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Author(s): Steven W. Kembel and James F. Cahill Jr.

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Plant Phenotypic Plasticity Belowground: A Phylogenetic Perspective on Root Foraging Trade-Offs

Steven W. Kembel^{*,†} and James F. Cahill Jr.^{*,‡}

Department of Biological Sciences, University of Alberta,
Edmonton, Alberta T6H 2E9, Canada

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ABSTRACT: Many plants proliferate roots in nutrient patches, presumably increasing nutrient uptake and plant fitness. Nutrient heterogeneity has been hypothesized to maintain community diversity because of a trade-off between the spatial extent over which plants forage (foraging scale) and their ability to proliferate roots precisely in nutrient patches (foraging precision). Empirical support for this hypothesis has been mixed, and some authors have suggested that interspecific differences in relative growth rate may be confounded with measurements of foraging precision. We collected previously published data from numerous studies of root foraging ability (foraging precision, scale, response to heterogeneity, and relative growth rate) and phylogenetic relationships for >100 plant species to test these hypotheses using comparative methods. Root foraging precision was phylogenetically and taxonomically conserved. Using ahistorical and phylogenetically independent contrast correlations, we found no evidence of a root foraging scale-precision trade-off, mixed support for a relative growth rate-precision relationship, and no support for the widespread assumption that foraging precision increases the benefit gained from growth in heterogeneous soil. Our understanding of the impacts of plant foraging precision and soil heterogeneity on plants and communities is less advanced than commonly believed, and we suggest several areas in which further research is needed.

Keywords: comparative method, foraging scale-precision trade-off, phenotypic plasticity, behavioral ecology.

Because of spatial variation in plant and consumer distributions (Pickett et al. 2000), inherently variable physical processes (Tinker and Nye 2000), and spatially variable rates of decomposition, mineral nutrients are distributed heterogeneously throughout the soil (Wilson 2000). This can result in significant variation in nutrient levels within the soil explored by a single plant (Jackson and Caldwell 1993), which can be exploited through a variety of physiological and morphological adaptations (Hodge 2004). The ecological implications of soil heterogeneity and plant foraging have been of interest to many researchers, with particular emphasis on changes in plant growth, competition, and species coexistence.

Early studies demonstrated that a variety of crop species proliferate roots in areas of high nutrient concentration and that plant nutrient concentration and yield could be higher in heterogeneous soil than in homogeneous soil (Garg and Welch 1967; Anghinoni and Barber 1980a; Borkert and Barber 1985; Yao and Barber 1986). Increased uptake and growth responses were attributed both to root proliferation increasing uptake potential and to the fact that a given soil volume has limited binding capacity, and thus as nutrient supply increases, a greater proportion of those added nutrients will remain in the soil solution (Anghinoni and Barber 1980b). The relative contribution of each of these processes is unclear and would be difficult to test directly. However, a related testable prediction does emerge: if root proliferation is essential for a plant to accrue growth benefits from heterogeneous soil, then those species with the strongest proliferation response should exhibit the greatest growth benefit from heterogeneous soils. Failure to find such a correlation would suggest that proliferation response itself is not a good indicator of the potential benefits of nutrient heterogeneity for a particular plant species.

Given that soil heterogeneity could alter individual plant growth, questions soon emerged about its potential role in structuring plant communities. The idea that small-scale nutrient heterogeneity could alter community structure became popular after the publication of an influential article by Campbell et al. (1991). The authors presented data

* The authors contributed equally to this work.

† E-mail: steve.kembel@ualberta.ca.

‡ Corresponding author; e-mail: jc.cahill@ualberta.ca.

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from eight species that suggested there was a trade-off between the spatial extent of a plant's root system (foraging scale) and its ability to respond to small nutrient patches (foraging precision). They suggested that adaptations that would allow large dominant species to forage for resources over large spatial scales were incompatible with the ability to proliferate root tissues precisely in small nutrient patches. Campbell et al. (1991, p. 537) proposed that increased foraging precision of small subordinate species could be a mechanism allowing for species coexistence and that "the average nutrient concentration in soil may be less important in determining the competitive success of species than their morphological flexibility in responding to ... enriched soil microsites." Not everyone agreed with this idea, and Tilman and Pacala (1993, p. 14) argue that "Because individual organisms can 'average' resource supply rates ... through the region in which they forage, the relevant components of spatial heterogeneity are the individual-to-individual differences in these averages." In this view, small-scale heterogeneity is important only in how it influences average resource capture and does not by itself alter the fundamental nature of plant interactions. Empirical support for a trade-off between foraging scale and precision is mixed (Einsmann et al. 1999; Farley and Fitter 1999; Wijesinghe et al. 2001; Bliss et al. 2002). Despite the mixed empirical support, Campbell et al.'s (1991) article continues to be very influential, with more than 100 citations to date (ISI Web of Science). As evidence of the article's continuing influence and impact, more than one-third of those citations have occurred 10 years after its initial publication (2001–2004).

