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Exploitation of phosphate from fertile soil microsites by three Great Basin perennials when in competition

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Abstract. The effectiveness of phosphate (P) exploitation from fertile soil microsites was investigated with a dual-radioisotope approach for three perennial Great Basin species. Three experiments with competing species pairs assessed the ability to acquire P in fertilized and control patches. The patches occupied less than 1% of the rooted soil volume. In all experiments, the plants acquired at least as much radioisotope from the enriched as from the control patches even though the isotopes in the enriched patches were diluted by a factor of 10^8 with added ^{31}P. The plants procured P from the enriched patches in proportion to its increased concentration relative to P in the control patches. The relative ability of the competing species to acquire P was very similar in control and enriched patches. *Artemisia tridentata* (Rydb.) Beetle was able to acquire much more P than *Pseudoroegneria spicata* (Pursh) A. Löve and was equivalent in ability to acquire P when in competition with *Agropyron desertorum* (Fisch. ex Link) Schult. However, when the *Agropyron* and *Pseudoroegneria* were together, they were unexpectedly similar in procuring P.

Key-words: Agropyron desertorum, Agropyron spicatum, Artemisia tridentata, competition, patch exploitation, *Pseudoroegneria spicata*, roots, soil phosphate

Introduction

Fertile microsites in soil have been suggested to be valuable sources of mineral nutrients for plants even though they may constitute a small fraction of the total rooted soil volume (Chapin, 1980; Grime, Crick & Rincon, 1986). When plant roots encounter fertile soil areas, they commonly respond by branching and proliferating to substantially increase the local root length density in the fertile patch (e.g. Passioura & Wetselaar, 1972). The physiological uptake capacity of roots in local fertile areas has also been shown to increase (Robinson & Rorison, 1983; Jackson, Manwaring & Caldwell, 1990). These morphological and physiological responses of roots suggest that such changes provide an advantage in exploiting the resources of fertile patches. The investment in local root mass and activity has been shown to pay dividends in nutrient solution studies (Drew & Saker, 1975, 1978). A study with individual potted plants in a mixture of soil and inert media showed that plants were very efficient in extracting P from small enriched patches relative to the added investment of root carbon in these patches (R.A. Black, J.H. Richards & J.H. Manwaring, unpublished observations).

Although fertile patches represent opportunities for plants, competition for nutrients in local fertile areas may be quite intense. While attention has been given to root proliferation in fertile microsites, the degree to which plants exploit nutrients from fertile microsites in the presence of neighbouring plant roots has not been investigated to our knowledge. Several questions emerge. In the presence of neighbouring plant roots, do plants derive a large proportion of newly available nutrients from fertile microsites compared to equal volumes of soil which have not been enriched? When neighbouring plant roots occupy the same microsites, is the ability of the neighbours to acquire nutrients proportionately the same in enriched and unenriched patches? If a species effectively acquires nutrients from an enriched patch, does the competing neighbour plant extract proportionately more of its resources from less fertile regions of the soil? Is the ability to procure nutrients from enriched patches associated with plant size?

This study involved three perennial species of the North American Great Basin which are all known to proliferate roots in fertile microsites, though the short-term dynamics of this proliferation differs among the species (Eissenstat & Caldwell, 1988; Jackson & Caldwell, 1989). All

three species exhibit sizeable increases in the physiological uptake capacity of roots in fertile microsites under field conditions (Jackson *et al.*, 1990). The species differ in general competitiveness (Caldwell & Richards, 1986; J.H. Richards, D.M. Eissenstat, M.M. Caldwell & J.E. Eriksson-Simonds, unpublished observations). Experiments with P isotopes have shown that the native tussock grass, *Pseudoroegneria spicata* (Pursh) A. Löve spp. *spicata* (Barkworth & Dewey, 1985) [syn: *Agropyron spicatum* (Pursh) Scribn.] is much less effective in acquiring phosphate than the exotic tussock grass, *Agropyron desertorum* (Fisch. ex Link) Schult. when in competition with the native shrub, *Artemisia tridentata* ssp. *vaseyana* (Rydb.) Beetle (Caldwell *et al.*, 1985). As in most soils, those of the Great Basin are expected to exhibit patchy distributions of nutrients, in part due to significant centimetre-scale variations in soil physical properties (Dobrowolski, Caldwell & Richards, 1990).

