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Root Exploitation of Fertile Soil Microsites

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ROOT EXPLOITATION OF FERTILE SOIL MICROSITES

by

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of the reqirements for the degree

of

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in

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Approved:

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ABSTRACT

Root Exploitation of Fertile Soil Microsites

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Root exploitation of enriched soil microsites was examined for the tussock grasses Agropyron desertorum and Agropyron spicatum and the shrub Artemisia tridentata. Two mechanisms of exploitation of the microsites were examined: root proliferation and changes in nutrient uptake capacity. One day after nutrient solution was applied to small soil patches, the mean relative growth rate of Agropyron desertorum roots in enriched patches was two to four times greater than for roots of the same plants in soil patches treated with distilled water. This rapid and striking root proliferation occurred in response to N-P-K enrichment as well as to P or N enrichment alone. Agropyron spicatum showed no tendency to proliferate roots in enriched soil patches during the 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 other experiments. The ability of

Agropyron desertorum to proliferate roots rapidly may partly explain its superior ability to exploit soil nutrients compared to Agropyron spicatum in Great Basin rangelands of North America.

Changes in nutrient uptake capacity in enriched soil patches were also studied for each species. Large and rapid changes in uptake capacity of plant roots from the field were observed after creation of nutrient-rich patches in the soil. Phosphate uptake of excised roots from enriched soil patches was as much as 80% greater than for roots of control patches treated with distilled water. These increases in uptake capacity took place within one week of patch treatment for all three species. A follow-up experiment showed increases within three days of patch treatment. These results showing rapid physiological plasticity in roots exploiting nutrient patches have important implications for nutrient acquisition and belowground competition among plants.

(38 pages)

CHAPTER I

OVERVIEW

The availability of mineral nutrients in the soil greatly influences plant abundance and productivity in many ecosystems. Soils are often characterized by the amount of nutrients that they contain and these characterizations are usually based on the average concentration of nutrients in the soil (e.g. Tilman 1988). While the bulk nutrient concentration is obviously important in explaining patterns of plant abundance and productivity, the occurrence and frequency of individual species at a given location may also be related to spatial and temporal patterns of nutrient availability at that location (Snaydon 1962; Chapin 1980).

The Great Basin ecosystem of the western United States contains a broad range of soil types and soil fertilities (West 1988). The sagebrush steppe of the northern portion of the Great Basin is dominated by sagebrush, Artemisia spp., and perennial tussock grasses (West 1988). Several studies have shown distinct spatial patterning in the availability of soil nutrients in this sagebrush steppe (Charley and West 1975, 1977; Doescher et al. 1984). Nitrogen and phosphorus concentrations were greater in soils beneath shrub canopies compared to shrub interspaces (Charley and West 1975; Doescher et al. 1984). Rates of nitrogen mineralization were also greater in soils under

shrub canopies (Charley and West 1977). Nitrogen and phosphorus abundance increased with decreasing depth in the soil (Charley and West 1975).

Patchiness in nutrient availability on a smaller scale than noted above can arise from such events as the localized decomposition of organic matter or soil disturbance by animals (Chapin 1980). Water also plays a role in the patchiness of nutrient availability (West 1988). Precipitation can increase the availability and mobility of soil nutrients and lead to a burst of microbial activity in the soil. In the Great Basin and many other ecosystems, there is a distinct water-induced seasonality to nutrient availability. All of these factors can lead to patchiness in the availability of mineral nutrients over both time and space.

Nutrient availability in some Great Basin soils can be poor and unpredictable, particularly the availability of soil phosphorus. Plants that grow in soils where nutrient availability is unpredictable are generally believed to have relatively low inherent growth rates, inflexible root-to-shoot ratios, low absorption rate capacity, and little morphological or physiological plasticity (Grime et al. 1986; Chapin 1988; Campbell and Grime 1989). Pulses of nutrients are believed to contribute a relatively large portion of the mineral nutrients absorbed by plants in nutrient-poor soils (Chapin 1988). Luxury consumption is also believed to be most important when nutrient

availability is unpredictable (Chapin 1980). Thus, patchiness in nutrient availability may be especially important for plants in Great Basin soils of low or unpredictable fertility.

Since patchiness in nutrient availability may be an important source of mineral nutrients for many plants in the Great Basin, competition for the nutrients in these nutrient-rich patches may also be important. Rapid exploitation of the soil patches should result in a large amount of nutrients captured per unit energy expended (Bloom et al. 1985). Plants exploiting nutrient-rich patches may use many mechanisms to capture the resources quickly; these potential mechanisms include root proliferation in the nutrient patches, increases in the kinetics of nutrient uptake by roots in the patches, changes in the frequency of mycorrhizal infection, and the use of root exudates to increase the mobility and flux of nutrients to the root surface (Chapin 1980).

In this study I examined the importance of two mechanisms, root proliferation and changes in root uptake capacity, for plants exploiting nutrient-rich soil patches. Three perennial species common to the Great Basin region were studied: the shrub Artemisia tridentata, the native tussock grass Agropyron spicatum, and the introduced tussock grass Agropyron desertorum. Data for each species on the timing and degree of root proliferation in enriched soil patches are presented in Chapter II. Chapter III

presents the results of four studies examining the ability of each species to increase nutrient uptake capacity in enriched and control soil patches.