Although Campbell et al.'s (1991) study is widely cited, several authors have raised questions about the underlying validity of their conceptual model. For example, interspecific variation in relative growth rates (RGR) may confound measures of foraging precision (Fransen et al. 1999a). Faster-growing plants will add more root tissue over a given period of time than slower-growing plants, and thus, even if two plants are equally "precise" in their foraging (e.g., they allocate an equal proportion of new root growth to nutrient-rich patches), one would find a biomass difference between patches for high-RGR plants sooner than for slower-growing, low-RGR plants (Fransen et al. 1999a). There is some empirical and modeling support for this idea, where if one controls for differences among species in RGR, there are few remaining differences in foraging precision (Fransen et al. 1999a; Aanderud et al. 2003). A related issue is that studies vary in duration, and thus the longer the study, the more likely a researcher is to find foraging precision among slower-growing species. However, soil nutrient patches can be very short-lived (Lamb et al. 2004), and thus, very long-duration studies of foraging precision may have little relevance to natural

systems. In either case, the relationship among RGR, study duration, and foraging precision is unclear.

Common to both the scale-precision and the RGR-precision models is that logistical limitations have necessitated that each experimental test of the models include a relatively low number of species. Further, no study has accounted for the phylogenetic relationships among species when evaluating trade-offs among root foraging and other plant traits. There is increasing acknowledgment that comparative studies should not treat species as independent data points because species are related through descent from common ancestors (Felsenstein 1985). As a result, the generality of either of these models is unclear but can best be resolved using a phylogenetically based comparative approach.

At an even more basic level, root proliferation in response to locally elevated soil resource levels is simply one example of morphological plasticity in response to an environmental signal, one of many forms of phenotypic plasticity exhibited by plants (Pigliucci 2001; Grime and Mackey 2002). Numerous studies have documented phylogenetic conservatism or convergence of plant species' ecological traits and niches (e.g., Ackerly 1999; Prinzing et al. 2001), but studies documenting the evolutionary history of phenotypic plasticity across a large number of plant species are extremely rare (e.g., Pigliucci et al. 1999), and studies describing the evolutionary history of plant foraging and behavioral ecology are nonexistent. By combining a current phylogenetic hypothesis with information on species root proliferation responses, we asked whether these ecological traits exhibit a phylogenetic signal. By using information on the evolutionary relationships among species, we can also control for potentially confounding effects of phylogenetic relatedness when addressing the ecological question of whether and how root foraging precision and plasticity are related to foraging scale and other traits.

We use previously published data on plant phylogenetic and taxonomic relationships and on plant root foraging ability to address the following questions: Are foraging precision, scale, plant response to nutrient heterogeneity, and RGR phylogenetically conserved or convergent traits? Are there interspecific correlations among plant foraging precision, foraging scale, RGR, study duration, and plant response to nutrient heterogeneity? Do interspecific correlations among traits differ when the evolutionary relationships among species are taken into account?

Methods

Data Sets

Following a thorough literature review of root foraging studies published between 1975 and August 2003, we chose

to use data from 13 articles that met a set of requirements (for details, see appendix in the online edition of the *American Naturalist*). To be included in this study, an article must have examined some measure of root response by individual plants to spatial variation in nutrient availability in experimentally created soil patches. When studies used multiple nutrient heterogeneity treatments, we selected the treatment most likely to maximize soil heterogeneity (fewest number of nutrient patches, most spatially separated patches, or largest patch/background contrast). Some data were reported in more than one format, in which case we used the highest quality data available (e.g., data from a table rather than extracting from a figure). We did not segregate studies on the basis of whether single resources (N, P) or multiple resources were manipulated, though most studies modified soil fertility as a whole.

