

Phosphorus acquisition by *Bromus madritensis* ssp. *rubens* from soil interspaces shared with Mojave Desert shrubs

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Summary

1. *Bromus madritensis* ssp. *rubens* (L.) Husnot (Red Brome) is an invasive annual grass that is associated with increases in fire frequency and decreases in perennial plant diversity. The success of Red Brome in the Mojave Desert has been attributed to its competitive ability, but competition between Red Brome and native shrubs for below-ground resources has not been investigated previously. In this study we present a modification of previous dual-isotope methods that assesses competitive interactions and responses among plants under field conditions. We then use this method to (i) determine if direct competition for phosphorus (P) occurs between Red Brome and native shrubs, and (ii) evaluate the effectiveness of phosphate acquisition by Red Brome from soil interspaces shared with different Mojave Desert shrub species.

2. Clipping Red Brome to remove $\approx 85\%$ of its foliage on the day prior to labelling soil interspaces with P isotopes did not have the desired effect of inhibiting phosphorus uptake by Red Brome. Therefore we were unable to verify that direct competition for P occurred between Red Brome and native shrubs.

3. Nonetheless, by sampling plant tissue from unclipped strips of Red Brome that were centred between two shrubs, we were able to evaluate the effectiveness of phosphate acquisition by Red Brome from interspaces shared with different shrubs. There were no differences in the amount of phosphorus acquired by Red Brome from soil interspaces shared with the evergreen shrub *Larrea tridentata* (D.C.) Cov. versus soil interspaces shared with the drought deciduous shrub *Lycium pallidum* Miers. However, Red Brome acquired more than six times as much P from soil interspaces shared with *Larrea* than from soil interspaces shared with the drought deciduous shrub *Ambrosia dumosa* Payne. Less P uptake by Red Brome from soil interspaces shared with *Ambrosia* suggests greater effectiveness of *Ambrosia* compared with *Larrea* to deplete soil P.

Key-words: *Ambrosia dumosa*, competition, *Larrea tridentata*, *Lycium pallidum*, Red Brome

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Introduction

Exotic plants have significantly altered the ecology of North American deserts (Smith, Monson & Anderson 1997). Of particular importance in Mojave Desert shrub communities is the invasion of exotic annual grasses in the genus *Bromus* (Hunter 1991). Eight species of *Bromus* occur in the Mojave Desert, six of which are introduced (Beatley 1976). Two of the species, *Bromus tectorum* L. (Cheatgrass) and *Bromus madritensis* ssp. *rubens* (L.) Husnot (Red Brome) have become widespread throughout southern Nevada, and significantly affect the ecology of the region (Hunter 1991). Cheatgrass occurs primarily at higher altitudes (above 1200 m) and is associated more strongly with

disturbance, whereas Red Brome occurs in greater densities at lower elevations and has become a thoroughly integrated member of undisturbed, native shrub communities (Beatley 1966; Hunter 1991). In the last three decades the relative dominance of Red Brome has increased significantly in Rock Valley and other Mojave Desert areas, such that in 1988 densities of Red Brome exceeded 2000 individuals m^{-2} , or 97% of the total annual plant biomass in Rock Valley (Hunter 1990, 1991). The invasion of Red Brome is of concern because increases in fire frequency (Beatley 1966; Brooks 1999) and decreases in species richness are associated with its establishment (Hunter 1990, 1991). Although the success of Red Brome has been attributed to its competitive ability, competition between Red Brome

and native shrubs for below-ground resources has not been investigated.

