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Root foraging for patchy resources in eight herbaceous plant species

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Abstract The root foraging strategy of a plant species can be characterized by measuring foraging scale, precision, and rate. Trade-offs among these traits have been predicted to contribute to coexistence of competitors. We tested for trade-offs among root foraging scale (total root mass and length of structural roots), precision (ln-ratio of root lengths in resource-rich and resource-poor patches), and rate (days required for roots to reach a resource-rich patch, or growth rate of roots within a resource-rich patch) in eight co-occurring species. We found that root foraging scale and precision were positively correlated, as were foraging scale and the rate of reaching patches. High relative growth rate of a species did not contribute to greater scale, precision, or rate of root foraging. Introduced species had greater foraging scale, precision, and rate than native species. The positive correlations between foraging scale and foraging precision and rate may give larger species a disproportionate advantage in competition for patchy soil resources, leading to size asymmetric competition below ground.

Keywords Root proliferation · Trade-offs · Foraging strategies · Resource heterogeneity

Introduction

Heterogeneity in soil resources is a ubiquitous feature of natural environments and is present at a range of scales. Spatial patterns have been detected for mineral resources and soil moisture at scales ranging from 1 to 50 m (Cain et al. 1999; Gross et al. 1995; Guo et al. 2002; Jackson and

Caldwell 1993a, b; Lechowicz and Bell 1991; Lister et al. 2000; Robertson et al. 1993; Ryel et al. 1996). Such large-scale resource heterogeneity influences plant community structure, for example by driving succession (Connell and Slatyer 1977), producing diversity gradients corresponding with resource gradients (e.g., Currie and Paquin 1987; Gross et al. 2000), or favoring coexistence through specialization of species on particular resources (Tilman 1982; Tilman and Pacala 1993) or through mass effects (Shmida and Ellner 1984).

Fewer studies have measured resource patterns at a scale detectable by individual plants, but at least two studies found substantial variation in resource availability over 20 cm (Farley and Fitter 1999b; Ryel et al. 1996). Much less is known about the patterns and consequences of plant responses to resource heterogeneity at this small scale. We do know that plants respond to resource-rich patches and that species differ in their responses. Many studies have shown that roots proliferate in resource-rich patches, but the extent of root proliferation differs among species (Caldwell 1994; Robinson 1994). Elevated resource uptake rates are also common in patches, with species differing in their abilities to increase uptake kinetics (Robinson 1994).

Comparison of foraging strategies is one approach to looking for patterns in species responses to small-scale resource heterogeneity and to predicting the potential consequences of response patterns. Campbell et al. (1991) suggest that root foraging has three components: scale, precision, and rate. The traits underlying these components include developing extensive root systems (high scale foraging), concentrating roots in high-resource patches (high precision foraging), or reaching or proliferating in patches quickly (high rate foraging). Separating these three aspects of root foraging allows species to be compared qualitatively and quantitatively.

Trade-offs among scale, precision, and rate of foraging might favor different species in different soil environments, or might promote coexistence of competitors. For example, Campbell et al. (1991) argue that a trade-off should exist between scale and precision of foraging, with

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dominant species using high-scale foraging and subordinate species persisting by foraging precisely on resource patches missed by the dominants.

Root foraging traits may also influence coexistence by their effects on the size symmetry of competition. Belowground competition is generally expected to be size symmetric: a plant's resource uptake and competitive effect should be proportional to its size. When soil resources are spatially or temporally patchy, however, larger plants might have a disproportionately large competitive effect (i.e., a greater per-gram effect) if they can reach and exploit patches faster than smaller plants, thereby preempting the resources in those patches (Schwinning and Weiner 1998). Size asymmetry is expected to lead to competitive exclusion, because larger plants can prevent smaller ones from meeting their minimum resource requirements through preemption of resources (Huston and DeAngelis 1994; Schwinning and Fox 1995; Zobel 1992).

If foraging scale is associated with large plant size, trade-offs between scale and precision (Campbell et al. 1991) or scale and rate of foraging could prevent larger plants from preempting resources from competitors with less extensive, but higher-precision or higher-rate foraging. On the other hand, if large size (and therefore extensive foraging scale) is positively associated with precise or high-rate foraging, then size-asymmetric root competition should be common in environments with small-scale resource heterogeneity.