Although few ecological studies use exactly the same methodologies, there was one decision made by several researchers that we felt excluded numerous studies from further consideration. There are two main approaches to creating soil heterogeneity: first, take a given amount of resources and either mix it evenly within the soil (homogeneous) or place it in small patches (heterogeneous) or second, take homogenous soil and either do nothing to it (homogeneous) or add nutrient patches (heterogeneous). In the latter approach, there is the confounding factor of increased soil fertility in the heterogeneous treatment relative to the homogeneous treatment, and we excluded the many studies that used this approach.

Significant differences in methodologies among studies necessitated dividing the data into three subsets: British flora (43 species), Great Plains flora (59 species), and combined biomass (78 species). The first two subsets represent large data sets derived from two articles (British flora: Grime and Mackey 2002; Great Plains flora: Johnson and Biondini 2001), with species selection of each limited to plants from a specific locale. Grime and Mackey (2002) chose species occurring in Britain in any of a variety of community types. The species chosen by Johnson and Biondini (2001) were all potentially co-occurring species of North American Great Plains grasslands. A major methodological difference between these studies is in how root responses to soil heterogeneity were measured, with Grime and Mackey (2002) measuring root biomass and Johnson and Biondini (2001) measuring root surface area. Since root surface area and biomass may not be directly comparable as measures of plant foraging responses (Hodge 2004), these two data sets were analyzed separately. Within each of these data sets, all plants were harvested at a single time (14 and 60 days, respectively), and thus any differences in foraging among species cannot be attributed to variation in study duration.

In contrast to the first two data subsets, the combined

biomass data set consists of the results of studies conducted on many species and presented in numerous articles by several authors (appendix). Common to all of these studies is that root biomass was the measure of root response to soil heterogeneity, and thus, this data set also includes the species tested by Grime and Mackey (2002). These studies varied in duration, and thus, this is the only data set that could be used to address the impact of study duration on measured root response to soil heterogeneity. Root proliferation responses were also measured using root length (15 species), specific root length (14 species), and root number/density (10 species) in several studies. However, to allow for biologically and statistically meaningful comparisons, relatively large numbers of species are needed, and thus, we analyzed only the three subsets of data described above.

Plant Trait Data

A variety of data were extracted from each study as well as a variety of other sources. When multiple studies measured foraging precision in the same species, each study was recorded separately in the database.

Root foraging precision. Foraging precision was measured as the proportion of a plant's root system biomass or surface area found in the high-nutrient treatment of an individual experiment. In all studies, the soil volume from which roots were extracted was the same for the patch and background cores, though the studies varied in whether these cores represented either the entire root system biomass (e.g., Campbell et al. 1991) or only a small subset (e.g., Cahill and Casper 1999). Measuring root response in patch and background soil could be done either by taking cores from similar locations in different pots of different treatments (heterogeneous vs. homogeneous) or by taking multiple cores within a single heterogeneous treatment (patch and background locations). We did not discriminate among these approaches in the collection of our data, and when both were available from a single study, we used the average of the two.

Root foraging scale. According to the original theory, Campbell et al. (1991, p. 537) state "Dominant plants tend to monopolize light and mineral nutrient capture by the development of extensive leaf canopies and root systems. We term this *high scale* foraging. This pattern of development necessitates an accompanying investment in long, large leaves and roots, in tall thick supporting stems and in long thickened roots." From this description, foraging scale has been interpreted as the spatial extent over which a plant forages. Quantifying foraging scale for a particular species could be done through two-dimensional excavations (e.g., Brisson and Reynolds 1994), through patterns of tracer uptake (e.g., Casper et al. 2000), or even better,

through three-dimensional analyses of root distributions. However, data for large numbers of species using any of these approaches are nonexistent. Instead, scale is generally measured using a proxy such as the size of a plant's root system (total surface area, root length, breadth, or biomass). Although comparing root biomass among species is probably a reasonable relative measure of scale within a study, differences in growing conditions (soil fertility, pot size, duration) prevent the use of this measure when comparing species from different studies. As a result, root biomass was available as a measure of scale only for the Great Plains data set. To provide a measure of foraging scale for the British flora and combined biomass data sets, we compiled data on the typical height at maturity for each species as reported in various floras and plant trait databases (Gleason 1963; Grime et al. 1988; Moss and Packer 1994; U.S. Department of Agriculture 2004). In an allometric study including numerous species, plant height was tightly correlated with lateral root spread (K. J. Niklas, H. J. Schenk, and R. B. Jackson, unpublished data) and thus should be another proxy measure of potential root foraging scale for all species. Within the Great Plains data set, plant height from the floras was correlated with total root biomass (table 1), further supporting our use of height as a measure of foraging scale.

