequate sample size.

Discussion

This study revealed striking differences among the three species in their ability to proliferate roots rapidly in small patches of nutrient-enriched soil and this behavior was generally consistent in the three experiments. *Agropyron desertorum* proliferated roots rapidly in each experiment. Root proliferation of *Artemisia tridentata* was less consistent than that of *Agropyron desertorum*. *Agropyron spicatum* showed no ability to proliferate roots in these two-week experiments. If the experiments had been longer, however, some proliferation of *Agropyron spicatum* roots might have occurred. Eissenstat and Caldwell (1988a) showed that *A. spicatum* could proliferate roots within 3 to 4 weeks of soil enrichment, but there too the response was less pronounced than for *Agropyron desertorum*.

The most unexpected result of the experiments was the rapidity with which root proliferation occurred. An analysis of variance of the first-day data for fertilized and control *Agropyron desertorum* roots in the N-P-K experiment was highly significant ($P<0.0001$, Fisher's LSD test). Though a nonrepeated-measures analysis of the data is inappropriate, the magnitude of the one-day response is apparent.

Although the responses of the grass species were qualitatively the same in the single- and multiple-nutrient experiments, the *Artemisia* response was more variable among experiments. Part of the variability in *Artemisia* proliferation may have been caused by changes in environmental factors apart from the nutrients applied. For example, ambient temperatures were much lower during the N-enrich-

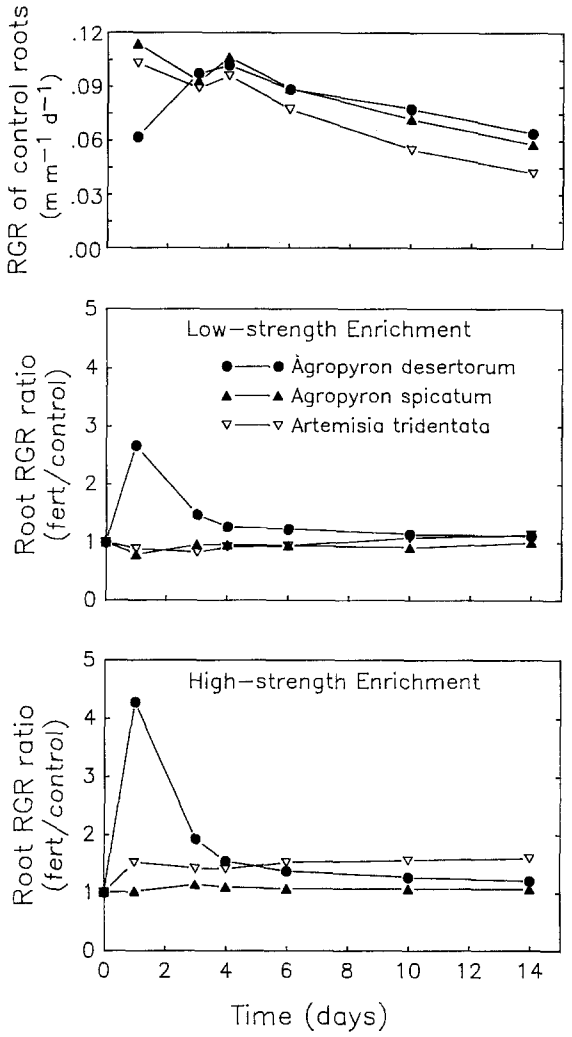

Fig. 2. Mean relative growth rates (RGR) of *Agropyron desertorum, Agropyron spicatum,* and *Artemisia tridentata* control roots (*upper graph*) and the ratios of mean RGR for roots in low-enrichment soil patches and control soil patches (*middle graph*) and high-enrichment soil patches and control soil patches (*lower graph*) for each species in the P-enrichment experiment ($n=8$ plants per species). A root RGR ratio of 1.0 means that roots in the enriched patches grew no faster than roots of the same plants in control patches treated with distilled water. Phosphorus enrichment occurred on day 0 and day 1

