Rapid shifts in phosphate acquisition show direct competition between neighbouring plants

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Direct demonstrations of competition between higher plants for specific soil resources are seldom possible[1-3]. Previous neighbour plant removal experiments in desert environments have shown increased growth and improved water status of the remaining plants[4-6]. However, these responses were only measured several months after the removal of neighbours, after which period there would have been ample time for major adjustments in the root distribution of surviving plants. We report here field experiments using dual-isotope labelling to measure opportunistic phosphate acquisition by shrubs within 2 weeks of partial defoliation of neighbouring grass plants. Phosphate isotope uptake from interspaces shared with defoliated grasses increased to as much as six times that of uptake from interspaces shared with unperturbed neighbours. The experiments indicate immediate competition for phosphate and the influence of root physiological activity on this competition.

We conducted two field experiments with *Artemisia tridentata* ssp. *vaseyana* (Rydb.) Beetle, a dominant shrub in western North America. One experiment was with a co-occurring grass, *Agropyron spicatum* (Pursh) Scribn. and Smith, and one with *Agropyron desertorum* (Fisch. ex Link) Schult., a grass from Eurasia widely seeded in this region. These two tussock grasses have very similar canopy structure, phenology, photosynthetic characteristics and biomass allocation[7-11]. Yet, *A. desertorum* is more competitive and more tolerant of grazing[3,7,12,13]. All three species have vesicular-arbuscular mycorrhizae of the genus *Glomus*[3].

To provide replicate plant sets, the experiments were conducted in field plots established with transplants seven years earlier. Soils are Typic Haploxerolls[7] and were not ploughed before transplanting. Bicarbonate-exchangeable phosphate is generally <6 p.p.m. The shrubs were interplanted with either grass species in an even 0.5-m spacing. Their roots intermingle extensively[3,7,13]. The experiments with the two grass species were in adjacent plots. Six replicate plant sets, each consisting of a shrub surrounded by four grass plants, were chosen for each experiment. The grass tussocks had basal diameter ~15 cm and the shrubs had canopies ~30-50 cm in diameter. Total canopy cover was similar to that in shrub/grass steppe communities. All three species were actively growing at the time of the experiments. Soils were moist throughout the rooting zone which is common at the time of year of the experiments[7,12]. On opposite sides of each shrub, ^{33}P and ^{32}P isotopes (18.5 MBq each, as carrier-free orthophosphoric acid) were injected into a series of ten 30-cm-deep holes previously created by inserting 6-mm-diameter rods into the soil. The holes were 2.5 cm apart in a row midway between the shrub and the grass and perpendicular to a line connecting the plants. The holes were then covered by soil. Phosphorus desorption tests indicate that 90-95% of added P is bound in these soils. The amount of total P injected in each row was less than 10^{-11} g cm^{-3}, which is below the concentration that might increase root growth[14].

On the day before labelling (23 May 1985), one of the grasses adjacent to a labelled interspace was clipped to 7 cm in height (~85% foliage removal). The clipped plant was next to a ^{32}P label in half the replicates and next to a ^{33}P label in the other half to compensate for possible isotope discrimination.

After 53 days, the experiments were terminated and the grasses harvested to estimate the P-isotope content of the shoots and crowns. Subsamples reduced to ashes (500° C) were digested in HCl, and scintillation counts were corrected for half-life, counting efficiency and energy overlap. As expected, the clipped

Table 1 Total quantities of P isotope in neighbouring grasses

	Agropyron spicatum		
	Control (kBq)		Defoliated (kBq)
Shoots	380 (92% ± 2%)	Regrowth shoots	12 (78% ± 5%)
		Older shoots	3 (19% ± 5%)
Crowns	35 (8% ± 2%)	Crowns	0.4 (3% ± 0.6%)
Total	415 ± 107	Total	15.4 ± 6
	Agropyron desertorum		
	Control (kBq)		Defoliated (kBq)
Shoots	686 (94% ± 2%)	Regrowth shoots	250 (86% ± 2%)
		Older shoots	36 (12% ± 2%)
Crowns	47 (6% ± 2%)	Crowns	7 (2% ± 0.4%)
Total	733 ± 234	Total	293 ± 115

Total quantities of P isotope in kBq (± one s.e.m.) and percentage allocated to plant parts (± one s.e.m.). In the experiment with each grass species $n = 6$.

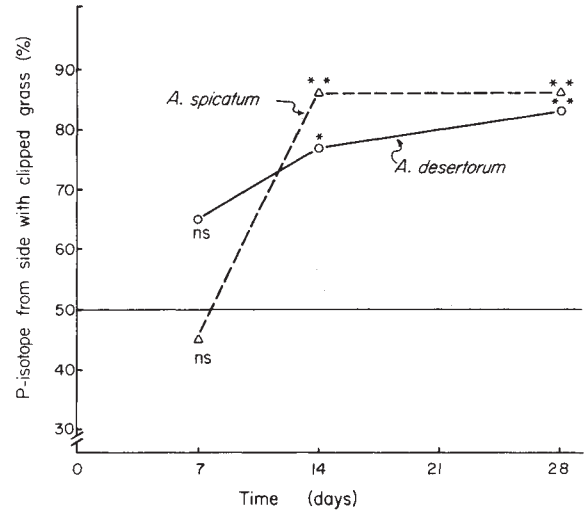

Fig. 1 The proportion of P isotope acquired by *Artemisia* from the labelled interspace shared with the partially defoliated grass at different times following defoliation and labelling. Each point represents the isotope proportion in the preceding time interval. This is shown for separate, but concurrent, experiments with both tussock grass species. As the two experiments were conducted in adjacent plots, comparison of the grass species is not appropriate[19]. Results of *t*-tests with square-root arcsin-transformed data at each time in each experiment are indicated thus: **, $P < 0.01$; *, $P < 0.05$; ns, not significantly different from the null hypothesis of 50% isotope from clipped side; $n = 6$ for each experiment.