CHAPTER II

THE TIMING AND DEGREE OF ROOT PROLIFERATION IN FERTILE-SOIL MICROSITES FOR THREE COLD-DESERT PERENNIALS

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.

Introduction

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.

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, N.Y.) 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 ($m\ m^{-1}\ day^{-1}$):

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

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 (Figure 1). Agropyron desertorum roots in enriched patches 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 (Figure 1).

Because the fertilized Agropyron desertorum roots proliferated so rapidly in this first experiment, accurate

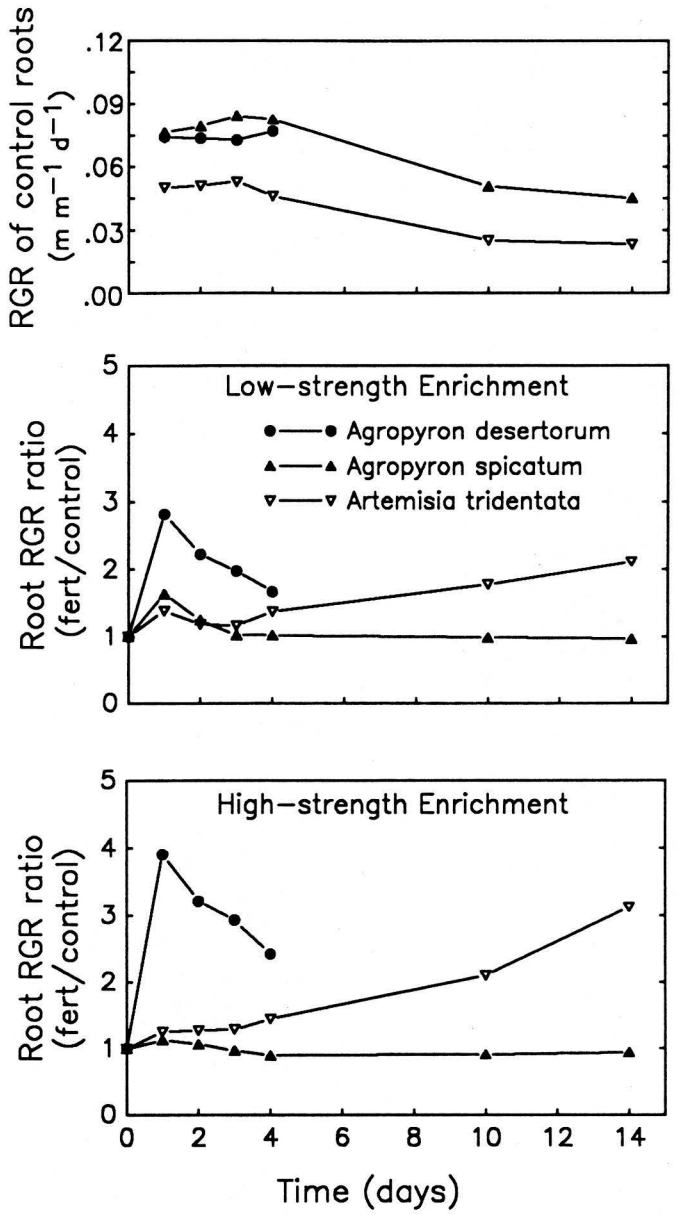

Fig. 1. Mean relative growth rates (RGR) of Agropyron desertorum, Agropyron spicatum, and Artemisia tridentata control roots (upper graph) and the ratios of mean RGR for roots in low-enrichment soil patches and control soil patches (middle graph) and high-enrichment soil patches and control soil patches (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.

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 (Figures 2 and 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 (Figure 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

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

	N-P-K Experiment		
Source	DF	MS	Fcalc
Species (1)	2	.264	20.6***
Error 1	24	.0128	
Fertilizer (2)	2	.0950	19.6***
Spec x Fert (2)	4	.0674	13.9***
Error 2	48	.00485	
Date (3)	3	.00996	16.5***
Error 3	24	.000603	
Spec x Date (4)	6	.00478	10.7***
Fert x Date (4)	6	.00316	7.11***
Spec x Fert x Date (4)	12	.00159	3.58***
Error 4	192	.000449	

