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Exploitation of Nutrient-Rich Soil Patches by Invasive Annual and Native Perennial Grasses

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Invasion of nutrient-poor habitats might be related to the ability of a species to exploit nutrient-rich microsites. Recent research suggests fast-growing species might have a greater ability to allocate root biomass to nutrient-rich microsites (root foraging precision) than slow-growing species. We examined if differences in relative growth rate (RGR) between invasive and native species were related to differences in foraging precision. We hypothesized that invasive species would: (1) have greater foraging precision than native species but (2) greater foraging precision would come at a cost in terms of root nutrient uptake rate. Foraging precision was evaluated on plants growing in soils with uniform or patchy nutrient distribution. Plants were harvested at a common time and a common developmental stage to separate indirect effects of RGR on foraging. Nutrient uptake rate was examined by exposing plants to a low or high nitrogen pulse. Invasives foraged more precisely than natives but had lower nitrogen uptake rate. Although these results support the idea of a positive relationship between RGR and foraging precision, biomass production in heterogeneous soils showed no relationship to foraging precision. Instead, species with greater RGR produced more biomass and root length across all treatments, allowing greater nutrient capture in heterogeneous soils. Although these results do not exclude a role for proliferation in influencing invasion of nutrient-poor systems or the potential for heterogeneity to influence population processes, these results suggest other traits may have an overriding importance in determining invader success in these systems.

Key words: Bunchgrasses, invasive, nutrients, rangeland, weeds.

Predicting the likelihood of invasion and the impact of invaders on ecosystems requires understanding the interaction between invader traits and ecosystem characteristics (Levine et al. 2003; Lonsdale 1999; Moyle and Light 1996). Early efforts to predict likelihood of invasion focused on correlating traits with invasiveness (Baker 1974; Newsome and Nobel 1986; Noble and Slatyer 1980). Success with these approaches was limited to a small group of species and many exceptions were identified, preventing a general theory of invasiveness from being developed (Mack et al. 2000; Perrins et al. 1992; Rejmanek and Richardson 1996). More recently, however, traits related to leaf and root tissue economics have been identified as important factors differentiating plant ecological strategies and valuable predictors of plant performance in different environments (Diaz et al. 2004; Wright et al. 2004). These traits also have emerged as useful predictors of invasiveness and habitat invasibility at multiple spatial scales (Grotkopp et al. 2002; Hamilton et al. 2005; Leishman et al. 2007).

At one end of the tissue economic spectrum are plants that construct thin, poorly-protected leaf and root tissue. This strategy permits quick return on resources allocated to roots and leaves, allowing rapid growth, but comes at a cost in terms of tissue life span (Westoby et al. 2002). At the opposite end of the spectrum are plants that produce thick, dense, and well-protected leaf and root tissue. This strategy causes a low rate of return on resources invested in tissue, resulting in slow growth, but increases tissue life span and allows plants a greater duration of return on resources allocated to leaves and roots (Berendse 1994; Coley 1988). The benefits of these contrasting traits are expected to depend on resource availability, with rapid growth and tissue turnover favored in nutrient-rich environments and construction of long-lived tissue favored in nutrient-poor environments.

Research in a number of systems has demonstrated that invasive species produce thinner leaf and root tissue than their native counterparts, allowing invasives to outperform

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Interpretive Summary

We examined if differences in ability to place roots in nutrient-rich soil microsites could be one mechanism contributing to the success of invasive annual grasses in perennial-dominated systems. By growing plants in uniform or patchy soil nutrient environments, we found that invasive annual grasses had greater precision in root placement than slow-growing native perennials. However, the noninvasive annual rye grass and some native perennial species showed root growth responses comparable to the invasive annuals. This suggests the ability to place roots in nutrient-rich microsites might not play a large role in the ability of annual grasses to establish and spread in nutrient-poor soils. Differences in seed production as well as germination and emergence timing rather than differences in root traits could contribute to the success of annual grasses in these systems.

natives following disturbance or increases in resource availability (Burns 2004; Grotkopp and Rejmanek 2007; James and Drenovsky 2007; Leishman et al. 2007). Although these responses are consistent with predictions based on leaf and root tissue economics, many invasives readily colonize undisturbed, nutrient-poor habitats as well (Funk 2008; James et al. 2006; Svejcar and Tausch 1991,). Although this could be due to a number of factors including escape from natural enemies or greater nutrient-use-efficiency (Blumenthal 2006; Funk and Vitousek 2007), it also could be due to a greater ability of invasive plants to forage for soil nutrients (Rajaniemi and Reynolds 2004).