Competition between plants for below-ground resources is often inferred from their response when the competitive environment is manipulated by adding or removing neighbours, or by changing resource levels through fertilization (Ehleringer 1984; Fonteyn & Mahall 1978; Robberecht, Mahall & Nobel 1983). However, measurement of plant responses well after a manipulation has occurred allows ample time for major adjustments in root distributions of the surviving plants, thus altering biotic interactions and outcomes. These manipulations can be avoided by the use of dual-isotope labelling techniques that allow *in situ* demonstration of direct competition for below-ground resources without disturbance to or manipulation of root distributions (Caldwell *et al.* 1985). For example, Caldwell *et al.* (1987) reported a field experiment in which a dual-isotope labelling technique was used to measure opportunistic phosphate acquisition by Sagebrush (*Artemisia tridentata*) within 2 weeks of partial defoliation of neighbouring grass plants (*Agropyron desertorum* and *A. spicatum*). A rapid shift in phosphorus (P) acquisition by Sagebrush following defoliation of the neighbouring grasses indicated direct competition for phosphate. Although P is not the single crucial resource in the balance of competition (Caldwell *et al.* 1987), P is needed for maximum nitrogen (N) mineralization and nitrification (West, Griffin & Jurinak 1984) and may be more limiting than N in many terrestrial ecosystems (Gutschick 1981; Lajtha & Schlesinger 1986; McGill & Christie 1983). In addition, effective moisture uptake facilitates absorption of P, and better P nutrition facilitates plants' capacity to acquire other nutrients and water (Caldwell & Richards 1986; Radin & Eidenbock 1984), which is the most limiting resource in arid environments (Smith & Nowak 1990). Therefore, plants that utilize P effectively should have a competitive advantage over species that do not.

In the current study, we introduce an innovative modification of previous P-isotope approaches that allows simultaneous determination of (i) direct competition between species for phosphate, and (ii) the relative ability of the species to acquire phosphate from shared soil interspaces under field conditions. We then use this technique to examine competitive interactions between Red Brome and three important shrub species in the Mojave Desert of western North America.

Materials and methods

STUDY SITE

Research was conducted at the Nevada Test Site (NTS), located between 36°35', 37°15' N latitude and 115°55', 116°35' W longitude. The NTS is 350 000 ha of arid and semiarid terrain that includes the transition zone between the Mojave and Great Basin deserts of western

North America. We refer the reader to Rundel & Gibson (1996) for excellent descriptions of climate gradients, vegetation patterns and physical geography for the region. Elevation of the study site is 970 m. Yearly rainfall at the NTS is highly variable, but generally ranges from 85 to 160 mm and rarely exceeds 250 mm year⁻¹ at elevations below 1000 m (Rundel & Gibson 1996). A soil classification map was not available for our study site, but soils located at similar elevations on the NTS belong to the Thermic family and would be classified as Entisols with an ochric epipedon (Rundel & Gibson 1996). Available P concentrations in these soils are low, and range from 2 to 2.5 mg kg⁻¹ (based on NaHCO₃ extraction) in the relatively thin (0–0.15 m) A1 horizon to 0.16 mg kg⁻¹ for C horizons at a depth of ≈1.5 m (Romney *et al.* 1973).

STUDY SPECIES

Three perennial shrub species were chosen for study. *Larrea tridentata* (D.C.) Cov. (Creosote Bush) is the dominant evergreen species in North American deserts. *Larrea* is a drought-resistant species that has the potential to grow at any time of the year (Oechel, Strain & Odening 1972). Due to *Larrea's* dominance in North American warm deserts, this genus has received a great deal of research attention (e.g. Mabry, Hunziker & DiFeo 1977). *Ambrosia dumosa* Payne (White Bursage) is one of the most abundant drought-deciduous species in the Mojave Desert and often forms co-dominant associations with *Larrea*. *Lycium pallidum* Miers (Desert Thorn) is another important drought-deciduous species in the Mojave Desert. For simplicity, we will refer to these species by their generic names in this paper. Both *Ambrosia* and *Lycium* are drought-avoiders and produce a major leaf cohort in the winter, but will produce a smaller leaf cohort in the summer given sufficient rainfall (Smith, Monson & Anderson 1997).