A trade-off between foraging scale and precision was found in a set of nine herbaceous species (Campbell et al. 1991). Einsmann et al. (1999), on the other hand, found that scale and precision were positively correlated for a set of ten coastal plain species. Among seven woodland herbs, only those with large root systems exhibited precise foraging (Farley and Fitter 1999a). None of these studies measured rate of foraging. We measured the scale, precision, and rate of root foraging for eight herbaceous perennial species, and asked whether those traits were positively or negatively correlated.

Materials and methods

Study system and species

Soil resource heterogeneity is expected to be most beneficial to competing plants in lower fertility soils (Reynolds and D'Antonio 1996). Thus, we chose species that commonly co-occur in infertile old fields (Goldberg 1987; Miller and Werner 1987; Rajaniemi 2001; Reader 1998). The species vary in growth form (Table 1), which may result in differences in rooting patterns and root foraging strategies. The eight species included four native species and four non-native species. All but two species were capable of clonal growth.

Experimental design, monitoring, and harvest

Individual plants were grown in 8 l, 20 cm diameter pots. Each pot had two circular, 5 cm diameter windows cut into the side to allow observation of roots. Windows were positioned with their top edges approximately 2 cm below the intended soil surface, and 90° from each other (Fig. 1). Windows were sealed with a piece of clear plastic secured inside the pot with duct tape. Except during observations, windows were kept covered with black plastic.

Pots were filled with a 1:1 mixture of field soil and sand. The field soil was collected from the top 30 cm at Bayles Field, an old field maintained by Indiana University, Bloomington, Ind., USA. The soil was sieved through a coarse mesh in the field to break up soil clods and remove stones larger than 1 cm. The soil and

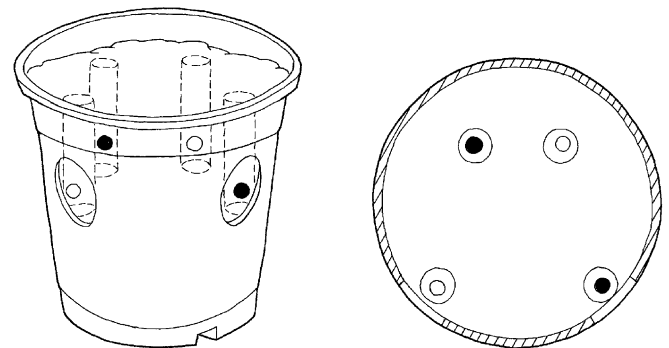


Fig. 1 Arrangement of windows and fertilizer and control patches in pots (left side view, right top view). Filled circles represent fertilizer patches, open circles represent control patches

Table 1 Growth form (USDA NRCS 2002) and origin (USDA NRCS 2002; Voss 1972, 1996) of species included in the study

Species	Growth form	Origin
<i>Achillea millefolium</i>	Rhizomatous rosette forb	Native
<i>Agropyron repens</i>	Rhizomatous grass	Introduced
<i>Aster pilosus</i>	Rhizomatous rosette forb	Native
<i>Bromus inermis</i>	Rhizomatous grass	Introduced
<i>Centaurea maculosa</i>	Rosette forb	Introduced
<i>Chrysanthemum leucanthemum</i>	Erect rhizomatous forb	Introduced
<i>Festuca rubra</i>	Rhizomatous grass	Native
<i>Schizachyrium scoparium</i>	Bunch grass	Native

commercial play sand were thoroughly mixed and homogenized in a cement mixer before pots were filled. This medium was intended to provide a well-mixed, low-resource background to which resource-rich fertilizer patches could be added. The soil was unsterilized to allow plants to associate and interact with mycorrhizal fungi and other soil microbes.

Plants were grown from seeds germinated directly in the pots. Seeds were obtained from commercial suppliers except for seeds of *Centaurea maculosa*, which were collected at the E.S. George Reserve in Pinckney, Mich., USA in 1998 and stored at 5°C until used. Three to five seeds of a single species were placed near the center of each pot and thinned to leave a single seedling after 3 weeks. Seeds were started on 21 January 2002 in 20 replicate pots for each species, for a total of 160 pots. This number was reduced by mortality over the course of the experiment, but at least ten replicates remained for each species.

The number of leaves and length of the longest leaf were measured for each plant on 4 March. These measurements were used in biomass regressions derived from additional seedlings to estimate initial total biomass (root plus shoot) of each plant.