Soil nutrient heterogeneity is common in nutrient-poor systems, and nutrient capture from short-lived patches can contribute to a large portion of a plants annual nutrient budget (Bilbrough and Caldwell 1997; Farley and Fitter 1999; Gross et al. 1995; Stark 1994). Plants have a number of mechanisms that allow exploitation of ephemeral nutrient patches. This includes increasing root biomass in patches (root proliferation), changing root morphology to increase root length in patches, and increasing nutrient uptake rate per unit root length (Hodge 2004). Variation in these foraging mechanisms can be important in determining nutrient capture and competitive ability among neighboring plants (Robinson et al. 1999) and could play a significant role in determining invader fate in nutrient-poor systems.

For example, a recent meta-analysis suggested root proliferation ability might be related to the major ecological strategies defined by root and leaf tissue economics (Kembel et al. 2008). This analysis showed that the ability to proliferate roots in nutrient patches was positively correlated with growth and negatively correlated with tissue lifespan and root tissue thickness. Although there has been little comparison of foraging strategies between co-occurring native and invasive species, this suggests foraging precision in nutrient-poor habitats might relate directly to the leaf and root resource economy strategies of plants and be an important suite of traits determining the ability of a species to invade nutrient-poor systems. However, species foraging ability is inextricably linked to growth rate, and large differences in growth rate among species can confound interpretation of differences in foraging ability among species. For example, even if invasive and native species have an equivalent ability to place roots in nutrient patches, if the invasive species has a greater relative growth rate (RGR) than the native species, it will be able to add more root tissue to a nutrient patch per unit time than the native species (Aanderud et al. 2003). Separating species-specific foraging ability from species differences in RGR requires making observation of root proliferation at a common time, as well as a common size or developmental stage where differences in RGR are minimized (Aanderud et al. 2003; Coleman et al. 1994). Lastly, there might be a trade-off between root foraging mechanisms. For example, a trade-off between ability to proliferate roots and the ability to increase nutrient uptake per unit root has long been proposed (Grime 1994; Hutchings and Dekroon 1994). If trade-offs occur, the value of any particular foraging trait would be a function of the soil nutrient environment. Gaining insight into any potential role root foraging and soil nutrient heterogeneity plays in invasion of nutrient-poor systems requires separating direct and indirect effects of life history traits (e.g., RGR) on foraging ability as well as understanding trade-offs among foraging traits.

The broad objective of this study was to compare the foraging ability of invasive annual grasses and native perennial grasses. We hypothesized that: (1) fast-growing, invasive annual grasses would demonstrate greater foraging precision than slow-growing native perennial grasses when observations were made at a common time and RGR differences contribute to differences in foraging ability; (2) differences in foraging precision among invasives and natives would diminish when observations were made at a common developmental stage to minimize RGR effects on foraging; and(3) there will be a trade-off between foraging precision and the ability to increase nitrogen (N) uptake rate per unit root length.

Methods

Study System and Materials. In spring 2006, approximately 3-wk-old seedlings of the eight study species (Table 1) were planted into large pots (25 cm diam by 30 cm deep [9.8 inches by 11.8 inches]) in an outdoor garden at the Eastern Oregon Agricultural Research Center, Burns, OR. The species selected for this experiment include three annual grasses, downy bromedowny brome (*Bromus tectorum* L.), medusahead [*Taeniatherum caput-medusae* (L.) Nevski], and rattlesnake brome (*Bromus briziformis*

Table 1. List of the eight species used in this study. Nomenclature follows the USDA PLANTS database (http://plants.usda.gov/). Common stage harvest indicates number days a species grew until the common stage harvest was made. Leaf area and specific leaf area (SLA) are for the first full leaf produced (mean ± SE, *n* =10).

Functional group	Common name	Species	Species abbreviation	Common stage harvest (d)	Leaf area (cm^2)	SLA ($m^2\ kg^{-1}$)
Perennial bunchgrass	bluebunch wheatgrass	*Pseudoroegenaria spicata*	(PSSP)	70	0.41 ± 0.02	20.3 ± 1.6
	squirreltail	*Elymus elymoides*	(ELEL)	65	0.31 ± 0.02	14.8 ± 0.2
	Idaho fescue	*Festuca idahoensis*	(FEID)	81	0.11 ± 0.01	18.3 ± 1.1
	Sandberg bluegrass	*Poa secunda*	(POSE)	81	0.05 ± 0.01	22.5 ± 2.1
Annual grasses	rattlesnake brome	*Bromus briziformis*	(BRBR)	58	0.27 ± 0.01	22.5 ± 0.7
	Downy brome	*Bromus tectorum*	(BRTE)	58	0.33 ± 0.02	19.8 ± 0.6
	Medusahead	*Taeniatherum caput-medusae*	(TACA)	62	0.34 ± 0.01	22.4 ± 0.7
	winter annual rye	*Lolium perenne*	(LOPE)	48	0.28 ± 0.01	13.9 ± 0.4