PLOT ESTABLISHMENT

Thirty plots were established at the NTS during October 1996. Each plot consisted of a pair of shrubs and three strips of Red Brome (Fig. 1). Ten of the plots consisted of *Larrea* paired with *Ambrosia*; 10 plots of *Larrea* paired with *Lycium*; and 10 plots of *Larrea* paired with *Larrea*. *Larrea-Larrea* plots were used as an experimental control. Red Brome seeds were broadcast in 0.25 m × 1.00 m strips (≈800 seeds per strip) on each side of the two shrubs so that a total of three strips of Red Brome were planted in each plot: one strip on each end of the plot and one strip centred between *Larrea* and the second shrub. The minimum distance between the bases of the two shrubs was 1 m and the maximum distance 2.5 m. No other perennial shrubs were allowed to grow within 3 m of the target shrubs. Annual plants beneath the

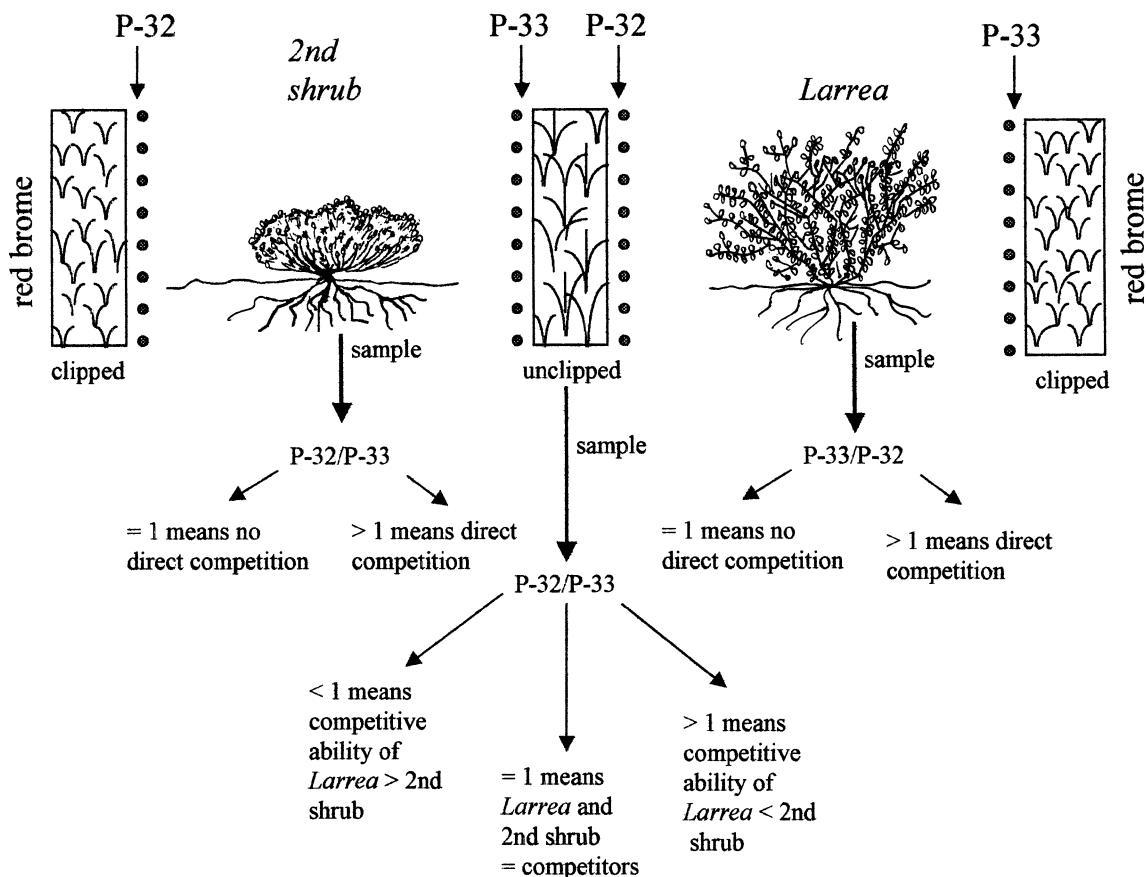


Fig. 1. Schematic diagram of study plot establishment and dual isotope labelling technique. Each plot consisted of a pair of shrubs (*Larrea* and a second shrub that was either *Larrea*, *Ambrosia* or *Lycium*) and strips of Red Brome planted on either side of each shrub. The two end strips of Red Brome were clipped to approximately two-thirds of their original height on the day prior to labelling. If clipping decreases P uptake and hence increases soil P availability, then P-isotope concentrations of shrub shoot samples indicate if direct competition between Red Brome and the shrubs is occurring. P-isotope concentrations of shoot samples from the centre, unclipped strip of Red Brome indicate if Red Brome acquires phosphate differentially from soil interspaces shared with different shrubs.

target shrubs and non-Red Brome annuals within the Red Brome strips were weeded. Because precipitation was below average, the plots were irrigated five times at 2–3-week intervals between November 1996 and March 1997 to facilitate Red Brome establishment and growth; each irrigation supplied an amount of water equivalent to 2.54 cm of rainfall.