Although phosphate is not necessarily the limiting mineral nutrient resource for these species in the Great Basin, available P in soils of the region occupied by these species can be quite low (e.g. Lentz & Simonson 1987) and they clearly compete for P (Caldwell *et al.*, 1985, 1987). There are several experimental advantages in using P rather than nitrogen, including the availability of two short half-life isotopes of P and the strong binding and immobility of P in these soils. This immobility ensures that the labelled patches remain localized and that uptake occurs within a few millimetres of the root or its associated mycorrhizas. We utilized a double-isotope technique to assess how effectively the study species acquired P from enriched soil microsites and from unenriched control patches of equal volume when the plants were in competition under field conditions.

Materials and methods

Field site

The experiments were performed near Logan, Utah (41° 45′N, 111° 48′W, 1460 m elevation) in a group of experimental field plots of evenly spaced plants (0·5 m between individuals) consisting of paired combinations of the three perennials in separate plots. Each individual was surrounded by four plants of the other species. The plots were established with transplants 11 years earlier for the plots of *Artemisia* mixed with either grass species and 6 years earlier for the plot containing the mixture of the two grass species. The soils are rocky Mollisols (Typic Haploxerolls), which were formed from alluvial material (Southard, Wilson & Erickson, 1978). The concentration of available (bicarbonate-extractable) phosphorus in these soils is generally *c* 8 $\mu g\ g^{-1}$ which is in the lower range of Great Basin soils where these species occur (Harner & Harper, 1973; Charley & West, 1975; Doescher, Miller & Winward, 1984). Further site details are in Caldwell *et al.* (1981).

The three combinations of species in separate plots constitute three concurrent experiments. Although the plots are no more than 60 m apart, variability in soil depth and microenvironment precludes considering these as a single experiment. The experimental unit was a set of four plants (as described below). There were six replicate plant sets in each experiment.

Isotope experiments

A plant set was a row of four plants alternating between two species (Fig. 1). Depending on the competitive balance, the individual plant size of the two species might differ (Table 1), but plant sets were chosen so that the size of the two individuals of the same species was similar. Three patches were involved in each plant set, one enriched patch in the centre of the plant set and two control patches between the adjacent plants (Fig. 1). Because naturally fertile microsites would seldom involve a single nutrient, enriched patches were created with solutions containing potassium, nitrogen and phosphate (250 ml 45 mM NH_4NO_3, 20 mM KH_2PO_4). Control patches were created with an equal volume of distilled water. To be able to measure P uptake from the patches, the isotopes, either ^{32}P or ^{33}P as 18·5 MBq (500 μCi) orthophosphoric acid, were included in the solutions for each patch such that one isotope was in the enriched and the other was in the two control patches. The enriched patch contained ^{32}P in half the replicates and ^{33}P in the other half to compensate for possible isotope discrimination. Since the radioactive orthophosphoric acid was carrier free, the amount of P added in the label itself was in the picogram range. The label solutions contained a trace of HCl (0·02 M) to ensure that the orthophosphate radioisotope remained in solution until injection into the soil.

The patches were small in volume, but planar in shape and perpendicular to a line connecting the plants. In this manner, the roots of both plants had a large probability of encountering the patch. The patches were created by injecting the solutions halfway between the neighbouring plants into a

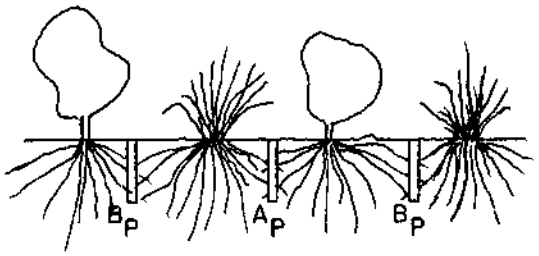

Fig. 1. Experimental plant set used in the isotope-labelling experiments. Two species were alternated in a row with even spacing. The enriched-nutrient patch was located in the centre and given a P isotope label (^{A}P) which was either ^{32}P or ^{33}P. Control patches were between the neighbours and centre plants. These received the other radioisotope label (^{B}P). The two centre plants were evaluated for isotope content.