Fisch. & C. A. Mey) that are native to Eurasia and the Mediterranean region but have extensively invaded over 50 million ha [123.5 million acres] in the western United States. The three annual grasses have comparable rooting patterns, but medusahead tends to occupy more clay-dominated soils and emerge later and maintain green leaves later in the growing season than rattlesnake brome and downy brome (James et al. 2008). We also included one introduced, noninvasive annual, annual rye (*Lolium perenne* L.) in the experiment to examine if any trait differences among annuals were unique to invaders or characteristic of the annual life form in general. The four native perennial grasses used in this study are commonly used in efforts to restore annual grass invaded systems. Bluebunch wheatgrass [*Pseudoroegenaria spicata* (Pursh) A. Löve], squirreltail [*Elymus elymoides* (Raf.) Swezey], and Idaho fescue (*Festuca idahoensis* Elmer) are deep-rooted bunchgrasses that tend to initiate leaf production later and maintain green leaves longer than the shallow rooted Sandberg bluegrass (*Poa secunda* J. Presl) (James et al. 2008).

Once seedlings of the eight species were planted, insulating foam was placed around the pots to minimize soil temperature fluctuations. Pots were filled with a 1 : 1 mixture of field soil and coarse sand to provide a low-nitrogen (N) soil medium. Field soil was collected from the top 20 cm at the Northern Great Basin Experimental Range (43°29′N, 119°43′W; about 1,400 m [4,480 ft] elev.), about 56 km (34.7 mi) west of Burns, Oregon. The soils at the site are Typic Durixerolls and are sandy loam to loamy sand (Lentz and Simonson 1986).

Experimental Design, Nutrient Treatments, and Harvests. In each of seven blocks, four plants of each species were assigned to one of two spatial patterns of nutrient availability (control or patch) and to one of two harvests (common time or common developmental stage) for a total of 224 plants (8 species by 2 spatial patterns of nutrient availability by 2 harvests by 7 blocks = 224). The nutrient patches were created before seedlings were planted by mixing 2 g of slow-release fertilizer (N : P : K 10–10–10) with field soil and placing this mixture in two, 2 mm, plastic mesh cores (6 by 10 cm). Mesh cores were placed in the 5 to 15 cm soil layer and centered approximately 7 cm from the edge of the pot. These cores were similar in dimension to those used by Aanderud et al (2003). The control treatment was created by mixing 2 g of the slow-release fertilizer with the entire 5–15 cm soil layer. A subsample of this mixture was then placed in a plastic mesh core and arranged in a manner similar to the nutrient patch treatment. The common time harvest was conducted 47 d after seedlings were planted. The common stage harvest was conducted at peak vegetative biomass for each species (Table 1). Over the duration of the experiment these nutrient additions increased soil inorganic N about 15-fold in the patches and about 2-fold in the bulk soil of the control treatment relative to field soil used in the experiment.

Measurements. To determine the RGR of each species, we destructively harvested 15, 3-wk-old seedlings of each species to develop regression equations to estimate initial biomass of each plant. These initial biomass estimates and the final plant biomass harvested at the end of the study were used to calculate relative growth rates (RGR) for each species during the experiment using the formula: $RGR = [\ln(M_f) - \ln(M_i)]/t_2 - t_1$ where M_f and M_i are final and initial plant biomass. At the beginning of the experiment, biomass and specific leaf area (SLA) were measured on the first leaf produced on 10 additional plants of each species.

Root cores were excavated in the control and patch treatment. Roots were gently washed from the soil in the cores over a fine screen to recover very fine lateral roots. Roots were then stored at 4 C until they were scanned for length with WinRHIZO (Regent Instruments Inc., Saint-

Foy, Canada) to determine root length density (RLD) and specific root length (SRL) (Bouma et al. 2000). Roots were then dried at 65 C and weighed. Root foraging precession was calculated using a log response ratio where *ln*RR = *ln* ($RLD_{enriched}/RLD_{control}$) (Hedges et al. 1999; Rajaniemi and Reynolds 2004). Increasing positive values indicate increasing precision in root placement.