SOIL LABELLING AND VEGETATION SAMPLING

At the end of March 1997, ^{33}P and ^{32}P (18.5 MBq each as carrier-free orthophosphoric acid) diluted in 250 ml distilled H_2O were injected separately on opposite sides of each shrub into a series of 10 15 cm deep holes that were 1.27 cm in diameter and adjacent to the edge of the Red Brome strips (Fig. 1). Twenty-five ml of solution were injected into each hole. The labelling solutions contained 0.02 M HCl to ensure that the orthophosphate radioisotope remained in solution until injection into the soil. The isotopes were injected adjacent to the Red Brome strips because competition for P can occur only when phosphate is

within a few mm of a root due to low diffusivity in soil (Nye & Tinker 1977). The lateral roots of desert shrubs can extend several metres beyond the base of the plant (Drew 1979; Rundel & Gibson 1996), but lateral roots of *Bromus* spp. extend only 20–30 cm (Hulbert 1955). The isotopes were injected at the 15 cm depth because *Bromus* spp. have the greatest concentration of roots in the top 20 cm of soil (Hulbert 1955), and each of the shrubs has a high concentration of roots at that depth (Wallace, Romney & Cha 1980). The concentrations of the isotopes were below those known to influence root or mycorrhizal growth (Schenk & Barber 1979). In order to account for possible discrimination between ^{32}P and ^{33}P , the form of isotope injected on the right and left sides of the shrubs was alternated.

To test for direct competition between Red Brome and the shrubs, the two strips of Red Brome on each end of the plot were clipped to remove $\approx 85\%$ of their foliage on the day prior to labelling (25 March 1997) following the procedures of Caldwell *et al.* (1987). At the time of clipping, the Red Brome was 4–5 cm high and many, but not all, of the plants had initiated

flowering. If direct competition for P was occurring between Red Brome and the shrubs, and if defoliation of Red Brome significantly decreased its P uptake, then more P should be available in the soil interspaces shared with the clipped Red Brome and the shrubs should acquire more P from that interspace (Fig. 1). If Red Brome and the shrubs were not competing directly for the same P, then the shrubs should not utilize the increased P availability in interspaces shared with clipped Red Brome. The relative P isotope acquisition by the shrubs was determined by sampling shrub shoot tissue 23 and 44 days after labelling (15 April and 6 May 1997, respectively); these dates corresponded with Red Brome anthesis and onset of senescence, respectively.

In order to address the second objective, to test the relative ability of Red Brome to acquire P from soil interspaces shared with different shrub species, shoot samples were collected from the unclipped strip of Red Brome centred between the two shrubs. If Red Brome was more effective at acquiring P from interspaces shared with one shrub than with another, then Red Brome should have relatively greater amounts of the radioisotope injected near that first shrub (Fig. 1). If Red Brome was equally effective, as would be expected for the *Larrea-Larrea* plots, then the ratio of the two P isotopes should be 1. The Red Brome shoot samples were collected at the same time that shrub shoot samples were collected for the first objective described above. To measure amounts of P-isotope label acquired by Red Brome and the shrubs, shrub and Red Brome shoot samples were reduced to ash (500 °C) and digested in HCl, and scintillation counts were corrected for half-life, counting efficiency and energy overlap (Black, Richards & Manwaring 1994).