Plant response to nutrient heterogeneity. The response of a plant to soil heterogeneity, measured as the ratio of whole plant biomass (root + shoot or shoot only) when grown in heterogeneous soil versus when grown in biomass in homogenous soil. Measures of plant performance were not taken in all studies, and as a result, this response variable is available only for the Great Plains data set and a subset of 18 species from the combined biomass data set.

Relative growth rate. RGR was measured as the per-week rate of plant growth as reported in various literature sources (Grime and Hunt 1975; Grime et al. 1988; Poorter and Remkes 1990; Levang-Brilz and Biondini 2002; Reich et al. 2003).

Study duration. Study duration was measured as the number of days plants were allowed to grow before harvest. These values varied within and among studies included in the combined biomass data set.

Taxonomic and Phylogenetic Data

Taxonomic names above the rank of genus (class, order, family) follow those used by Cronquist (1998) and the APG II phylogenetic classification of flowering plants (APG II 2003), while genus and species nomenclature follow Kartesz (1994). We constructed hypotheses for the phylogenetic relationships among the species included in each of the three data sets using Phylomatic (Webb and Donoghue 2004), an online phylogenetic database and tree

assembly tool kit. We used the maximally resolved Phylomatic tree version R20031202 as the backbone of our phylogenetic hypothesis. This tree is not a true supertree (sensu Sanderson et al. 1998) but rather has been assembled by hand on the basis of data from numerous published vascular plant phylogenies, with the backbone of the tree based on a recent interpretation (Stevens 2004) of the APG II (2003) phylogenetic classification of angiosperm plant orders and families. The tree produced by Phylomatic was well resolved to the family level but placed all genera as polytomies within families and species as polytomies within genera.

Phylogenetic and Taxonomic Trait Variation

The degree of evolutionary conservatism of root plasticity and other traits was assessed in two ways. First, we conducted variance components analyses (VCA) using Proc Nested (SAS 2001) to determine the relative amounts of variation in measured traits among classes, orders, families, genera, and species (Harvey and Mace 1982; Ackerly 1999; Prinzing et al. 2001). Second, we estimated the quantitative convergence index (QVI; Ackerly and Donoghue 1998; Ackerly 1999) for each variable. QVI measures the magnitude of phylogenetic signal in a phenotypic trait as the degree of phylogenetic conservatism or convergence relative to that expected by chance. Possible QVI scores range from 0 (maximally conserved trait evolution, maximum phylogenetic signal) to 1 (maximally convergent trait evolution, minimum phylogenetic signal). QVI was calculated for each variable using CACTUS 1.13 (Schwilk 2001; Schwilk and Ackerly 2001), and the statistical significance of each QVI score was evaluated by comparison with QVI values for 1,000 random reshufflings of species across the phylogeny. Because CACTUS 1.13 requires a fully resolved phylogenetic tree in order to calculate QVI, we randomly resolved all polytomies in the tree 100 times using Mesquite 1.05 (Maddison and Maddison 2004) and repeated the QVI analysis on each of the randomly resolved trees. In all cases, results from these randomly resolved trees were comparable, indicating that the uncertainty in the original tree did not have a significant effect on our results.

Ahistorical and Phylogenetically Independent Correlations among Traits

We assessed relationships among plant foraging precision, foraging scale, response to heterogeneity, RGR, and study duration in several ways. We first examined ahistorical relationships among variables, treating each species as an independent data point and evaluating correlations among all pairs of traits. All variables were $\ln(x + 1)$ transformed

Table 1: Correlations (ahistorical and phylogenetically independent contrasts [PIC]) among root foraging traits