After the soil cores were removed, aboveground biomass was clipped, dried at 65 C, and weighed. A subsample of shoot material was then triple rinsed with distilled water, dried at 65 C, weighed and ground to a fine powder. Shoot N was measured on a carbon/nitrogen (C/N) analyzer (Carlo Erba, Milan, Italy). Shoot phosphorous (P) samples were dry-ashed, dissolved in 1 N HCl, and analyzed colorimetrically following reaction with phosphomolybdate blue and ascorbic acid. The biomass of the bulk root system was estimated by gently excavating the remaining root system from the soil remaining in the pot.

Root N uptake rate was measured following the approach used by Campbell and Grime (1989). Given logistical constraints associated with measuring root N uptake rate, subsets of species were selected for these measurements. This included the two most widespread invasive annual grasses, downy brome and medusahead, and two native perennial grasses most commonly used in annual grass restoration projects, bluebunch wheatgrass and squirreltail. Nitrogen uptake measurements were made on a separate set of plants. Plants of each species were randomly assigned to receive a low N pulse (0.04 mM N) or a high N pulse (0.4 mM N). Half the plants were harvested immediately before the pulse and the second half were harvested 7 d following the pulse. Each treatment was replicated 10 times in a completely randomized design. Changes in whole-plant N pool and total root length over the 7-d period were used to calculate N uptake rate per unit root length. The limitations of this approach are that it does not provide an instantaneous value of N uptake rate and measures an average N uptake rate across the entire root system. The advantages of this approach are it allows measurements on intact roots, avoiding confounding effects of measuring uptake on excised roots, and ensures roots are uniformly exposed to the same concentration of N.

Statistical Analysis. Data were analyzed with ANOVA and regression (SAS 2001). To compare effects of functional group, harvest time, and nutrient treatment on the suite of traits considered, the ANOVA model included block, functional group (annual or perennial), harvest time (common time or common developmental stage), and nutrient treatment (control, or patch). Assumptions of ANOVA were evaluated using the Shapiro–Wilk test for normality and Levene's test for homogeneity of variance. When these assumptions were violated, data were weighted by the inverse of the variance (Neter et al. 1990). Following ANOVA, linear contrasts were used to test a priori hypothesis about differences in N capture and root responses between perennial grass and annual grass functional groups. Specifically, the first set of contrasts was tested if annual grasses differed from perennials in the suite of traits examined (e.g., foraging precision, RLD, N uptake rate). The second set of contrasts was tested if trait differences between annual and perennials were influenced by harvest time. The third set of contrasts was tested if the responses of the noninvasive annual, annual rye, differed from the average response of the three invasive annual grasses. When these comparisons were not orthogonal, sequential Bonferroni corrections were made to maintain an experiment-wise error rate of $\alpha = 0.05$ (Rice 1989). We used Tukey's studentized range test to examine individual species responses to our nutrient availability and developmental stage treatments. Regression analysis was used to examine the relationship among traits.

Results

All but two species, Idaho fescue and Sandberg bluegrass, showed significant root foraging precision in at least one of the harvests (Figure 1a; *t*-test for *ln*RR > 0). Across groups, however, annuals showed greater root foraging precision than perennials ($P = 0.02$). The magnitude of difference in root foraging between annuals and perennials did not change between the common time and common developmental stage harvests ($P = 0.54$). Foraging precision of the noninvasive annual, annual rye, was lower than the average foraging precision of the three annual grasses ($P = 0.004$). Annuals maintained a greater RLD, SRL, root to weight ratio(RWR), and RGR than perennials (Figure 1b–d; Figure 2, $P < 0.001$) and the magnitude of these differences did not vary between the common time and common stage harvests ($P > 0.05$). Across nutrient treatments, annuals maintained higher SRL than perennials ($P < 0.001$). Of the grasses analyzed for N uptake, the two perennial grasses had higher root N uptake rates than the two annuals ($P < 0.001$). Further, the perennials increased root N uptake rate when exposed to a 0.4 mM N pulse to a greater degree than annuals ($P < 0.001$) (Figure 3). Averaged across the control and patch treatments, annuals captured more N and P and produced more biomass than perennials (Figure 4a–c; $P < 0.001$). Biomass production by the study species did not differ between the control and patch treatments ($P > 0.05$). Surface area of first leaf produced was greater for annuals than perennials ($P = 0.007$; Table 1) but the first leaf produced by perennials had a greater specific leaf area (SLA) than the first leaf produced by annuals ($P = 0.025$; Table 1).