Soil heterogeneity was created by installing two patches of fertilizer in each pot on 7–9 March. Four soil cores (2 cm diameter, 5 cm deep) were removed from each pot, one immediately behind each window and two 4 cm from the opposite edge of the pot (Fig. 1). Two of the holes (at the right-hand window and opposite; Fig. 1) received approximately 1 g of Osmocote fertilizer (19-6-12 NPK; Scotts-Sierra Horticultural Products, Marysville, Ohio, USA) mixed with 1:1 soil: sand, then all holes were refilled with 1:1 soil: sand. In the field, similarly constructed patches increased available nitrogen approximately twofold after 3 weeks and fourfold after 12 weeks (T. Rajaniemi, unpublished data). Thus, each pot had two fertilized patches, one near a window to allow observations of root growth and one away from the pot edge to control for pot edge effects on root growth. Each pot also had one window and one non-window control patch, to control for the disturbance of patch creation.

Windows were checked for root growth three times per week, beginning 11 March, 50 days after seeds were planted, and continuing until harvest. When roots were visible at a window, the position of those roots was traced onto a sheet of clear plastic. The traced pattern was scanned and analyzed for total root length using a WinRhizo root image analysis system (Regent Instruments, Quebec, Canada). Traced images for each window were not erased between observation dates; instead, new roots were added to the image as they appeared and cumulative root growth at the window was measured.

Plants were harvested from 7 to 15 May, beginning 107 days after seeds were started. By this date, all plants had roots visible in at least one window; 90% of plants had roots visible by day 89 and 80% by day 80. Also by this date, window root lengths for four plants were beginning to level off. Therefore, by the harvest date all plants had

time to exploit fertilizer patches, but few showed signs of having reached the maximum possible root length in patches.

The shoots of each plant were collected, dried at 60°C for 48 h and weighed. Soil cores (2.5 cm diameter, the full depth of the pot) were collected from the positions of the two fertilized and two control patches. These cores were stored at 5°C and later the roots were washed from each core and scanned and analyzed for total root length. The remaining roots in each pot were washed at the time of harvest, dried, and weighed. After drying, the dried bulk roots were manually separated into fine roots (those which crumbled easily when handled) and structural roots (thicker roots which remained intact). Structural roots were scanned and their total length calculated. Relative growth rate of each plant was calculated as $[\ln(\text{harvest biomass}) - \ln(\text{initial biomass})]/64$ days, using summed root and shoot biomass.

Quantifying foraging traits

Foraging scale was quantified in two ways. Ideally, scale should represent the extent to which a plant is able to explore the soil volume. To capture the total volume of soil that a plant's roots might access, we used total root mass, excluding roots harvested from patches (so that foraging precision would not influence root mass). To capture the distance a plant's roots might travel from the center of the plant, we used length of structural roots. Both root mass and structural root length were natural-log transformed for normality.

Foraging precision was measured as a log response ratio, $\ln\text{RR} = \ln(\text{root length in fertilized patches}/\text{root length in control patches})$. A value of zero indicates equal root growth in resource-rich and resource-poor soil, and no precision of foraging. Increasing positive values indicate increasing precision. Within each species, the log response ratios calculated for patches near the windows were highly correlated with ratios for patches away from windows ($0.632 \leq r^2 \leq 0.865$, $P \leq 0.002$ for all eight species). Therefore, precision was calculated using the summed root lengths of the two fertilized and two control patches.

Two aspects of foraging rate were quantified. The first measure of rate was the number of days from planting of seeds until a root was first observed in the window with the fertilized patch. The second was the growth rate, in centimeters per day, of roots in that window. Root growth rates were calculated as the slope of a linear regression of total cumulative root length on day of observation for each plant. Few plants showed any indications of non-linearity in the root length-day relationship. Root growth rates were natural-log transformed for normality.

Analysis

To compare traits among species and test for trade-offs, we calculated values of foraging scale (\ln root mass,

In structural root length), foraging precision (lnRR), and foraging rate (day reaching window and ln growth rate) for each individual plant, and mean values for each species. We tested for species differences using separate one-way ANOVAs for each of these traits. Pearson correlations of the species mean values were used to test for trade-offs among the five traits. The critical *P*-values for the ANOVAs and for pairwise comparisons among species were Bonferroni-corrected. Because the correlations involved only seven or eight points and therefore had low power, we chose not to apply a correction to these.

Given the limited time plants were allowed to grow in pots, faster-growing species might have had a greater opportunity to forage and therefore might have higher foraging scale, precision, and rate simply because they had more time to express those traits. To examine the importance of growth rate, we used ANOVA to test for species differences in RGR, and Pearson correlation to test for relationships between RGR and the five foraging traits.