row of 10 30-cm-deep holes, 2·5 cm apart, previously created by inserting 6-mm-diameter rods into the soil. The holes were then covered by soil. Since the volume of solution injected was threefold greater than the volume of holes, the solution would coalesce in the soil between the holes and beyond, forming the planar patch. Most of the P would be bound in the soil close to the sites of application. Assuming a pore volume of 50% in these silty soils, the volume of a patch created by the solution was approximately 0·7% of the total rooted soil volume of an individual plant in the upper 30 cm of the profile.

The labelling and creation of patches were conducted on 5 July 1989 and the final sampling was 5 weeks later. This period is typically warm and dry. Soil water potentials (Ψ_s) at the experimental site were measured at 10 locations with screen-cage soil psychrometers (J.D. Merrill Specialty Equip., Logan, Utah). At the initiation of the experiment, Ψ_s was generally in the range of −0·5 to −1·3 MPa at 35 cm. The soils at this depth dried to −1·0 to −2·2 MPa after 1 week and to −1·3 to −3·0 MPa after 3 weeks following labelling. Soils at greater depths tend to be more moist (Richards & Caldwell, 1987; Caldwell & Richards, 1989) and the plants at this time of year maintain active photosynthesis and growth (Caldwell *et al.*, 1981). Nevertheless, to prevent the roots in the upper soil layers from becoming entirely water limited during this dry period, we applied 50 mm of water over a 5-day period ending 5 days before the final harvest on 9 August.

For the final harvest, the entire above-ground portion of the grasses and 10 shoots from the shrubs were reduced to ashes (500 °C), digested in 6 M HCl, and scintillation counts were corrected for half-life, counting efficiency, and energy overlap of the two isotopes. A few wood samples from the shrubs were also taken from the branches where the leaf and green stem material was sampled to assess the general level of specific activity. The entire above-ground isotope content of the shrubs was calculated using allometric relationships between canopy volume and shoot biomass and between shoot biomass and wood fractions (r^2 = 0·97). The wood component was treated separately because it generally had at least an order of magnitude lower specific activity. Acquisition by the plants of the P added to the patches was based on total P radioisotope content of the shoots. In addition to the final harvest at 5 weeks, five to 10 grass tillers and five shrub shoots were collected 1 and 3 weeks after labelling and

Table 1. Total radioisotope content in above-ground biomass of the competing plants derived from the control and enriched patches in each experiment. The average shoot biomass is also given. The numbers in square brackets refer to the average above-ground biomass of the shrubs which was not in the heavy wood component. The numbers in parentheses refer to standard errors of the mean (n = 6). The asterisks denote significant differences between pools derived from the enriched and control patches within a given species and experiment ($P < 0·05$ after Bonferroni adjustment of a paired t-test).

Experiment and species	Radioisotope pools (KBq)					Shoot biomass (g)	
	Control patch			Enriched patch			
Pseudoroegneria	1·55	(0·55)		2·95	(0·77)	27·5	(5·0)
Agropyron	1·69	(0·94)		1·96	(1·20)	19·9	(2·8)
Pseudoroegneria	0·94	(0·39)	*	3·34	(0·99)	7·7	(1·8)
Artemisia	8·05	(2·30)	*	21·64	(3·31)	145·7 [29]	(25·9)
Agropyron	18·07	(8·06)		18·10	(6·82)	56·6	(11·4)
Artemisia	5·95	(1·59)		19·09	(9·81)	290·0 [62]	(51·6)

similarly processed to determine an approximate time course of isotope accumulation. (These samples represented less than 9% of the total above-ground biomass and corrections were made in the final harvests for the removal of the earlier samples.)