Regression analysis provided no evidence for a general positive relationship between foraging precision and RGR

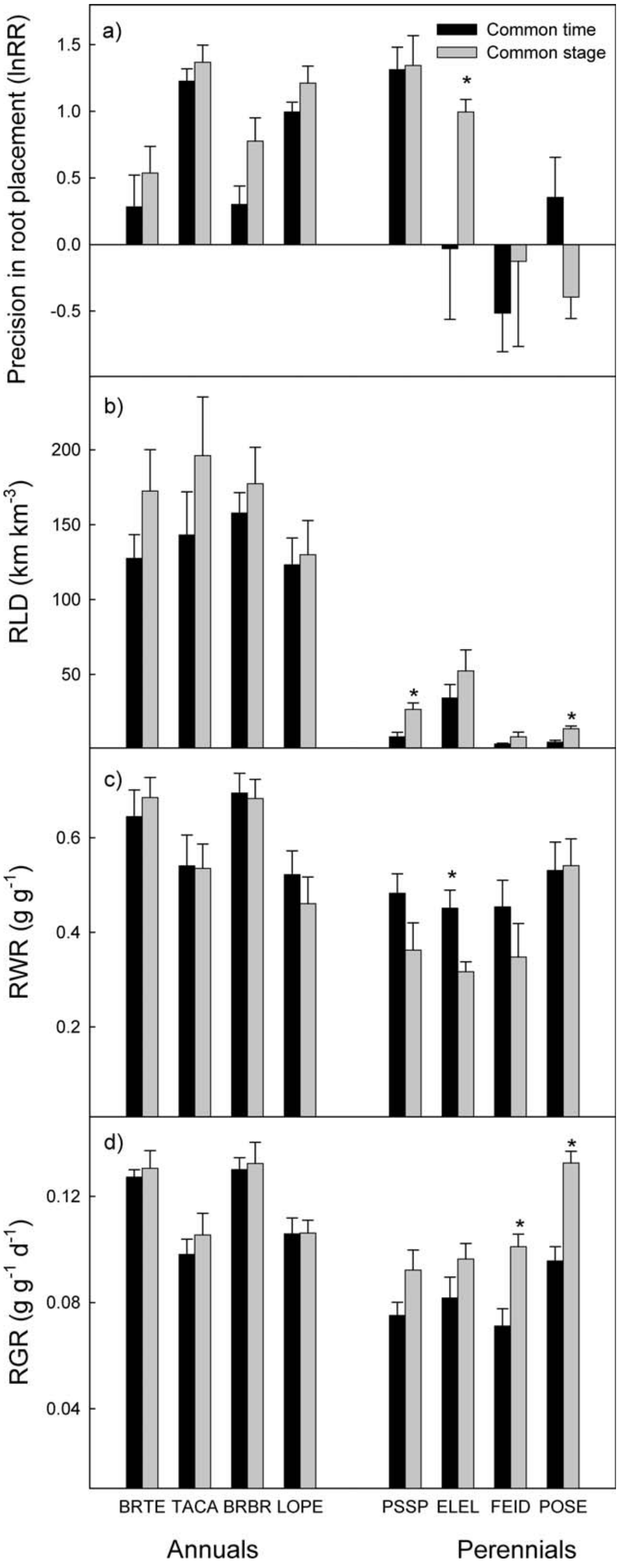

Figure 1. (a) Root placement precision, (b) root length density (RLD), (c) root weight ratio (RWR), and (d) relative growth rate (RGR), of eight grasses measured at a common time or common developmental stage (mean + SE, *n* =14). Values are averaged over nutrient treatments. Species abbreviations follow Table 1.

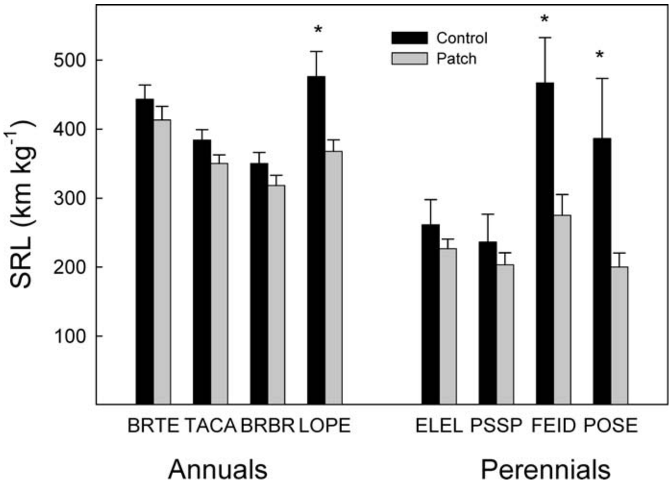

Figure 2. Specific root length (SRL) of the grasses in the control and patch nutrient treatments (mean + SE, *n* =14). Values are averaged over the two harvest treatments. Asterisks over bars indicate significant differences between nutrient treatments within a species as determined with Tukey pairwise comparisons ($P < 0.05$).