Results

The species differed significantly in scale and precision of foraging (Fig. 2a–c). They also differed significantly in the mean number of days until roots were observed at a window, but not in growth rate of roots in windows (Fig. 2d, e). *Schizachyrium* tended to be the least effective forager and *Bromus* the most effective. In general these aspects of foraging differed little by species nativity (Fig. 2; ANOVA comparing native and introduced species:

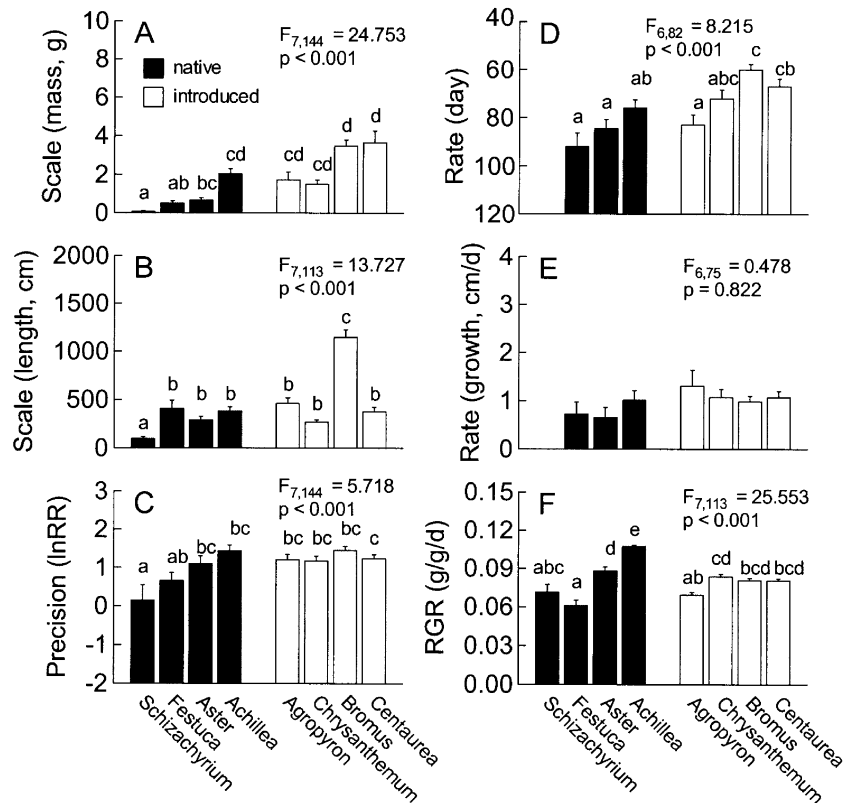
for scale (root mass) $F_{1,6}=4.983, P=0.067$, for scale (structural root length) $F_{1,6}=2.805, P=0.145$, for precision $F_{1,6}=2.255, P=0.184$, for rate (day) $F_{1,6}=5.937, P=0.051$, for rate (growth) $F_{1,5}=8.271, P=0.035$). *Achillea millefolium*, which tended to have trait values most similar to the introduced species, is represented by both native and introduced genotypes in North America (Voss 1996).

Our two measures of foraging scale were strongly and positively correlated (Fig. 3). Plants that produced high root biomass and were therefore able to place roots throughout a large volume of soil also produced extensive structural roots, which would allow them to explore soil at greater distances.

No trade-offs were observed among the foraging traits. Instead, scale and precision of foraging were strongly and positively correlated (Fig. 3; for structural root length $R=0.876, P=0.004$). Foraging scale was also strongly and positively correlated with one aspect of foraging rate, the speed at which roots reached the window near a fertilizer patch (Fig. 3; for structural root length $R=-0.698, P=0.054$). Thus, species with high foraging scale reached patches early and foraged more precisely within patches. The relationship between precision and the day at which roots reach a patch also had a high correlation coefficient ($r=0.694$), but was only marginally significant ($P=0.056$). A clearer pattern of foraging ability by species origin is evident when traits are correlated against one another. Native species typically fall out as poor foragers compared to naturalized and invasive exotics (Fig. 3).