*** Significant at P<0.001

** Significant at P<0.01

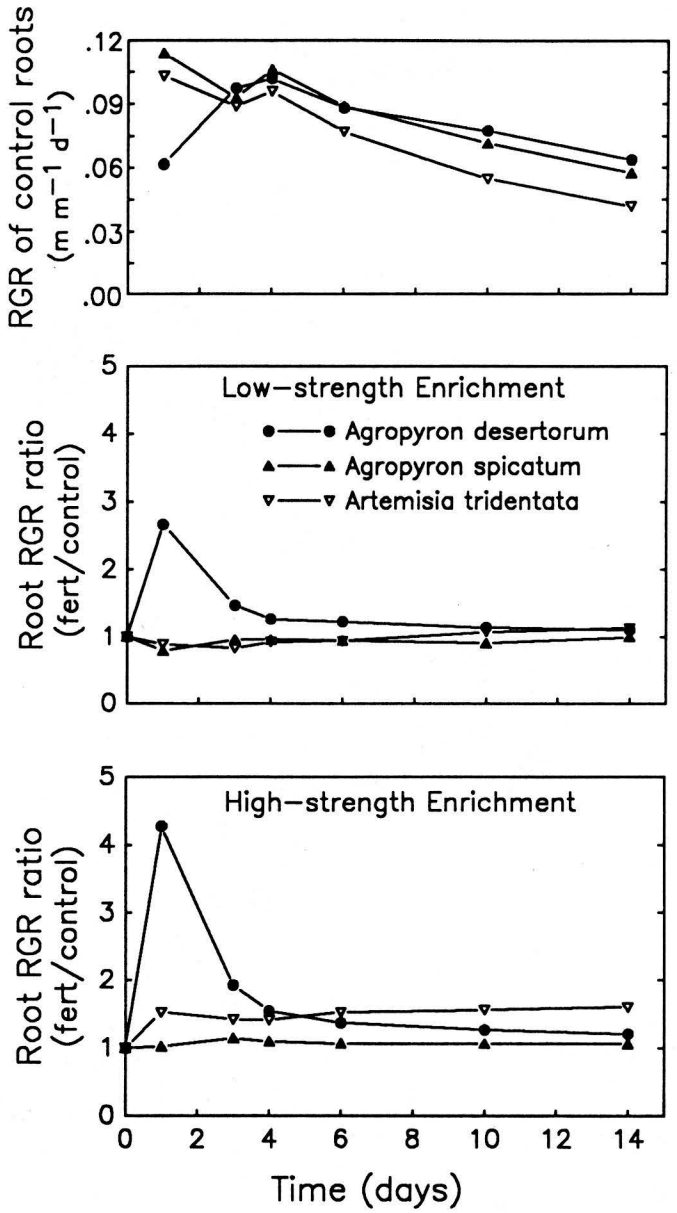

Fig. 2. Mean relative growth rates (RGR) of Agropyron desertorum, Agropyron spicatum, and Artemisia tridentata control roots (upper graph) and the ratios of mean RGR for roots in low-enrichment soil patches and control soil patches (middle graph) and high-enrichment soil patches and control soil patches (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.

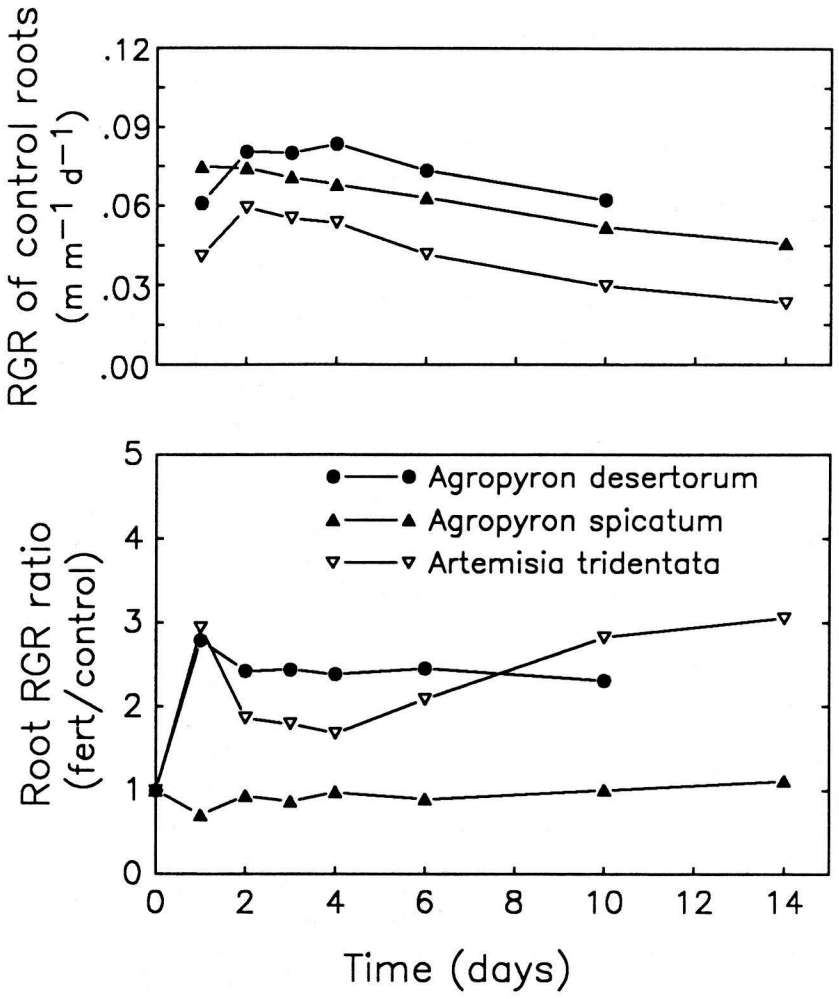

Fig. 3. Mean relative growth rates (RGR) of Agropyron desertorum, Agropyron spicatum, and Artemisia tridentata control roots (upper graph) and the ratios of mean RGR for roots in high-enrichment soil patches and control soil patches (lower graph) for each species in the N-enrichment experiment (n=9 plants 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.

entire two-week experiment (Table 2). Relative growth rates from the N-enrichment experiment were analyzed only through day 10 (Table 3); 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

Table 2. Repeated-measures analysis of variance for relative growth rate data from the P-enrichment experiment (n=8 plants per species). The data were analyzed through day 14 of the experiment. The numbers in parentheses refer to the appropriate error-term number.