(Figure 5). Variation in N and P capture among species was not positively related to foraging precision but was strongly and positively related to RLD. Variation in root length density, in turn, appeared to be a function of variation in biomass. Variation in biomass among species appeared to be most related to variation in RGR among species, not due to variation in initial leaf area produced among species.

Discussion

In support of our first hypothesis, there was a positive relationship between growth rate and foraging precision at the functional group level, with annual grasses demonstrating greater foraging precision than perennial grasses. Research examining the relationship between growth rate and foraging precision has been mixed, partly because most studies have not separated the direct effects of life history traits associated with RGR from the indirect effects of RGR on measurements of species foraging ability (Aanderud et al. 2003). The few studies that have controlled indirect effects of RGR generally have found that once these indirect effects are removed, fast- and slow-growing species do not differ in foraging ability (Aanderud et al. 2003; Fransen et al. 1999). However, recent work that considered

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Asterisks over bars indicate significant differences between harvests within a species as determined with Tukey pairwise comparisons ($P < 0.05$).

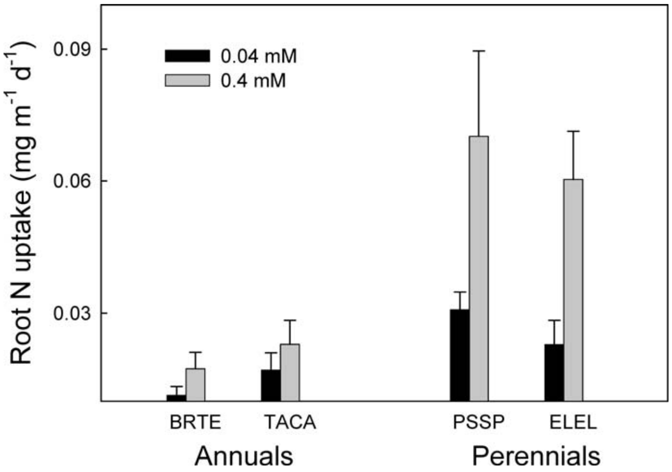

Figure 3. Root N uptake rate of the four grasses over 7 d exposed to a low (0.04 mM) or high (0.4 mM) uniform pulse of N (mean + SE, *n* =10).

the role of phylogeny in these responses found some support for a correlation between growth rate and precision (Kembel et al. 2008). In this current study, there was no evidence suggesting that differences in foraging ability between these groups was solely due to differences in growth rate because differences in foraging precision also were observed during the common-stage harvest where species were allowed to grow until vegetative production stopped and plants began to shift resources to reproductive growth. This suggests that differences in foraging precision observed between these two groups are not due to fast-growing species occupying and proliferating roots in patches more rapidly than slow-growing species. Instead these results support the idea put forth by Kembel et al. (2008) that high foraging precision is related to a suite of traits that make up one end of the tissue economic spectrum and allow rapid return on dry matter allocated to leaves and roots.

At the species level, however, there was no clear relationship between RGR and precision. For example, medusahead and annual rye had the lowest growth rates but the highest foraging precision of the annuals, whereas the perennial grasses bluebunch wheatgrass had a lower growth rate than the two annuals, downy brome and rattlesnake brome, but a higher foraging precision than these species. Therefore, although this study provides evidence for a general relationship between foraging precision and growth rate, it also indicates that phylogeny or other factors can obscure this relationship when considering subsets of co-occurring species (Kembel and Cahill 2005; Larigauderie and Richards 1994).

Foraging precision averaged across the three invasive annual grasses did not differ from that of the introduced noninvasive annual grass annual rye. Although only one noninvasive annual grass was included, meaning a general pattern has yet to be elucidated, these initial observations suggest high foraging precision is not a trait unique to invaders in this system. A number of traits can contribute to success of invasive annuals in nutrient poor systems, including earlier and faster growth, more abundant seed production and ability to set seed before seasonal drought