Statistical analyses were performed with SAS software (SAS Institute, Inc., Cary, NC, USA). Two-tailed *t*-tests were used to compare amounts of P isotope taken up by clipped versus unclipped strips of Red Brome and to compare amounts of P isotope taken up by the centre, unclipped strip of Red Brome from soil interspaces shared with different shrubs. Box plots and normal probability plots of residuals were used

to assess normality and outliers. P-isotope concentration data were log-transformed to meet assumptions of normality. Statistical power in this experiment was low because of the small sample size and high variability common in field experiments. Therefore we considered differences in P-isotope concentrations to be statistically different at $P < 0.10$. This approach may increase the chance of type I errors (concluding treatment differences when there are none), but type II errors (concluding no treatment effect when there is one) are reduced. The log-likelihood ratio or *G*-test (Zar 1996) was used to determine if the frequency with which Red Brome acquired more P from soil interspaces shared with *Larrea* versus soil interspaces shared with *Ambrosia* or *Lycium* was significantly different than expected (50% in each category).

Results

RED BROME-SHRUB DIRECT COMPETITION

A critical assumption of the first study, to test for direct competition between Red Brome and shrubs, is that defoliation of Red Brome would decrease its P uptake and subsequently increase P availability in the soil interspaces adjacent to clipped Red Brome stands. Contrary to our expectations, the clipping treatment did not decrease P uptake by Red Brome (mean for two sample dates + SE = 2536 + 805 and 2129 + 881 KBq g⁻¹ for clipped and unclipped Red Brome, respectively). In fact, the clipped Red Brome reached similar heights and produced comparable numbers of seeds to unclipped Red Brome (visual observation). In addition, P-isotope concentrations in shrub shoot samples indicated that all of the shrub species acquired equal amounts of P isotope from soil interspaces shared with clipped and unclipped Red Brome (Table 1). Consequently, we were unable to verify direct competition between Red Brome and the shrubs.

EFFECTIVENESS OF PHOSPHATE ACQUISITION FROM SHARED INTERSPACES

By measuring the ratio of ³²P and ³³P in samples collected from the unclipped strip of Red Brome centred between the two shrubs, we were able to examine the effectiveness of Red Brome in depleting soil P from soil interspaces shared with different shrubs. Within the *Larrea-Larrea* control plots there were no significant differences in the frequency that Red Brome acquired more P from the left versus the right soil interspace for either sample date (Table 2). Furthermore, the mean concentration of P isotope acquired by Red Brome from the left and right interspaces over the two sample periods was similar (Table 3). Equal P uptake by Red Brome from both soil interspaces in the *Larrea-Larrea* plots validates this experimental design.

For the *Larrea-Lycium* plots, the frequency that Red Brome acquired more P isotope from soil interspaces

Table 1. Results of *t*-tests comparing concentrations of P isotopes in shrub shoot samples over two sample periods. Concentrations indicate amounts of radioisotope acquired from soil interspaces shared with clipped versus unclipped Red Brome. The large sample size for *Larrea* reflects each *Larrea* plant over all three shrub combinations

Shrub	N	Treatment	Mean P isotope concentration	
			(kBq g ⁻¹) ± SE	<i>P</i> value
<i>Larrea</i>	80	clipped	21 ± 9	0.63
	80	unclipped	27 ± 9	
<i>Lycium</i>	20	clipped	8 ± 4	0.85
	20	unclipped	7 ± 3	
<i>Ambrosia</i>	20	clipped	296 ± 189	0.92
	20	unclipped	271 ± 158	

Table 2. Percentage of plots from which Red Brome acquired more P from interspaces shared with *Larrea* versus interspaces shared with second shrub. For *Larrea-Larrea* plots the second shrub is the interspace to the left of the centre Red Brome strip

Shrub pair	Days after labelling	Percentage of plots where more P isotope was acquired from	
		<i>Larrea</i> interspace	Second shrub interspace
<i>Larrea-Larrea</i>	23	60	40
	44	50	50
<i>Larrea-Lycium</i>	23	60	40
	44	40	60
<i>Larrea-Ambrosia</i>	23	70	30
	44	80*	20

*Significant differences between interspaces ($P < 0.10$; $N = 10$).