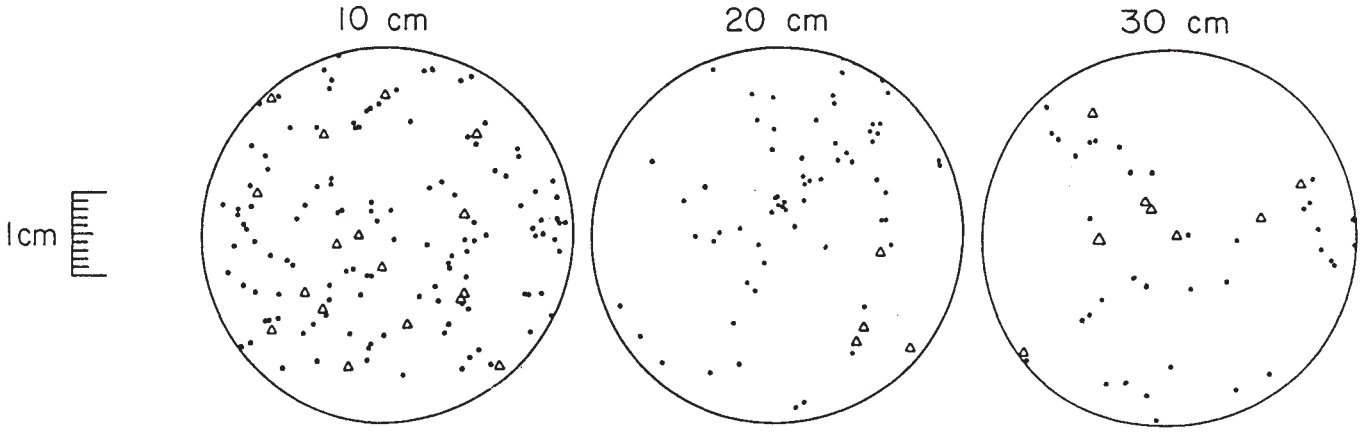

Fig. 2 The distribution of individual fine roots in cross-sections of soil in the interspace between *Artemisia* (△) and *A. desertorum* (●) at three depths. Parcels of soil previously frozen with liquid nitrogen were excavated and then sectioned at −70° with a lapidary saw. The position of individual roots intersecting the cut plane was mapped from the cut soil sections and from enlarged photographs of them. To determine whether the individual roots belonged to *Artemisia* or the grass, a fluorescence technique has been developed and tested on roots of *Artemisia* and *Agropyron* of different age and phenological status. On partial thawing of the soil, individual root segments (~1 cm) were removed from the soil and dried. A basic extract of the roots (2N NaOH) was dried on chromatography paper and the spots observed under a UV-A lamp. The *Artemisia* and *Agropyron* roots are clearly distinguished by colour and intensity of fluorescence.

grasses acquired less isotope than the unperturbed grasses even though they were rapidly regrowing (Table 1).

If the shrubs and grasses are competing for the same resource at the same time, reduced uptake by the grass should be reflected in increased resource acquisition by the shrub. The relative P-isotope acquisition by the shrub from the two labelled interspaces was determined by the ratio of P isotopes in small shoot samples at different times[3,15]. Within two weeks following defoliation, the proportion of P isotope acquired by *Artemisia* from the interspaces shared with the clipped grasses increased substantially (Fig. 1). This response was very similar in experiments with both grass species, even though these grass species differ greatly in their ability to recover from defoliation and to compete[3,7,12,13]. After 53 days when the grasses were harvested, the proportion of P isotope acquired by the shrubs from the interspaces shared with the clipped grasses was 68 and 76% in the experiments with *A. spicatum* and *A. desertorum*, respectively (both significantly different from 50% at $P < 0.05$; Wilcoxon rank sum test).

Competition for P is very localized. Because phosphate ions are almost immobile in soils, the effective uptake zone is within a few millimetres of a root and its associated mycorrhizae[16]. Thus, individual roots of neighbouring plants must be very close to each other to compete for the same phosphate ions at the same time. The distance between individual roots depends both on the average rooting densities (root length divided by soil volume) and the distribution patterns of individual roots. As shown in Fig. 2, individual roots of neighbouring plants were close enough to compete directly for phosphate.

The proximity of the neighbouring plant roots and the rapid and sizeable shift in P uptake exhibited by the shrub indicate an immediate competition for P. This competition, in turn, appears to be substantially influenced by the physiological activity of the roots rather than simply by general root morphology and distribution in the soil. Processes such as root phosphate absorption, continued fine-root maintenance and extension, and support of mycorrhizae all depend on a continuing energy supply to the roots and on plant demand for P. Treatments such as shading and defoliation can curtail root growth and nutrient uptake within 24 h (refs 17 and 18). In our experiments, the reduced P absorption by the clipped grass plants (Table 1) was rapidly reflected in the acquisition patterns of the shrub (Fig. 1) even though the physiological activity and general distribution of the shrub roots would not be directly affected by the clipping treatments.

The rapid shift in resource acquisition demonstrated in these experiments not only indicates immediate resource competition, but also shows how quickly the balance of competition might change in the event of herbivory. We have focused on competition for phosphorus because of the sensitivity of the dual-isotope approach. We do not, however, feel that P is the only, nor necessarily the pivotal, resource in the competitive balance of these plants[3].

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