Species differences in foraging traits and the positive correlations among traits were not due to greater foraging

Fig. 2a–f Mean plant traits for each species: foraging scale (a total root mass, b structural root length), foraging precision (c), foraging rate (d days to reach fertilizer patch, e root growth rate in fertilizer window), and relative growth rate (f). The scale for foraging rate (days until root appears in window) is inverted, so that high-rate foraging (few days to reach the window) is reflected in a high position on the y-axis. Error bars are one standard error. Scale (both root mass and length) and growth rate were ln-transformed for analysis; back-transformed values are shown here. Bars marked with different letters are significantly different (pairwise comparisons with $P<0.05$ after Bonferroni adjustment). *F*- and *P*-values are given for the overall ANOVA results. Species are arranged by origin. There were insufficient data to calculate foraging rates for *Schizachyrium*



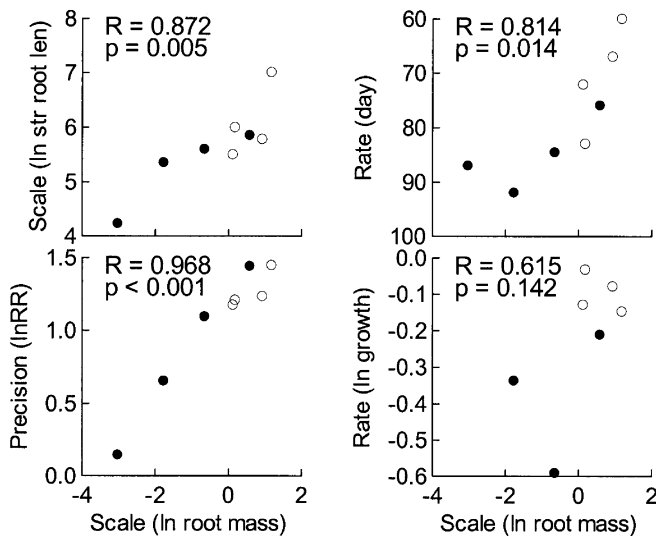


Fig. 3 Correlations among root foraging traits of the eight species. Native species are indicated with *filled circles*, introduced species are indicated with *open circles*. The scale for foraging rate (days until root appears in window) is inverted, so that high-rate foraging (few days to reach the window) is reflected in a high position on the y-axis

by fast-growing species. Species differed in relative growth rate (Fig. 2), but RGR was not correlated with any foraging trait [root mass $R=0.501$, $P=0.206$; structural root length $R=0.257$, $P=0.538$, precision $R=0.584$, $P=0.128$; rate (day) $R=-0.430$, $P=0.287$; rate (growth) $R=-0.099$, $P=0.833$].

Discussion

We observed differences among species in root foraging traits, but no trade-offs among the traits. Species such as *Bromus inermis* and *Centaurea maculosa* exhibited high foraging scale, precision, and rate, while *Festuca rubra* and *Schizachyrium scoparium* had low foraging scale, precision, and rate. These patterns may have important implications for the performance of these species in complex communities.

Species differences in foraging ability are likely to strongly influence competitive outcomes in these co-occurring species. High scale foraging may contribute to the greater competitive effect of larger individuals (e.g., Goldberg and Landa 1991; Goldberg and Werner 1983). High foraging precision may also confer a competitive advantage. In competition between two species, the species with greater root proliferation in enriched patches takes up more nitrogen from those patches (Hodge et al. 1999; Robinson et al. 1999). Fransen et al. (2001) showed that, when two grass species competed, the species with the greater proliferation response to patches was the stronger competitor in heterogeneous, but not homogeneous soils. The ability to reach resource patches quickly might also provide a competitive advantage: given similar root growth rates within the patch (Fig. 2d), the first plant to reach a patch is likely to acquire most of the resources.

Although we did not observe differences in rate of root growth *within* resource-rich patches, this trait has the potential to enhance nutrient gains from high precision foraging, by increasing the speed at which roots proliferate within patches. Jackson and Caldwell (1989) observed differences in root growth rates in P-enriched patches between two species, although these differences were not reflected in resource uptake (Caldwell 1994). Our experimental design may not have been able to detect patterns in within-patch root growth rate: only a subset of plants provided enough data for calculation of growth rate, and patterns may have been hidden by large amounts of random variation. Gross et al. (1993) also failed to detect growth rate differences between species, with only small sample sizes. Given that foraging precision varied among species, root growth within patches does appear to be an important response to heterogeneous resources. If species exhibit higher precision but do not vary in within-patch growth rate, they must vary in absolute time spent in growth in patches, in root death rates in patches (Gross et al. 1993), or in root architecture within patches, which controls whether new roots remain within the patch or grow beyond it (Fitter 1994; Fransen et al. 2001). Other potentially important responses to resource-rich patches include increases in physiological uptake rates (Caldwell 1994; Fransen et al. 2001; Robinson 1994) or investment in mycorrhizal growth in a patch (Hodge 2003; Hodge et al. 2001).