Results

The quantities of P radioisotope (*P, designating either ^{32}P or ^{33}P) acquired from fertile and control patches were of the same order of magnitude for each species in all three experiments (Table 1) even though the *P in the enriched patch solution was diluted by a factor of 10^8 with ^{31}P compared to the solution added to the control patches. Only in the experiment with *Artemisia* and *Pseudoroegneria* did the plants differ in *P ratios between control and enriched patches. Both species obtained proportionately more *P from the enriched patch than from the control patch ($P < 0.05$ after Bonferroni adjustment of paired *t*-tests with $\sin^{-1/2}$-transformed data).

Fig. 2 shows the total P acquired by the competing pairs of plants from the P solutions added to the patches (P_a). In addition to the *P from both types of patches, the plants acquired ^{31}P added to the fertile patches ($^{31}P_a$) which could be calculated based on the mole fractions of *P added to the enriched patches. The shrubs clearly obtained much more P than did the *Pseudoroegneria* tussocks. The difference was similar in both the enriched and control patches ($P < 0.05$ after Bonferroni adjustment of paired *t*-tests) despite the orders of magnitude difference in P_a acquired from the two types of patches. In the experiments with the shrubs and *Agropyron* tussocks, the ability of the two species to acquire P_a was similar in the enriched patches. Although the grass appears to have procured more isotope from the control patches in Fig. 2, this difference is not statistically significant. Surprisingly, when the two grasses were together, they were very similar in acquisition of P_a in both control and enriched patches.

There was no indication that a large amount of *P was accumulated by the plants early in the experiment (Fig. 3). The concentration of *P in shoot tissues after 1 week was always less than 20% of that at the final sampling and in most cases was less than 10%. The large increase in *P late in the experiment was probably in part due to the water application 5 days before the final harvest.

Correlations between above-ground biomass at the end of the experiment and *P pools among plants of the same species in the six replicate plant sets of each experiment did not reveal patterns. There was no consistent relationship between plant size and total *P pools derived from either control or enriched patches, nor between plant