Table 3. Mean \pm SE ($N = 20$) and proportions of P isotope concentrations (kBq g⁻¹) in Red Brome samples indicating relative amounts of phosphate acquired from interspaces shared with different shrubs over two sample periods. P values are results of t -tests comparing log-transformed concentrations

Shrub pair			P value
<i>Larrea-Larrea</i>	Right interspace	Left interspace	0.50
	2057 \pm 665 (50%)	2021 \pm 835 (50%)	
<i>Larrea-Lycium</i>	<i>Larrea</i> interspace	<i>Lycium</i> interspace	0.38
	1683 \pm 690 (54%)	1432 \pm 530 (46%)	
<i>Larrea-Ambrosia</i>	<i>Larrea</i> interspace	<i>Ambrosia</i> interspace	0.07
	6677 \pm 4622 (86%)	1065 \pm 846 (14%)	

shared with *Lycium* versus soil interspaces shared with *Larrea* was also not significantly different during either sample period (Table 2). Also, the mean concentration of P isotope acquired by Red Brome from each interspace over the two sample periods was nearly equal (Table 3).

Within the *Larrea-Ambrosia* plots, Red Brome acquired more P from *Larrea* soil interspaces seven out of 10 and eight out of 10 times for the first and second sample dates, respectively. The differences in frequency were significant only for the second sample date ($P = 0.038$). Over the two sample periods, the mean concentration of P isotope acquired by Red Brome from soil interspaces shared with *Larrea* was six times greater than the mean concentration of P isotope acquired by Red Brome from interspaces shared with *Ambrosia* (Table 3).

Discussion

Because clipping Red Brome did not have the desired effect of increasing P-isotope availability in the soil interspaces adjacent to the clipped stands of Red Brome, we were not able to verify that direct competition occurred between Red Brome and the shrubs. However, our experimental design enabled us to use samples from the centre, unclipped strip of Red Brome to determine if Red Brome acquires phosphate differ-

entially from soil interspaces shared with the evergreen shrub *Larrea* versus soil interspaces shared with either of the drought deciduous shrubs *Lycium* or *Ambrosia*. We found no significant difference in Red Brome's capacity to obtain phosphate from soil interspaces shared with *Larrea* versus soil interspaces shared with *Lycium*. However, Red Brome acquired more than six times as much P from soil interspaces shared with *Larrea* than from soil interspaces shared with *Ambrosia*, which suggests that *Ambrosia* is more effective than *Larrea* at depleting soil P.

An underlying assumption of this inference is that each shrub has more roots than its neighbour on the near side of the centre strip of Red Brome, and less than its neighbour on the far side. Each of the shrub species in this study has lateral roots that can extend 1.6–4.5 m from the base of the plant (Cannon 1913; Gile, Gibbons & Lenz 1998; Markle 1917). Furthermore, each of these species can deplete water in soil interspaces that are 0.5–1.5 m from the base of the plants (Yoder & Nowak 1999). Therefore, all three species probably had their roots completely beneath the centre Red Brome strip, and thus possibly obtained P isotope from both sides of the centre strip. If the shrubs were able to obtain P isotope equally well from both near and far sides of the centre Red Brome strip, then the shrubs would have obtained P isotopes from three locations (the right and left sides of the shrub plus the far side of the centre Red Brome strip). Thus the shrubs would have taken up more of one P isotope than the other, and P-isotope ratios in the shrubs would have been >1 . Because no significant differences in P-isotope ratios occurred for any shrub species (Table 1), we conclude that the shrubs did not acquire significant quantities of P isotope from the far side of the centre Red Brome strip. If, however, P-isotope ratios >1 had occurred, further investigation would have been required to determine if the ratios were the result of direct competition between Red Brome and the shrubs, or if the shrubs were obtaining P tracer from both sides of the unclipped Red Brome. Hence, in future studies of this type determination of maximum lateral rooting, as well as relative root length density of each shrub on both sides of the centre strip, would be necessary.

Several morphological and physiological traits may affect P acquisition, including rooting density and root surface area; mycorrhizal associations or root hair characteristics; root architecture or degree of branching; physiological uptake capacities; and proton or phosphatase excretions that facilitate nutrient uptake. Many of these factors have not been investigated for these species; however both *Larrea* and *Ambrosia* are colonized by vesicular-arbuscular mycorrhizal fungi (Bethlenfalvay, Dakessian & Pacovsky 1984), and Wallace & Romney (1972) report an abundance of mycorrhizal fungi associated with living and dead roots of all three shrub species. Hence mycorrhizal associations probably played an important role in P

acquisition by these plants. In contrast, physiological uptake capacities were probably not as critical as growth and morphological parameters because phosphate concentration at the root surface is quickly restored to equilibrium, and phosphate diffusion through the bulk soil is usually more limiting than absorption by roots (Clarkson 1985).