		P Experiment	
Source	DF	MS	Fcalc
Species (1)	2	.0390	1.05
Error 1	21	.0372	
Fertilizer (2)	2	.0573	19.8***
Spec x Fert (2)	4	.0142	4.90**
Error 2	42	.00289	
Date (3)	5	.0489	27.3***
Error 3	35	.00179	
Spec x Date (4)	10	.00233	3.02**
Fert x Date (4)	10	.00452	5.87***
Spec x Fert x Date (4)	20	.00319	4.14***
Error 4	280	.000771	

*** Significant at P<0.001

** Significant at P<0.01

Table 3. Repeated-measures analysis of variance for relative growth rate data from the N-enrichment experiment (n=9 plants per species). The data were analyzed through day 10 of the experiment. The numbers in parentheses refer to the appropriate error-term number.

N Experiment

Source	DF	MS	Fcalc
Species (1)	2	.128	14.6***
Error 1	24	.00875	
Fertilizer (2)	1	.207	23.0***
Spec x Fert (2)	2	.0884	9.83***
Error 2	24	.00900	
Date (3)	5	.00534	12.2***
Error 3	40	.000439	
Spec x Date (4)	10	.000833	1.36
Fert x Date (4)	5	.000180	.293
Spec x Fert x Date (4)	10	.000924	1.51
Error 4	200	.000613	

*** Significant at P<0.001

** Significant at P<0.01

Agropyron desertorum roots in the N-P-K experiment was highly significant ($P<.0001$, 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-enrichment 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, Crick, and Rincon, 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 important 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.

CHAPTER III

RAPID ROOT PHYSIOLOGICAL ADJUSTMENT TO LOCALIZED SOIL ENRICHMENT

Fertile soil microsites are an important source of mineral nutrients for plants in many environments (Chapin 1980; Robinson and Rorison 1983; Bloom et al. 1985; Grime et al. 1986). Patchiness in belowground nutrient availability is analogous to resource availability in canopy gaps above ground (Torquebiau 1988). Though physiological changes of sun and shade leaves in canopy gaps are well known (Taylor and Pearcy 1976; Boardman 1977; Adams 1988), we know of no studies showing analogous physiological changes of roots in enriched soil patches. We present evidence of large and rapid changes in the uptake kinetics of plant roots after creating nutrient-rich soil patches in the field. Phosphate uptake for roots from enriched soil patches was as much as 80% greater than for roots of control patches treated with distilled water. The changes took place within days of patch treatment. This degree of plasticity was unexpected for plants growing in soils of very low available phosphorus. Our results showing rapid physiological plasticity of roots in fertile soil microsites have important implications for theory and modeling of nutrient uptake in all soils.

Field experiments were performed with three perennial species common to the Great Basin region of North America:

a prominent shrub, Artemisia tridentata ssp. vaseyana (Rydb.) Beetle, an introduced tussock grass, Agropyron desertorum (Fisch. ex Link) Schult., and a native tussock grass, Agropyron spicatum (Pursh) Scribn. and Smith (syn: Pseudoroegneria spicata (Pursh) A. Löve ssp. spicata (Barkworth and Dewey 1985)). The experiments were conducted in monoculture field plots of evenly spaced plants (0.5-m spacing) established ten years earlier. Soils are Typic Haploxerolls (Caldwell et al. 1987), generally contain <6 p.p.m. bicarbonate-exchangeable phosphate (Caldwell et al. 1985), and have a solution phosphate concentration of approximately 1 μM. The first three experiments were conducted in May and June, 1989, with moist soil throughout the rooting zone. The fourth experiment was conducted one month later; the soil was drier and, therefore, water was applied prior to the experiment. Plants were actively growing during all experiments. Pairs of soil patches were treated by using wicks to place 750 ml of distilled water on one side of a plant and 750 ml of nutrient solution (45 mM NH_4NO_3, 20 mM KH_2PO_4) on the other side of the plant. Samples of the soil patches were removed in soil cores (12 cm diam., 25 cm deep) one week after treatment in the first three experiments and three days after treatment in the fourth experiment.

The excised roots from each soil patch were sieved from the soil, retained if <0.5mm in diameter (Chapin 1981), and separated into five random subsamples. Excised root assays

provide a comparative test and phosphate uptake in excised roots is more representative of intact-root uptake than for other ions such as nitrate or potassium (Bloom and Caldwell 1988). Subsampled roots in small cheesecloth bags were equilibrated in a 0.5-mM $CaCl_2$ solution for one hour at 20°C (Chapin and Bloom 1976) and were placed for 10 min. in 1, 3, 5, 10, or 20-μM solutions of NaH_2PO_4 at 20°C. The NaH_2PO_4 solutions contained 20 to 40 μCi/l of ^{32}P-labeled orthophosphoric acid. The roots were then rinsed three times for at least 2 min. in 200-μM unlabeled NaH_2PO_4 solution at 5°C to replace any adsorbed radioisotope (Chapin et al. 1986). Roots were oven-dried, weighed, and counted by liquid scintillation using Cerenkov radiation (Läuchli 1969), with corrections for half-life and counting efficiency. All solutions were buffered to pH 6.0, were well mixed and aerated, and contained 0.5 mM $CaCl_2$ (Chapin et al. 1986). Apparent Michaelis-Menten parameters were fitted to the phosphate-uptake data:

$$V = ([S] \times Vmax)/([S] + Km)$$

where V is the measured phosphate uptake (μmol g^{-1} hr^{-1}), [S] is the phosphate concentration in solution (μM), Vmax is the maximum phosphate uptake (μmol g^{-1} hr^{-1}), and Km is the binding affinity of enzyme for phosphate (μM).