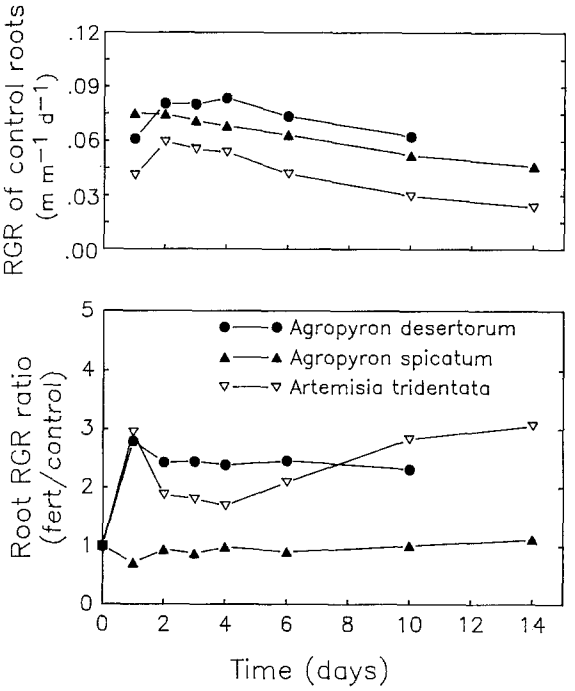

Fig. 3. Mean relative growth rates (RGR) of *Agropyron desertorum, Agropyron spicatum,* and *Artemisia tridentata* control roots (*upper graph*) and the ratio of mean RGR for roots in high-enrichment soil patches and control soil patches (*lower graph*) for each species in the N-enrichment experiment ($n=9$ plants per species). A root RGR ratio of 1.0 means that roots in the enriched patches grew no faster than roots of the same plants in control patches treated with distilled water. Nitrogen enrichment occurred on day 0 and day 1

ment experiment than during either of the first two experiments.

Root proliferation in fertile-soil microsites is likely an important mechanism of effective competition for soil resources by plants. However, there are substantial costs associated with this morphological plasticity (Grime et al. 1986). Therefore, plants might be expected to regulate the degree of root proliferation in accordance with their demand for nutrients. If either the growth rate of the plant is slow or the nutrient status of the bulk soil is high, then root proliferation in fertile patches may be minimal. Duncan and Ohlrogge (1958) found that young corn plants proliferated roots after N-P or P enrichment but not after N enrichment. The *Artemisia* roots in our study proliferated after both N-P-K and N enrichment but only slightly in the P-enriched soil. The lack of proliferation may be understandable if growth of the plants was not being limited by the nutrient supplied in the fertile patch. Although such experiments suggest some regulation of root proliferation, whether or not plants do regulate the degree of root proliferation according to their nutrient demand is still an open question.

Our study also suggests that plants may modulate the degree of root proliferation depending on the concentration of nutrients available in an enriched soil patch. Root proliferation in the soil patches treated with low-strength solutions was apparent at the same time, but with a lesser magnitude, as root proliferation in the high-strength patches. The degree of proliferation was approximately proportional to the degree of enrichment; root proliferation in low-strength patches was roughly half the magnitude of proliferation in the high-strength patches.

The exploitation of a nutrient-rich soil patch by roots involves both encountering a patch and the uptake of the nutrients from the patch. In this study, roots were always present in the patches prior to nutrient enrichment. We, therefore, did not test whether the species differed in their likelihood of encountering a nutrient-rich soil patch. In nature, however, encountering a nutrient-rich patch is a necessary precursor to effective root proliferation. Caldwell and Richards (1986) showed that *Agropyron desertorum* and *Agropyron spicatum* plants in the field had similar root biomass per soil volume, but *A. desertorum* had up to 50% more root length per unit root biomass than *A. spicatum*. *Agropyron desertorum* had much thinner roots and a larger number of lateral roots. Thus *A. desertorum* roots would have a greater likelihood of encountering enriched soil patches. The greater general rooting density and superior ability to proliferate roots in enriched patches may be im-

portant characteristics of *A. desertorum* enabling it to encounter and exploit temporary patches of nutrient-rich soil more quickly than *A. spicatum*.

Plants in the field compete for soil resources by several potential mechanisms. Tilman (1982, 1988) has hypothesized that species compete for soil nutrients by depleting the nutrients in the bulk soil to levels inaccessible to other species. Alternatively, plants may compete for nutrients by preferentially exploiting nutrient-rich soil patches, without necessarily depleting nutrients of the bulk soil to a great degree. Patch exploitation may be particularly important when nutrients are dispersed very unevenly in the soil. Seasonal pulses in nutrient availability would also increase the importance of nutrient patchiness for belowground competition (Chapin 1980). Eissenstat and Caldwell (1987) grew *Agropyron desertorum* and *Agropyron spicatum* plants over a range of N and P solution concentrations and found little difference in relative growth responses of the two species to a range of nutrient concentrations. The average nutrient concentration of P and N may, therefore, be less important in determining differences in the competitive potential of these two species than their morphological flexibility in responding to enriched soil microsites.

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