Variable 1	Variable 2	<i>N</i>	Ahistorical correlation (<i>r</i>)	<i>P</i> value	PIC correlation (<i>r</i>)	<i>P</i> value
Combined biomass species (multiple studies):						
Precision	Scale (height)	78	-.15	.2021	-.18	.1123
Precision	RGR	56	-.02	.8678	-.04	.7864
Precision	Response to heterogeneity	31	.23	.2205	.15	.4391
Precision	Study duration	78	-.54	.0000	-.60	.0000
Scale (height)	RGR	56	-.20	.1355	-.08	.4675
Scale (height)	Response to heterogeneity	31	-.07	.6910	-.12	.4909
Scale (height)	Study duration	78	.49	.0000	.25	.0297
Study duration	Response to heterogeneity	31	.00	.9968	-.04	.7964
Study duration	RGR	56	-.24	.0832	-.14	.3097
RGR	Response to heterogeneity	18	.14	.2860	.07	.3399
British flora (Grime and Mackey 2002):						
Precision	Scale (height)	43	.00	.9960	-.03	.7338
Precision	RGR	36	-.23	.1845	-.26	.1348
Scale (height)	RGR	36	.42	.0106	.52	.0029
Great Plains flora (Johnson and Biondini 2001):						
Precision	Scale (height)	59	-.02	.8869	-.03	.7128
Precision	Scale (root system size)	59	.17	.1914	.15	.2982
Precision	Response to heterogeneity	59	-.04	.7540	-.11	.4571
Precision	RGR	54	.24	.0758	.33	.0282
Scale (height)	Scale (root system size)	59	.20	.1259	.31	.0274
Scale (height)	Response to heterogeneity	59	-.05	.7194	-.11	.4439
Scale (height)	RGR	54	.26	.0570	.29	.0505
Scale (root system size)	Response to heterogeneity	59	.18	.1799	.22	.1172
Scale (root system size)	RGR	54	.43	.0013	.40	.0051
RGR	Response to heterogeneity	54	-.03	.8257	-.05	.6811

Note: PIC correlation *P* values based on comparison of observed correlations with correlations obtained for 1,000 random trees generated by shuffling species across the tree. All correlations calculated using $\ln(x + 1)$ transformed data. PIC correlations and *P* values represent the means from analyses of 100 trees generated by randomly resolving all polytomies in the original phylogeny; in all cases, results from these randomly generated trees were comparable (i.e., traits with significant [$P < .05$] ahistorical or PIC correlations were significant across >80% of randomly resolved trees). *N* = number of species; RGR = relative growth rates.

before analysis to meet assumptions of normality. All analyses were performed separately on each of the three data sets.

Relationships among all variables were also analyzed in an evolutionary context using phylogenetically independent contrasts (PICs). This method contrasts the difference in two variables between daughter nodes for each node in a phylogeny, with ancestral states reconstructed using linear parsimony analysis (Felsenstein 1985; Garland et al. 1992), avoiding the assumption that species represent statistically independent data points. Raw contrasts at each node were standardized by dividing them by their standard deviation, with standard deviation defined as the square root of the sum of branch lengths for a contrast (Garland et al. 1992).

We calculated PICs among all pairs of traits for which

we had calculated ahistorical correlations using CACTUS 1.13 (Schwilk 2001; Schwilk and Ackerly 2001) and the PDAP:PTREE module (Midford et al. 2002) in Mesquite 1.05 (Maddison and Maddison 2004) using $\ln(x + 1)$ transformed values for all traits. We obtained estimates of branch lengths for the phylogeny using BLADJ (Webb 2004), which assigned branch lengths on the basis of clade age estimates (Wikstrom et al. 2001), with undated nodes assigned equal branch lengths between nodes for which age estimates were available. To evaluate our choice of branch lengths, we compared plots of the absolute value of standardized independent contrasts versus the standard deviation of contrasts (the square root of the sum of branch lengths for a contrast) assuming equal branch lengths and using branch lengths provided by BLADJ, and we found that equal branch lengths provided the most

adequate standardization of contrasts (Garland et al. 1992). We therefore assumed all branch lengths were equal when conducting PIC analyses, a method that has been shown to provide proper Type I error rates in comparative analyses when true branch lengths are uncertain or unavailable (Díaz-Uriarte and Garland 1996; Ackerly 2000).

We calculated correlations between standardized contrasts for all pairs of traits for which we had calculated ahistorical correlations. We calculated the statistical significance of all PIC correlations using a randomization method that compared observed contrast correlations to a null distribution of correlations obtained from 1,000 random reshufflings of species across the phylogeny (Ackerly 2000). All analyses were repeated for 100 phylogenetic trees generated by randomly resolving all polytomies in the original tree to allow linear parsimony reconstruction of ancestral states.