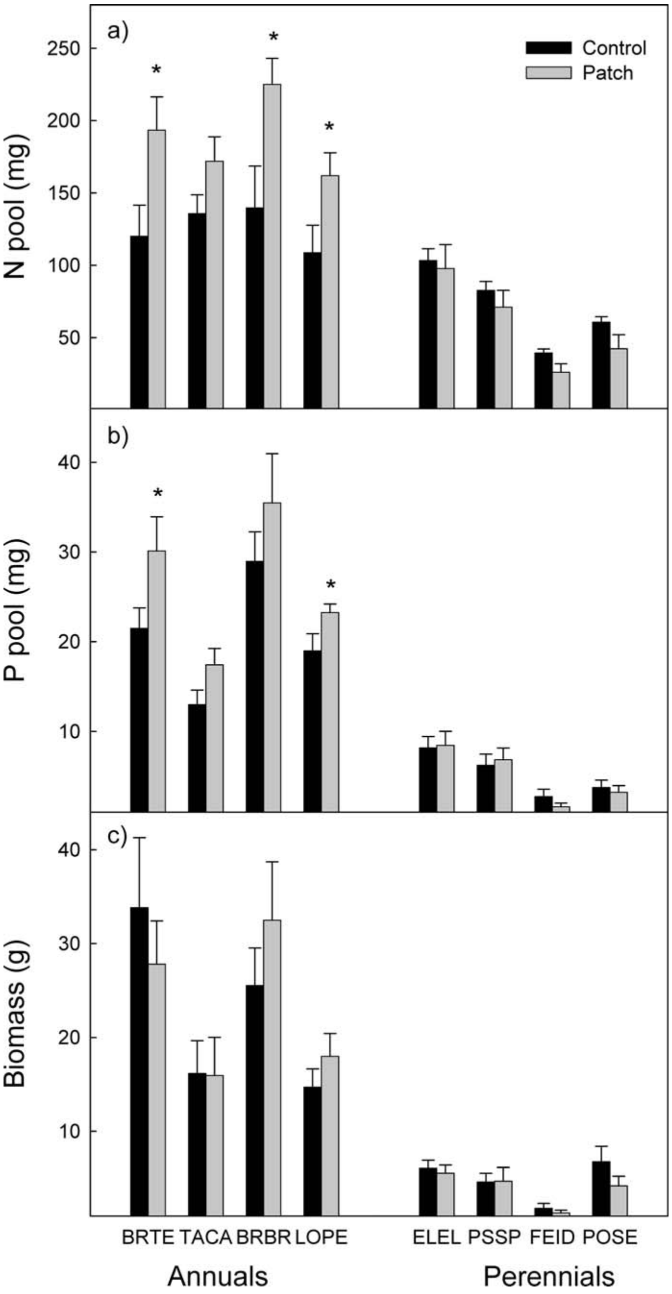

Figure 4. Plant (a) N pool, (b) P pool, and (c) total biomass of the grasses in the control or patch nutrient treatments (mean + SE, *n* =14). Values are averaged over the two harvest treatments. Asterisks over bars indicate significant differences between nutrient treatments within a species as determined with Tukey pairwise comparisons ($P < 0.05$).

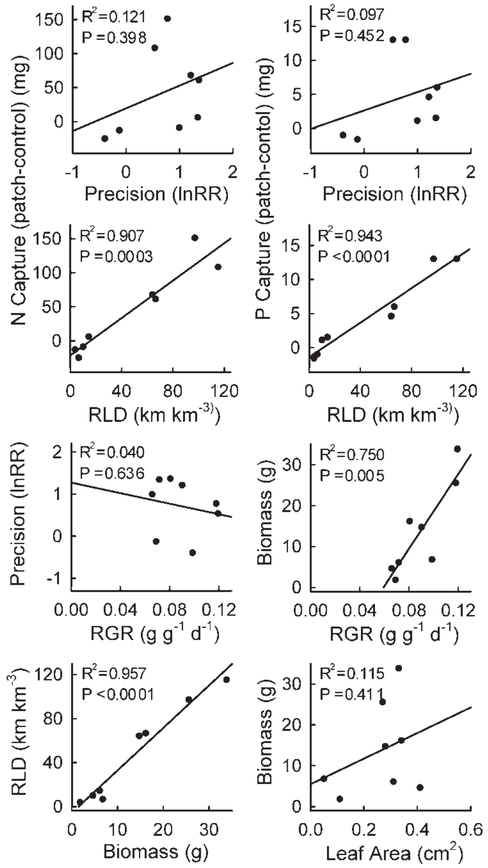

Figure 5. Simple linear regressions among traits for the eight study species. Nitrogen and P capture is expressed as the difference in total N and P captured between the patch and control treatments. This provides a measure of the relative benefit a species conferred by growing in soils where nutrients were distributed in heterogeneous soils compared to when the same amount of nutrients were distributed uniformly through the soils. Root length density (RLD), root foraging precision (precision), whole plant biomass (biomass), and relative growth rate (RGR) are values from the common developmental stage harvest where all plants were allowed to reach maximum biomass. Leaf area is the amount of leaf area on the first full leaf produced by seedlings of each species.