If plant roots respond physiologically to nutrient-rich soil patches, then increases in uptake capacity for soil nutrients are expected. Indeed, we saw striking increases in phosphate uptake per unit root mass of as much as 80% for

roots in enriched compared to distilled-water patches (Fig. 4). The treatment effect was significant at $P<0.05$ for each of the single-species experiments (Tables 4-6). Michaelis-Menten parameters Vmax and Km were fitted to the data (Table 7); calculated Vmax values were always greater for roots in enriched compared to control soil patches.

Because we obtained such consistent differences in uptake kinetics one week after soil-patch treatment, we performed a follow-up experiment coring patches three days after establishing enriched and control patches. A single plot planted with Agropyron spicatum and Agropyron desertorum was used to compare directly the phosphate uptake of the two tussock grasses. Again we found clear differences in phosphate uptake of roots in enriched and control patches (Fig. 5). The treatment effect was significant at $P<0.05$; the species term was not significant (Table 8). Fitted Vmax values were greater for roots of each species in enriched compared to control patches (Table 9).

Many factors are important for the uptake of soil nutrients by plants. Rooting density and root length are particularly important for the uptake of relatively immobile nutrients like phosphorus, especially when soil phosphorus levels are low and the buffering power of the soil is high (Barber 1984). Enhanced nutrient uptake capacity is not normally considered to contribute to increased phosphorus uptake because diffusivity usually limits P uptake from the soil (Barber 1984; Nye and Tinker 1977). As soil solution

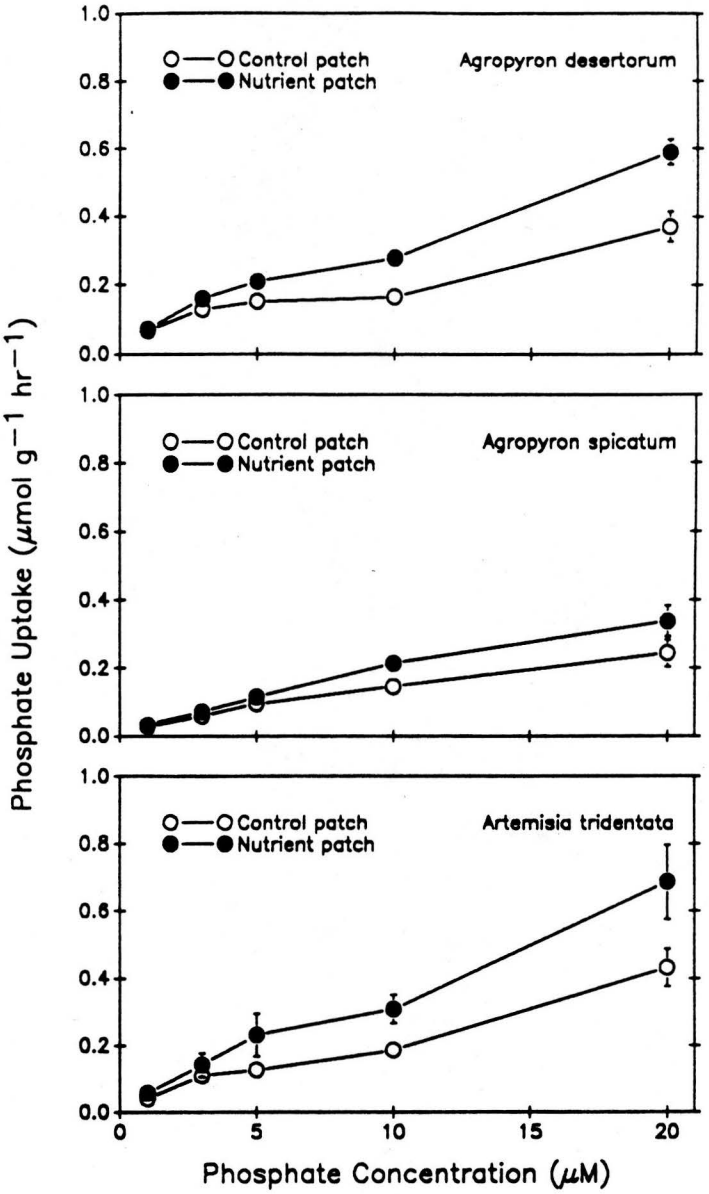

Fig. 4. The rate of phosphate uptake for roots from enriched and control soil patches as a function of solution phosphate concentration (mean ± standard error; n=6 for Agropyron desertorum, n=8 for Agropyron spicatum and Artemisia tridentata). Soil patches on opposite sides of plants in monoculture field plots were treated with 750 ml of nutrient solution or distilled water. Samples of the soil patches were cored one week after treatment. Roots from each core were subsampled and immersed in radioactive phosphate solutions. The three single-species experiments were conducted at different times and in separate field plots; direct comparison of results among species is therefore inappropriate. The treatment effect was significant at $P<0.05$ for each species (two-factor split-plot analyses of variance set out in blocks).

Table 4. Analysis of variance (two-factor split-plot design set off in blocks) for the Agropyron desertorum experiment (n=6). The numbers in parentheses refer to the appropriate error-term number.