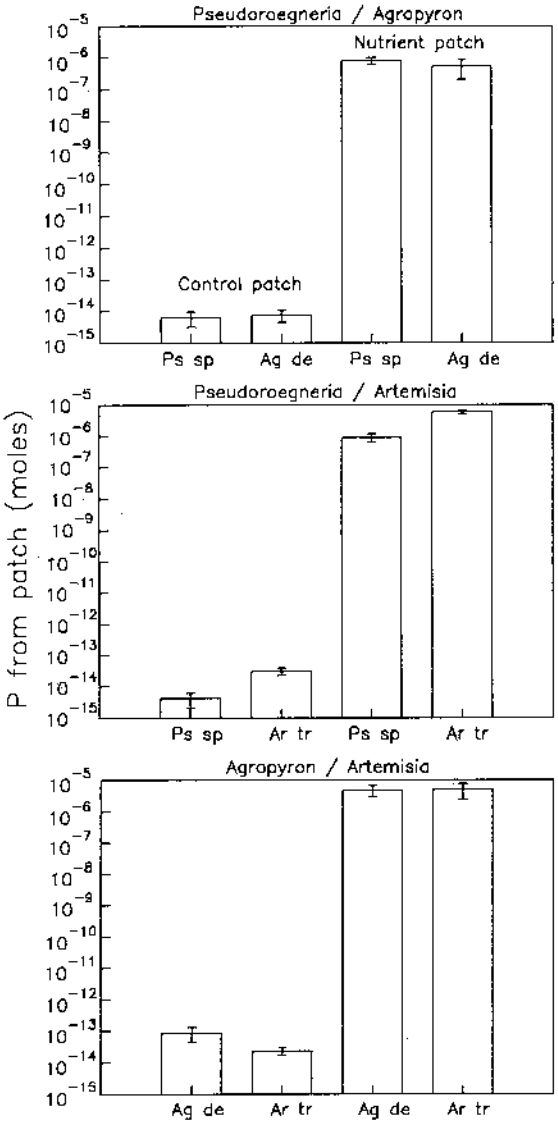

Fig. 2. The total quantity of added phosphate (P_a), both as radioisotope (*P) and ^{31}P, derived from the control and enriched patches and appearing in the above-ground biomass of the competing plants at the end of the experiments. The total P_a derived from the control patches was only in the form of *P. The vertical bars representing standard errors of the mean ($n = 6$) are included only to illustrate the variation among replicates; the results were analysed using paired *t*-tests. The only significant differences were with the *Pseudoroegneria* and *Artemisia* combination ($P < 0.05$ after Bonferroni adjustment) in which case uptake by *Artemisia* was greater than for *Pseudoroegneria* in both the control and enriched patches.

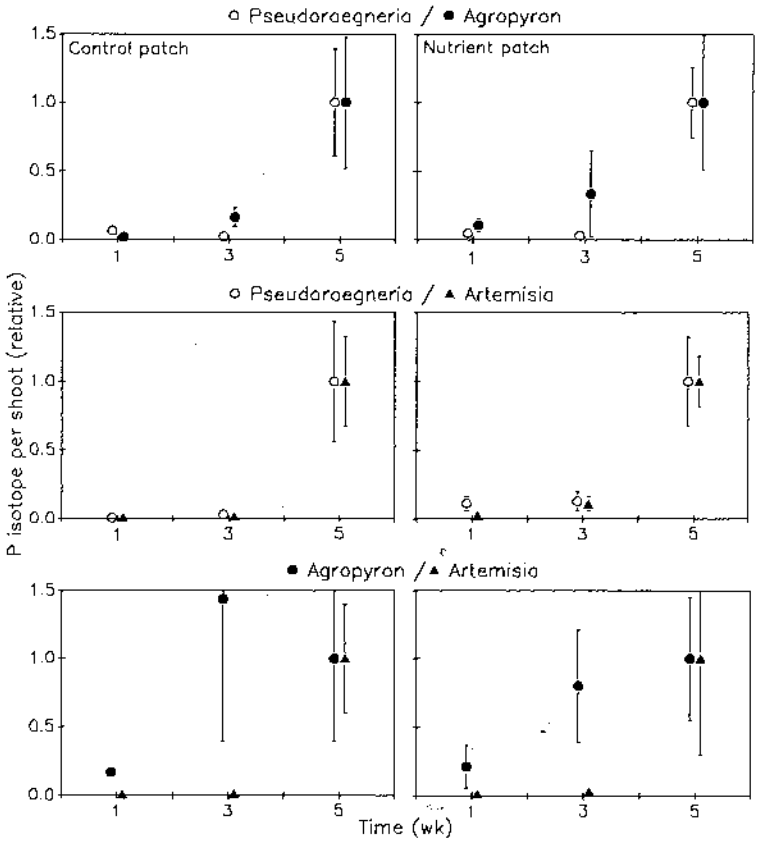

Fig. 3. The concentrations of *P in shoot tissues of the plants 1 and 3 weeks following labelling relative to the concentrations at the end of the experiment. The vertical bars representing standard errors of the mean ($n = 6$) are for illustrative purposes only; an attempt to stabilize variances would be necessary if statistical tests were to be performed.

size and the proportion of *P derived from the fertile and control patches.

Discussion

Acquisition of P from enriched patches

Even though the *P in the enriched patches was diluted with ^{31}P in the injected solutions (a factor of 10^8 compared to the control patches), the plants acquired the same magnitude of *P from the enriched and control patches. Since the *P was well mixed with ^{31}P in the solutions used to create the enriched patches, the plants clearly acquired 10^8 more P from the solutions added to the enriched patches compared to those added to the control patches. Yet, this speaks only of the P added (P_a) to the patches. The plants, of course, also had access to indigenous soil P (P_i) in both the control and enriched patches.