Results

Average foraging precision (mean proportion of the total measured root biomass in high nutrient treatment \pm SE) was 0.77 ± 0.01 for the British flora (BF), 0.75 ± 0.01 for the combined biomass (CB) species, and 0.67 ± 0.02 for the Great Plains flora (GPF). Plants were generally slightly larger when grown in heterogeneous soil relative to homogeneous soils, with an average response (ratio of plant biomass in heterogeneous vs. homogenous soil \pm SE) of 1.07 ± 0.06 in the CB data set and 1.25 ± 0.11 among the GPF.

Phylogenetic Structure of Trait Variation

Root foraging precision is a phylogenetically and taxonomically conserved trait. Approximately 82% (BF) and 52% (GPF) of taxonomic variation in root foraging precision occurred above the level of species, and QVI scores for root foraging precision were lower (GPF: $P = .002$) or marginally lower (BF: $P = .073$) than expected by chance in two of the three data sets we examined (fig. 1; table 2). A large proportion of the total variation in root foraging precision was among classes (e.g., monocots vs. dicots; fig. 1; table 2). There was also substantial variation in foraging precision among genera within families in both the BF and CB data sets (table 2).

The CB data set showed significant phylogenetic conservatism of foraging scale (plant height) and relative growth rate (table 2). Much of the variation in foraging scale was among classes (e.g., gymnosperm trees vs. predominantly herbaceous monocots and dicots) and orders within classes, while variation in RGR was largely among families. Phylogenetic signal in all other measured traits was not significantly different from random (table 2).

Trait Relationships

There were no significant ahistorical or phylogenetically independent contrast correlations among root foraging precision, foraging scale, or plant response to nutrient heterogeneity (figs. 2, 3, 5; tables 1, 3). In the GPF data set, there was a positive correlation between our two measures of foraging scale (table 1), supporting our use of plant height as a proxy measure for foraging scale. RGR was significantly positively correlated with foraging precision for the GPF data set (fig. 3; table 1; phylogenetically independent contrasts) and positively correlated with foraging scale (table 1) for both the BF and GPF data sets. For the CB species, there was a strong negative correlation between study duration and foraging precision (fig. 4; table 1) and a positive relationship between study duration and foraging scale because of the fact that studies that included the tall tree species tended to be of longer duration. The negative correlation between study duration and foraging precision in the CB data set remained significant when results from Grime and Mackey's (2002) study were removed from that data set ($r = -0.40$, $N = 35$, $P = .017$).

Discussion

The Evolution of Plant Phenotypic Plasticity and Root Foraging Ability

The ability of plants to modify their root morphology in response to soil nutrient heterogeneity is one kind of phenotypic plasticity, and this study is among the first studies to demonstrate phylogenetic and taxonomic conservatism of phenotypic plasticity across a wide range of plant species (table 2). The general pattern of lower root proliferation response by monocots relative to dicots (fig. 1) was noted previously by the original researchers of the GPF and BF data sets (Johnson and Biondini 2001; Grime and Mackey 2002). Despite the general conservatism of plasticity at the class level in these two data sets, similar findings were not found in the CB data set. Additionally, there were exceptions to the broad differences among classes in all data sets such that both precise and imprecise foragers were found in both classes (fig. 1).

A major challenge that remains to be resolved is disentangling the relationships of various morphological and physiological traits with root foraging precision. It is unclear whether the phylogenetic history of root foraging precision is a result of direct selection on the ability of plants to proliferate roots in response to environmental signals or as a result of selection on other morphological or physiological characters correlated with foraging precision. Shared derived characters such as the adventitious roots produced by many monocots may be partly respon-