Source	DF	MS	Fcalc
REPS (1)	5	.0101	
DAYS	2	.00944	
REPS/DAYS	3	.0105	
TREATMENT (1)	1	.0954	27.7**
ERROR 1	5	.00345	
PHOSPHATE (2)	4	.276	126.3***
PHOSP X TRTMNT (2)	4	.0194	8.88***
ERROR 2	40	.00218	

Table 5. Analysis of variance (two-factor split-plot design set off in blocks) for the Agropyron spicatum experiment (n=8). The numbers in parentheses refer to the appropriate erroe-term number.

Source	DF	MS	Fcalc
REPS (1)	7	.0238	
DAYS	3	.0422	
REPS/DAYS	4	.0101	
TREATMENT (1)	1	.0321	8.57*
ERROR 1	7	.00374	
PHOSPHATE (2)	4	.171	75.2***
PHOSP X TRTMNT (2)	4	.00585	2.57*
ERROR 2	56	.00228	

*** Significant at P<0.001
** Significant at P<0.01
* Significant at P<0.05

Table 6. Analysis of variance (two-factor split-plot design set off in blocks) for the Artemisia tridentata experiment (n=8). The numbers in parentheses refer to the appropriate error-term number.

Source	DF	MS	Fcalc
REPS (1)	7	.0620	
DAYS	3	.0879	
REPS/DAYS	4	.0426	
TREATMENT (1)	1	.226	14.6**
ERROR 1	7	.0154	
PHOSPHATE (2)	4	.618	43.8***
PHOSP X TRTMNT (2)	4	.0358	2.54
ERROR 2	56	.0141	

*** Significant at P<0.001
** Significant at P<0.01

Table 7. Fitted Michaelis-Menten parameters for the three single-species experiments.

	Vmax	Km
Agropyron desertorum (nutrient)	1.61	37.8
Agropyron desertorum (control)	.625	16.5
Agropyron spicatum (nutrient)	.861	30.9
Agropyron spicatum (control)	.548	25.3
Artemisia tridentata (nutrient)	4.75	120.9
Artemisia tridentata (control)	4.50	192.6

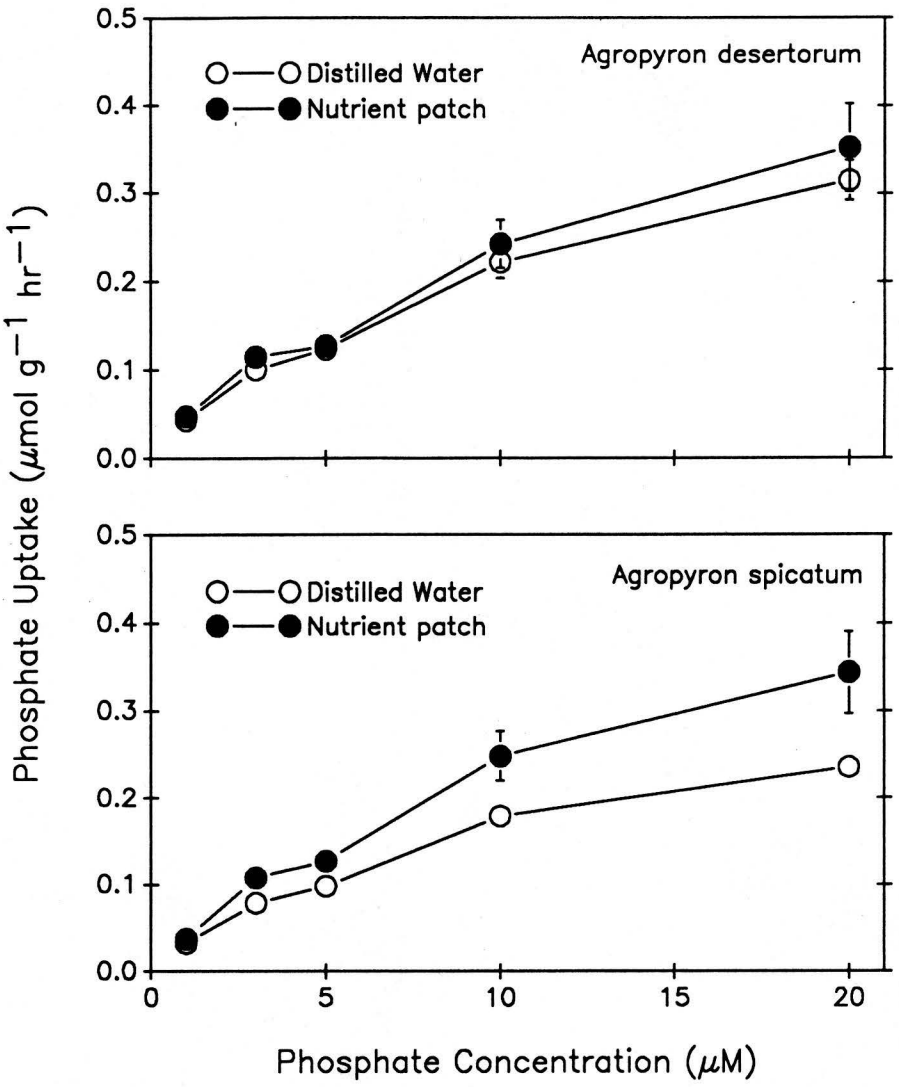

Fig. 5. The rate of phosphate uptake for roots from enriched and control soil patches as a function of solution phosphate concentration (mean ± standard error; n=7). The experimental procedure was the same as outlined for Fig. 4 except that soil patches were cored only three days after treatment, no Artemisia plants were tested, and results for the Agropyron species may be compared directly. The treatment effect was significant at $P<0.05$ but the species term was not significant (three-factor split-plot analysis of variance set out in blocks).