We estimate the acquisition of P_i to be comparable in the control and enriched solutions based on the similar amount of *P acquired from the control and enriched patches. When the *P was applied, there would be a rapid isotopic exchange of *P with $^{31}P_i$ in the soil solution and with some of the $^{31}P_i$ adsorbed on soil particle surfaces. Since the injected volume of liquid, the *P concentration and the size and configuration is the same for the enriched and control patches, isotopic exchange should have occurred to the same degree in both kinds of patches. Therefore, since the plants acquired the same magnitude of *P from the control and enriched patches, the same amount of P_i should have been procured in the two types of patches. (This should not be complicated by the $^{31}P_a$ in the enriched patches since the ratio of *P to $^{31}P_i$ would be equivalent in the control and enriched patches.)

The plants acquired not only the same amount of P_i from the enriched and control patches, but also P_a in the enriched patches in proportion to its contribution to the total P concentration in the

enriched patches, i.e. proportional to $(P_a+P_i)/P_i$. In the case of the experiment with *Artemisia* and *Pseudoroegneria*, the effectiveness of P acquisition from the enriched patches was even greater than the proportion $(P_a+P_i)/P_i$ (Table 1).

The effective P enrichment in the fertile patches would change through time during this 5-week experiment. Initially there would have been very high soil solution P concentrations. However, a rapid exchange between the soil solution and P adsorbed on soil particle surfaces takes place (Barber, 1984). In well-mixed soil samples under defined conditions, the fraction of soil P that exchanges rapidly, i.e. within 1–2 days, is thought to be the more available, or labile, P adsorbed on soil particles. Exchange also occurs in a slower equilibration process and this is considered to involve a non-labile fraction of P adsorbed on particles and precipitated in various compounds (Barber, 1984). Much of the slower exchange is completed in about 1 week (Mattingly, 1957; Nye & Tinker, 1977). In our experiment, the exchange would likely occur more slowly since these solutions were injected and not forcibly mixed with the soil. In the calcareous soils of our study site, a considerable adsorption and precipitation of P occurs into the non-labile form.

Although the available P concentrations in the enriched patches changed during the period of this experiment, most of the *P uptake took place after 3 weeks when much of the equilibration should have been completed. The approximate time courses of *P uptake in these experiments (Fig. 3) showed that after 1 week a very small proportion of the *P tissue concentrations had been attained compared with concentrations at the end of the experiment upon which we are basing our conclusions. The relative time courses were very similar for *P uptake from both the control and enriched patches in all three experiments. The large proportion of *P uptake late in the experiment was probably attributable to the water application as mentioned earlier. Had the soils been uniformly moist during the entire period of the experiment, the time course and total acquisition by the species could have been different.

This is the first time to our knowledge that the potential for nutrient acquisition in small fertile microsites has been tested in the field, especially when the plant roots were competing with those of neighbours. This test was made possible by the application of dual-isotope labelling which provided the opportunity to estimate acquisition of both P_i and P_a. The use of the unenriched patches not only provided the second isotope comparison but also controlled for the inevitable effects of installing the patches in the soil environment including mechanical disturbance and soil wetting.

The total amount of P obtained from the enriched patches over the 5-week period was only a very minor portion of the total P acquisition of these plants for the growing season. Nevertheless, these small patches, representing less than 1% of the rooted soil volume in the upper 30 cm of the profile, indicate the potential capacity of the plants to exploit enriched patches. Although much of the P_a should have been bound and precipitated in these calcareous soils and not available to the plant, the plants were very efficient in acquiring P from the enriched patches when compared with the control patches.