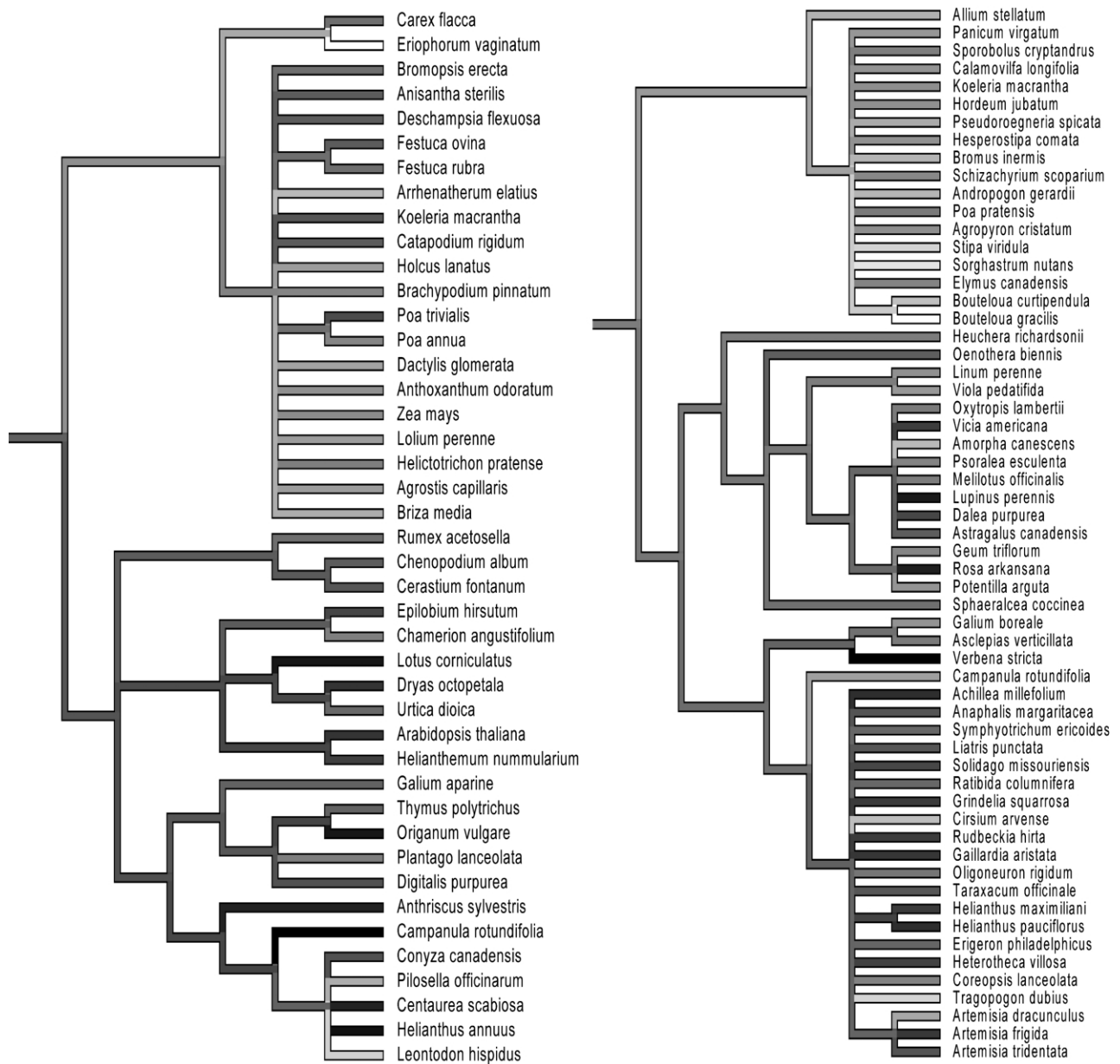


Figure 1: Phylogenetic history of root foraging precision (relative ability to proliferate roots in nutrient patches) for British flora (*left*; Grime and Mackey 2002) and Great Plains flora (*right*; Johnson and Biondini 2001) species. Branch shading indicates relative root foraging precision, from white (low precision, low plasticity) to black (high precision, high plasticity). Ancestral states were reconstructed using squared-change parsimony analysis. Branch lengths in the figure are arbitrarily scaled to allow visual interpretation of phylogenetic patterns.

sible for the lower root foraging precision of this clade (Grime and Mackey 2002). However, numerous other traits are shared by the monocot clade, and undoubtedly, some of these traits are also correlated with root foraging precision. It remains to be seen how multivariate interactions among plant functional traits are related to root morphological plasticity.