Our results suggest that effective foraging, in terms of scale, precision, and rate, may in part explain the success of introduced plant species. Typically, 'r-selected' life history traits, such as rapid maturation and frequent production of many, small seeds, have been correlated with invasiveness (e.g., Rejmanek and Richardson 1996). Recently, belowground attributes, such as allelopathy (Callaway and Aschehoug 2000; Ridenour and Callaway 2001) and plant-microbe interactions (Callaway et al. 2003) have also been shown to be important to invasive success. Release from enemies (Mitchell and Power 2003) may allow introduced species to allocate more energy to resource acquisition strategies. Our study, while not explicitly designed to compare native and exotic species, suggests that traits allowing rapid exploitation of belowground resources deserve more study in this context.

Fast-growing species are expected to be more plastic in their growth and more responsive to resource-rich patches than slower-growing species (Campbell and Grime 1989; Crick and Grime 1987). In a greenhouse experiment of limited duration, slow growth rate might also constrain foraging: even if fast-growing and slow-growing species had the same potential foraging scale or precision, slow-growing species might not be able to fully express that potential in the time available. For example, Aanderud et al. (2003) found that fast-growing species had greater root foraging precision, but that precision did not differ among species when relative growth rate was controlled for by harvesting species at a common size. In this study, neither potential effect of growth rate on foraging was observed: RGR was unrelated to foraging scale, precision, or rate.

The relationships among the foraging traits provide further insight into the potential effects of those traits on community structure. A trade-off between foraging scale and precision, or between other pairs of traits, could contribute to species coexistence. We found no evidence of such a trade-off, and similar studies examining groups of co-occurring species (Einsmann et al. 1999; Farley and Fitter 1999a) also failed to detect a trade-off between root foraging scale and precision. Campbell et al. (1991), on the other hand, found a trade-off between precision and foraging for eight herbaceous species from a wide range of habitats. Species exclusive to fertile habitats appeared to have high foraging scale, while species typical of infertile habitats foraged more precisely. The conflict between this study and the others might be resolved by considering the groups of species examined. Trade-offs between scale and precision of foraging may contribute to explaining species distributions along environmental gradients (e.g. Campbell et al. 1991), but not coexistence of species in any given environment (e.g. Einsmann et al. 1999; Farley and Fitter 1999a; this study).

The positive relationships we observed between foraging scale and precision, and between foraging scale and rate, may in fact reduce coexistence by promoting size-asymmetric root competition. If species with an advantage in size also have an advantage in reaching and proliferating roots within, and thus preempting, resource-rich microsites, they may exert a competitive effect disproportionate to their advantage in size. The positive relationships between foraging scale and precision observed here and in other studies (Einsmann et al. 1999; Farley and Fitter 1999a) suggest that size-asymmetric interactions belowground are potentially widespread. Plant size is only one potential component of foraging scale; however, we found that size and foraging scale were closely related. Root biomass was correlated with length of structural roots (Fig. 3) and within each species root biomass and shoot biomass were strongly correlated ($0.902 > R > 0.721$), so that both measures of scale are good indicators of plant size.

Only one study has yet detected size asymmetry in root competition (Rajaniemi 2003). However, many of the experiments showing size symmetry of root competition have used homogenized soil (Newbery and Newman 1978; Weiner et al. 1997; Wilson 1988). Belowground size asymmetry requires small-scale heterogeneity of resources. The importance of soil heterogeneity was confirmed in a study of competition between two grasses in homogeneous and heterogeneous soils (Fransen et al. 2001). Although competition was not restricted to belowground, populations in fine-grained heterogeneous soils (6 cm × 6 cm patches) exhibited greater size inequality, indicative of size-asymmetric interactions, than plants in homogeneous soils or coarse-grained heterogeneous soils (15 cm × 15 cm patches). More work is needed to determine the degree of small-scale resource heterogeneity in the field, to assess the potential importance of belowground size asymmetry in natural plant communities.

Belowground plant interactions can have important effects on individual fitness (e.g., Cahill 1999; Peltzer et al. 1998) and community diversity (Rajaniemi et al. 2003). Species' strategies for foraging for patchy soil resources will almost certainly prove to be an important component of these higher-level effects.

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