Root proliferation of these three species has been demonstrated to occur in response to fertilization of soil microsites (Eissenstat & Caldwell, 1988; Jackson & Caldwell, 1989). However, an experiment conducted at the same time as this isotope study showed that while root densities of *Agropyron* and *Artemisia* were greater in the enriched than control patches, roots of *Pseudoroegneria* proliferated to the same extent in the two types of patches (Caldwell, Manwaring & Durham, 1991). Therefore, root proliferation should have contributed materially to the difference in P acquired from the control and enriched patches for *Agropyron* and *Artemisia*, but not for *Pseudoroegneria*. Other changes of the roots in fertile soil microsites have been shown. Increased physiological P uptake capacity has been demonstrated in fertile soil microsites (Jackson *et al.*, 1990) and this probably contributed to the effective exploitation of P in the enriched patches. The solution culture experiments of Drew & Saker (1978) showed that when a small portion of the root system of phosphate-deficient plants was exposed to high P concentrations, a localized increase of P uptake compensated for the rest of the root system remaining in totally phosphate-deficient solution. This was attributed both to localized root proliferation and to increased uptake rates per mass of root tissue of as much as five-fold.

Apart from changes in root characteristics in fertile patches, alterations of the soil solution P concentrations and diffusivity also could contribute to improved acquisition of P in the enriched patches. Simulations with a mechanistic root uptake model have shown that even without changes in the root system surface area or uptake capacity, placing the same amount of P fertilizer in a small fraction of the rooted soil volume leads to

substantially greater acquisition of the added P than if the same fertilizer is placed in a large proportion of the soil volume (Kovar & Barber, 1989). The effective exploitation of P from enriched patches in our study may be similarly attributed, in part, to increased solution P and diffusivity in the enriched patches. However, this warrants greater scrutiny.

Competition in patches

Fertile soil microsites may represent important resources for plants, but competition for nutrients in these patches may be intense. Acquisition of P from both control and enriched patches in these experiments was always in the presence of neighbouring plant roots. In both control and enriched patches, *Agropyron* and *Artemisia* acquired the same amount of P when they were together while *Artemisia* procured about six to seven times more P than did *Pseudoroegneria* (Fig. 2). This corresponds with an earlier experiment, in which *Artemisia tridentata* was located between neighbours of *Agropyron desertorum* and *Pseudoroegneria spicata* and labelled, unfertilized patches were placed in the interspaces. The shrub acquired six times more *P from the soil interspace shared with *Pseudoroegneria* than from the interspace shared with *Agropyron* even though the shrub had the same investment in root length and mycorrhizal infection in both soil interspaces (Caldwell *et al.*, 1985). Surprisingly, in the experiment with the two grasses, they were equivalent in their acquisition of P from both control and enriched patches (Fig. 2).

There is some correspondence between plant shoot biomass and competition for P in these experiments, especially if the heavy wood component of the shrub is ignored, since this is largely necromass (Table 1). Only for the experiment with *Artemisia* and *Pseudoroegneria* was there a sizeable difference in average shoot biomass and in acquisition of P between the two species. The other two species combinations involved plants of comparable size and similar P acquisition, if the heavy *Artemisia* wood is not considered. Nevertheless, interspecific comparisons of shoot size and competitive ability are tenuous since they do not necessarily account for factors such as differences in allocation to fine roots. In this study, no relationships emerged between intraspecific differences in shoot biomass and competitive ability for P even though plant size varied by factors of 2·5–5 among replicates of each species in these experiments. However, others have found that differences in plant size appear to be of greater importance for light competition than for competition below ground (Weiner, 1986; Wilson, 1988).

Concluding thoughts

Returning to the questions presented at the outset of this paper: the study species were very effective in exploiting the additional P in enriched microsites compared with acquisition from control microsites. Despite the large differences in P fertility of control and enriched microsites, the relative ability of the neighbouring species to acquire P from the two types of patches was very similar. There was no tendency for the plants to procure proportionately more P from control patches, if they were not effective in acquiring P from enriched patches in competition with their neighbours. Finally, there was no indication that intraspecific differences in shoot biomass bore a relationship with the ability to acquire P from either enriched or control patches.

The ability of plants to exploit nutrient resources from fertile soil microsites may be an important element of their capacity to compete. Root systems that exhibit plasticity in growth and physiological characteristics would likely confer an advantage in spatially heterogeneous environments. However, the root adaptations advantageous in exploiting spatial heterogeneity may reflect, in part, selection for rapid response to temporal changes in soil nutrient availability (e.g. Campbell & Grime, 1989).

Acknowledgments

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