Table 8. Analysis of variance (three-factor split-plot design set out in blocks) for the comparative experiment of Agropyron desertorum and Agropyron spicatum (n=7). The numbers in parentheses refer to the appropriate error-term number.

Source	DF	MS	Fcalc
DAYS (1)	6	.00722	
SPECIES (1)	1	.0143	3.24
TREATMENT (1)	1	.0359	8.14*
SPEC X TRTMNT (1)	1	.00897	2.03
ERROR 1	18	.00442	
PHOSPHATE (2)	4	.326	136.7***
SPEC X PHOSP (2)	4	.00132	.553
TRTMNT X PHOSP (2)	4	.00505	2.12
SPEC X TRTMNT X PHOSP (2)	4	.00133	.557
ERROR 2	96	.00239	

*** Significant at P<0.001

* Significant at P<0.05

Table 9. Fitted Michaelis-Menten parameters for the experiment comparing nutrient uptake capacity of Agropyron desertorum and Agropyron spicatum.

	Vmax	Km
Agropyron desertorum (nutrient)	0.649	17.0
Agropyron desertorum (control)	0.554	15.2
Agropyron spicatum (nutrient)	0.635	16.7
Agropyron spicatum (control)	0.390	12.8

concentrations increase, however, uptake capacity increases in relative importance (Chapin 1980). When soil nutrient distribution is patchy, increased uptake capacity may contribute to rapid exploitation of the nutrients in the patches.

Uptake capacity is greatly influenced by tissue nutrient concentrations and, hence, plant demand for nutrients (Chapin 1988). Studies of uptake kinetics can be confounded by the inherent variability of plant nutrient demand among individual plants (Barta 1977). The results of this study, however, were not confounded by changes in total nutrient demand since the same plants were exposed to both enriched and control patches.

A common response of plant roots encountering fertile soil patches is to branch and proliferate, thus increasing local rooting density (Tilman 1988). These species differ in their relative ability to proliferate roots in nutrient-rich soil patches (Chapter II). Agropyron desertorum was shown to begin root proliferation within one day of patch enrichment, while Agropyron spicatum did not proliferate roots within two weeks of enrichment in any of the experiments (Chapter II). In our current study, the excised roots of Agropyron desertorum may therefore have consisted of both newly proliferated and existing roots. However, at least for Agropyron spicatum, the increases in uptake capacity occurred in roots present in the patches before treatment.

Plants in nutrient-poor soils are believed to have root systems exhibiting little morphological or physiological plasticity (Chapin 1980, Chapin 1988; Campbell and Grime 1989). Plants in nutrient-poor soils also have generally low phosphate absorption capacities (Chapin 1988), even when grown in more fertile soils (Chapin 1980). Though the three species we studied typically grow in nutrient-poor soils, they each had the physiological plasticity to rapidly and substantially increase uptake capacity after phosphorus levels in the soil increased. This unexpected plasticity implies that nutrient uptake capacity is much more important to mineral nutrient capture than previously believed. As patchiness in nutrient availability is explicitly modeled, changes in uptake capacity may be found to be important for nutrient capture by plants in soils.

LITERATURE CITED

Adams WW III (1988) Photosynthetic acclimation and photoinhibition of terrestrial and epiphytic CAM tissues growing in full sunlight and deep shade. In: Evans JR, von Caemmerer S, Adams WW III (eds) Ecology of photosynthesis in sun and shade. CSIRO, Australia, pp 123-134

Barta AL (1977) Uptake and transport of Calcium and Phosphorus in Lolium perenne in response to N supplied to halves of a divided root system. Physiol Plant 39:211-214

Barber SA (1984) Soil nutrient bioavailability. John Wiley & Sons, New York

Barkworth ME, Dewey DR (1985) Genomically based genera in the perennial Tritaceae of North America: identification and membership. Am J Bot 72:767-776

Bloom AJ, Caldwell RM (1988) Root excision decreases nutrient absorption and gas fluxes. Plant Physiol 87:794-796

Bloom AJ, Chapin FS III, Mooney HA (1985) Resource limitation in plants - an economic analysis. A Rev Ecol Syst 16:363-392

Boardman NK (1977) Comparative photosynthesis of sun and shade plants. A Rev Plant Physiol 28:355-377

Caldwell MM, Eissenstat DM, Richards JH, Allen MF (1985) Competition for phosphorus: differential uptake from dual-isotope-labeled soil interspaces between shrub and grass. Science 229:384-386

Caldwell MM, Richards JH (1986) Competing root systems: morphology and models of absorption. In: Givnish TJ (ed) On the economy of plant form and function. Cambridge University Press, Cambridge, pp251-273

Caldwell MM, Richards JH, Johnson DA, Nowak RS, Dzurec RS (1981) Coping with herbivory: photosynthetic capacity and resource allocation in two semiarid Agropyron bunchgrasses. Oecologia (Berlin) 50:14-24