In addition to mycorrhizal associations and rooting densities, a potential mechanism that could contribute to differential P uptake by Red Brome from interspaces shared with *Ambrosia* and *Larrea* is root segregation (Schenk, Callaway & Mahall 1999). Root-system segregation may lead to competitive advantages because dominating below-ground space promotes competitive ability (Brisson & Reynolds 1997; Casper & Jackson 1997). Both *Larrea* and *Ambrosia* exhibit root segregation, but they have different mechanisms to induce it: *Larrea* appears to actively create and maintain space around its roots via a root-produced 'allelochemical' in order to segregate soil space for its exclusive use, whereas *Ambrosia* uses a root-recognition response to help reduce intraspecific competition by segregating soil space among different *Ambrosia* individuals (Mahall & Callaway 1991, 1992, 1996). These different root segregation mechanisms may have contributed to *Ambrosia*'s greater effectiveness than *Larrea* at depleting soil P. For instance, self-incompatibility of *Larrea* roots (intraspecific and intraindividual root segregation) may limit *Larrea*'s ability to make root distribution and architectural changes that are necessary to exploit immobile soil resources such as P (Caldwell & Richards 1986; Caldwell 1994; Fitter 1994). That is, because *Larrea* roots remain several millimetres apart (Mahall & Callaway 1991, 1992), they may explore soil less intricately than species that do not exhibit root segregation. Alternatively, *Larrea* may have depleted soil P less effectively than *Ambrosia* because soil P may be less limiting to *Larrea* than to *Ambrosia*. For example, growth and reproduction of evergreen species are not as closely coupled to soil nutrient availability as they are in deciduous species, due to nutrient storage and high redistribution efficiency in evergreen leaves (Gray & Schlesinger 1983). *Larrea* has strong P reabsorption prior to leaf abscission (Lajtha 1987), which is an effective P conservation mechanism. However, because Red Brome acquired phosphate differentially from soil interspaces shared with *Ambrosia* but not *Lycium*, factors other than those related to leaf phenology must have affected phosphate absorption among these species. Irrespective of the mechanism, differential P uptake by Red Brome indicates that *Ambrosia* is more effective than *Larrea* at depleting soil P. Holzapfel & Mahall (1999) demonstrated experimentally that *Ambrosia* positively influences biomass and seed production of annuals, including *Bromus*, growing under shrub canopies. However, the positive effects they observed were probably due to the effect of shading by shrub canopies on soil temperature and water availability (Holzapfel & Mahall

1999). These positive effects will not occur in shrub interspaces. Hence, in interspaces where shrub roots are numerous but positive canopy effects on soil temperature and water availability are absent, differential nutrient acquisition among shrub species may have considerable influence on long-term biotic interactions and outcomes between annuals and shrubs.

Conclusions

We have presented a novel modification to previous P-isotope approaches that simultaneously tests for direct competition and relative competitive ability between species. Our experimental manipulations were not entirely successful because clipping Red Brome did not decrease P uptake by Red Brome. Subsequently, we were unable to verify direct competition between Red Brome and native Mojave Desert shrubs. However, we were able to use an unclipped row of Red Brome that was centred between two shrubs to examine the relative competitive ability of Red Brome to acquire P from interspaces shared with different shrubs. Red brome was equally effective at acquiring P from soil interspaces shared with the evergreen shrub *Larrea tridentata* and the drought-deciduous shrub *Lycium pallidum*. However, Red Brome was up to six times as effective at acquiring P from interspaces shared with *Larrea* relative to those shared with the drought-deciduous shrub *A. dumosa*. These results suggest that *Ambrosia* is better able than *Larrea* to deplete soil P at the expense of Red Brome. Further investigation will be required to elucidate long-term competitive outcomes between these species and to identify mechanisms that contribute to the effectiveness of below-ground resource acquisition for each species.

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