(DiVittorio et al. 2007; Dyer and Rice 1999; Harris 1967). Although nutrient heterogeneity has been well-documented in nutrient-poor systems (Jackson and Caldwell 1993; Ryel et al. 1996), these results do not indicate that greater foraging precision contributes to the success of invasive annuals in these systems.

Counter to our initial hypothesis of a tradeoff between foraging precision and nutrient uptake rate per unit root length, the two perennial species examined exhibited higher root N uptake rates following both low and high N pulses compared to the two invasive annuals examined. These two perennials also demonstrated foraging precision comparable to the invasive annuals during at least one of the harvests. Given the large variation in foraging precision among species, it might be that a trade-off between foraging precision and uptake rate would be more evident if a larger number of species were included. Nevertheless, these observations do suggest that perennial species are able to rapidly adjust N uptake rate and/or reduce N efflux from the root to a greater degree than annuals, but contrary to earlier work, this does not appear to involve a trade-off in foraging precision (Campbell and Grime 1989; Crick and Grime 1987).

There was no relationship between foraging precision and the amount of N or P a species captured in soils where nutrients were distributed in patches compared to when nutrients were distributed evenly in the soil. The relationship between foraging precision and nutrient capture in heterogeneous soils reported in previous studies has been mixed (e.g., Bilbrough and Caldwell 1995; Fransen et al. 1998; Hodge et al. 1998; Robinson 1994) and other mechanisms might contribute to species differences in nutrient capture from patches, including physiological plasticity, differences in root demography or soil nutrient supply processes (Barber 1995; Eissenstat and Yanai 1997; Jackson et al. 1990). The shorter root life span of annuals (Ryser 1996), as well as their lower N uptake rates per unit root length, suggests root demography and physiological plasticity are unlikely to explain the greater N and P capture by annuals in heterogeneous soils. The greater nutrient capture by annuals likely is a function of the higher RLD of annuals in patches and the higher local concentration of nutrients in patches. As the same amount of N and P becomes concentrated in a smaller area, less N and P is bound by soil and more nutrient becomes available in the soil solution, allowing nutrient uptake rate per unit root length to increase even without physiological adjustment to the root (Jackson and Caldwell 1996). Even though perennials demonstrated greater N uptake per unit root than the annuals, the 2- to 3-fold higher RLD of annuals might have allowed annuals to capitalize on the local increases in nutrient availability in the patch treatments to a greater extent than perennials.

Soil nutrient heterogeneity and differences in foraging ability did not differentially affect biomass production by the study species. In fact, none of the species produced more biomass in the patch treatment compared to the control. Differences in species biomass in this experiment appeared to be due almost entirely to differences in RGR, not initial leaf area. Variation in RGR appeared to contribute to differences in final biomass among the species. Although root proliferation has been interpreted as an adaptive response to nutrient heterogeneity, our study found little evidence that greater foraging precision translates into greater biomass production in heterogeneous soils supporting some earlier observations (Einsmann et al.

1999; Fransen et al. 1998; Kembel and Cahill 2005; Wijesinghe et al. 2001). A recent meta-analysis indicated that species biomass response to soil nutrient heterogeneity could be positively related to species photosynthetic rate and negatively related to root respiration rates (Kembel et al. 2008). Although it would be reasonable to expect these traits to differ among invasive and native grasses used in our study, there was no evidence that these differences would confer a benefit in terms of increased yield in heterogeneous environments. It is possible that other parameters related to fitness, such as seed production or viability, could have shown a positive response to heterogeneity (O'Dell and Claassen 2006).

Although plants in nutrient-poor systems can acquire a large portion of their nutrients from fertile microsites, taken together, our findings argue against the notion that invasive species have an inherently greater ability to exploit nutrient-rich microsites through changes in root biomass allocation or root physiological adjustments. Instead, greater nutrient capture from patches by invasive grasses was related to a higher RLD. Plants with higher RGR tended to produce more biomass and consequently more root length. Therefore, the greater RGR typically displayed by annual grasses appears to be one of the traits allowing annuals to capture more nutrients in heterogeneous environments. Although these results do not exclude a role for proliferation in influencing invasion of heterogeneous, nutrient-poor habitat, or the potential for heterogeneity to influence neighborhood, population, or community processes (Day et al. 2003; Fransen et al. 2001; Wijesinghe et al. 2005), these results add to the growing body of literature questioning the adaptive value of root proliferation for individual plants and suggests a number of other trait differences might be more important in determining success of invaders in these systems.

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