Caldwell MM, Richards JH, Manwaring JH, Eissenstat DM (1987) Rapid shifts in phosphate acquisition show direct competition between neighbouring plants. Nature 327:615-616

Campbell BD, Grime JP (1989) A comparative study of plant

responsiveness to the duration of episodes of mineral nutrient enrichment. New Phytol 112:261-268

Chapin FS III (1980) The mineral nutrition of wild plants. Ann Rev Ecol Syst 11:233-260

Chapin FS III (1981) Field measurements of growth and phosphate absorption in Carex aquatilus along a latitudinal gradient. Arct Alp Res 13:83-94

Chapin FS III (1988) Ecological aspects of plant mineral nutrition. Adv Min Nutrition 3:161-191

Chapin FS III, Bloom A (1976) Phosphate absorption: adaptation of tundra graminoids to a low temperature, low phosphorus environment. Oikos 26: 111-121

Chapin FS III, Van Cleve K, Tryon PR (1986) Relationship of ion absorption to growth rate in taiga trees. Oecologia 69:238-242

Charley JL, West NE (1975) Plant induced soil chemical patterns in some desert shrub-dominated ecosystems in Utah. J Ecol 63:945-964

Charley JL, West NE (1977) Micro-patterns of nitrogen mineralization activity in soils of some shrub-dominated ecosystems of Utah. Soil Biol Biochem 9:357-366

Crick JC, Grime JP (1987) Morphological plasticity and mineral nutrient capture in two herbaceous species of contrasted ecology. New Phytol 107:403-414

Doescher PS, Miller RF, Winward AH (1984) Soil chemical patterns under eastern Oregon plant communities dominated by big sagebrush. Soil Sci Soc Am J 48:659-663

Drew MC, Saker LR (1975) Nutrient supply and the growth of the seminal root system in barley. II. Localized, compensatory increases in lateral root growth and rates of nitrate uptake when nitrate supply is restricted to only part of the root system. J Exp Bot 26:79-90

Drew MC, Saker LR (1978) Nutrient supply and the growth of the seminal root system in barley. III. Compensatory increases in growth of lateral roots, and in rates of phosphate uptake, in response to a localized supply of phosphate. J Exp Bot 29:435-451

Duncan WG, Ohlrogge AJ (1958) Principles of nutrient uptake from fertilizer bands. II. Root development in the band. Agron J 50:605-608

Eissenstat DM, Caldwell MM (1987) Characteristics of successful competitors: an evaluation of potential growth rate in two cold desert tussock grasses. Oecologia (Berlin) 71:167-173

Eissenstat DM, Caldwell MM (1988a) Seasonal timing of root growth in favorable microsites. Ecology 69:870-873

Eissenstat DM, Caldwell MM (1988b) Competitive ability is linked to rates of water extraction: a field study of two aridland tussock grasses. Oecologia (Berlin) 75:1-7

Grime JP, Crick JC, Rincon JE (1986) The ecological significance of plasticity. In: Jennings DH, Trewavas AJ (eds) Plasticity in plants. Cambridge University Press, Cambridge, pp 5-29

Gurevitch J, Chester ST Jr. (1986) Analysis of repeated measures experiments. Ecology 67:251-255

Läuchli A (1969) Radioassay for ß-emmiters in biological materials using Cerenkov radiation. Int J Appl Radat Isot 20:265-270

Newman EI (1966) A method of estimating the total length of root in a sample. J Appl Ecol 3:139-145

Nye PH, Tinker PB (1977) Solute movement in the soil-root system. University of California Press, Berkeley, Los Angeles

Passioura JB, Wetselaar R (1972) Consequences of banding nitrogen fertilizers in soil. II. Effects on the growth of wheat roots. Plant Soil 36:461-473

Richards JH (1984) Root growth response to defoliation in two Agropyron bunchgrasses: field observations with an improved root periscope. Oecologia (Berlin) 64:21-25

Robinson D, Rorison IH (1983) A comparison of the responses of Lolium perenne L., Holcus lanatus L., and Deschampsia flexuosa (L.)Trin. to a localized supply of nitrogen. New Phytol 94:263-273

Snaydon RW (1962) Micro-distribution of Trifolium repens L. and its relation to soil factors. J Ecol 50:133-143

St. John TV, Coleman DC, Reid CPP (1983) Growth and spatial distribution of nutrient-absorbing organs: selective exploitation of soil heterogeneity. Plant Soil 71:487-493

Taylor RJ, Pearcy RW (1976) Seasonal patterns of the CO_2

exchange characteristics of understory plants from a deciduous forest. Can J Bot 54:1094-1103

Tennant D (1975) A test of a modified line intersect method of estimating root length. J Ecol 63:995-1001

Tilman D (1982) Resource competition and community structure. Princeton University Press, Princeton, New Jersey

Tilman D (1988) Plant strategies and the dynamics and structure of plant communities. Princeton University Press, Princeton, New Jersey

Torquebiau EF (1988) Photosynthetically active radiation environment, patch dynamics and architecture in a tropical rainforest in Sumatra. In: Evans JR, von Caemmerer S, Adams WW III (eds) Ecology of photosynthesis in sun and shade. CSIRO, Australia, pp 327-342

West NE (1988) Intermountain deserts, shrub steppes, and woodlands. In: Barbour MG, Billings WD (eds) North American Terrestrial Vegetation. Cambridge Univ. Press, New York, pp 210-230