If future research is to be conducted with individual potted plants, effort should be directed toward selecting study taxa that will help understand the overall evolutionary pattern of root plasticity in plants. This evolutionary work would be greatly strengthened if it were coupled with gene sequencing that allowed for mapping of the evolution of the gene families associated with root

Table 2: Phylogenetic and taxonomic structure of variation in plant species foraging precision, foraging scale, study duration, relative growth rate (week^{-1}), and response to heterogeneity

Variable	N	Mean QVI	Mean expected QVI	P value	Percent of total variance accounted for by taxonomic ranks				
					Class	Order	Family	Genus	Species
Combined biomass species (multiple studies):									
Precision	78	.840	.838	.342	11.8	2.0	.0	21.9	64.3
Scale (height)	78	.546	.905	.001	55.6	35.6	3.9	4.6	.3
Study duration	78	.808	.822	.346	2.6	.2	2.7	.0	76.6
RGR	56	.662	.855	.002	.0	8.0	54.4	22.9	14.7
Response to heterogeneity	31	.941	.881	.181	.0	78.8	.0	15.9	5.4
British flora (Grime and Mackey 2002):									
Precision	43	.741	.845	.073	38.9	.0	1.0	41.7	18.4
Scale (height)	43	.824	.851	.320	.0	10.6	10.1	78.6	.7
RGR	36	.814	.858	.242	.0	4.1	60.0	19.0	16.8
Great Plains flora (Johnson and Biondini 2001):									
Precision	59	.664	.846	.002	43.6	8.1	.0	.0	48.3
Scale (height)	59	.818	.835	.271	.0	2.1	.0	.0	79.9
Scale (root system size)	59	.919	.886	.225	.0	43.6	.0	44.2	12.1
RGR	54	.839	.844	.298	.0	52.3	.0	16.0	31.8
Response to heterogeneity	59	.858	.854	.294	.3	7.5	.0	.0	92.2

Note: Quantitative convergence index (QVI) *P* values indicate significance of observed QVI relative to expected QVI from random reshuffling of taxa across phylogeny 1,000 times. QVI scores significantly lower than expected indicate phylogenetic trait conservatism. Expected QVI and *P* values are mean values from 100 random resolutions of polytomies in the original phylogenetic tree; in all cases, results from these randomly resolved trees were comparable (i.e., trees were either all significant or all nonsignificant for a given trait). Variance accounted for at different taxonomic ranks was calculated using hierarchical nested variance components analysis (SAS 2001). All analyses were conducted using $\ln(x + 1)$ transformed data. *N* = number of species; RGR = relative growth rates.

proliferation. At a most basic level, we do not know whether this form of phenotypic plasticity is an ancestral or derived trait in plants.

Correlations among Foraging Precision, Scale, Study Duration, and Plant Growth Rates

In this comparative study using 121 species, there was no relationship between root foraging precision and scale in any of the three data sets examined (table 1). The large number of species considered in this study, the consistency of patterns regardless of how species responses to nutrient heterogeneity were measured, and the fact that the criteria for species inclusion varied among data sets lead us to conclude that there is no convincing evidence for a widespread trade-off between plant root foraging scale and precision.

Further, from a mechanistic basis, it is unclear why plant foraging scale should be expected to be related to the ability of a plant to proliferate roots in nutrient patches. Recent molecular studies indicate that root proliferation responses in *Arabidopsis thaliana* are controlled by a network of signaling genes that induce root initiation and growth in

direct response to the availability of different soil nutrients (Zhang and Forde 1998; Forde 2002; Casson and Lindsay 2003; López-Bucio et al. 2003; Malamy 2005; Tonsor et al. 2005). For the scale-precision trade-off to occur, these genes would need to be found or expressed only in relatively small or subdominant species, and there is no clear reason why large dominant plants would lack these particular genes. The increasing knowledge of the genetic basis of root proliferation responses may eventually allow direct comparisons between measured variation in root proliferation ability and variation in the genetic networks that control root proliferation. On the basis of the available evidence, we suggest the scale-precision hypothesis is supported by neither comparative data nor current molecular understanding.

In contrast to the lack of support for a scale-precision relationship, the relationship between RGR and precision is more ambiguous. In both the CB and BF data sets, there was no relationship between RGR and foraging precision (fig. 3; table 1), but there was a significant positive relationship between RGR and precision of phylogenetically independent contrasts in the GPF data set (table 1). The lack of a relationship in two of the data sets is probably

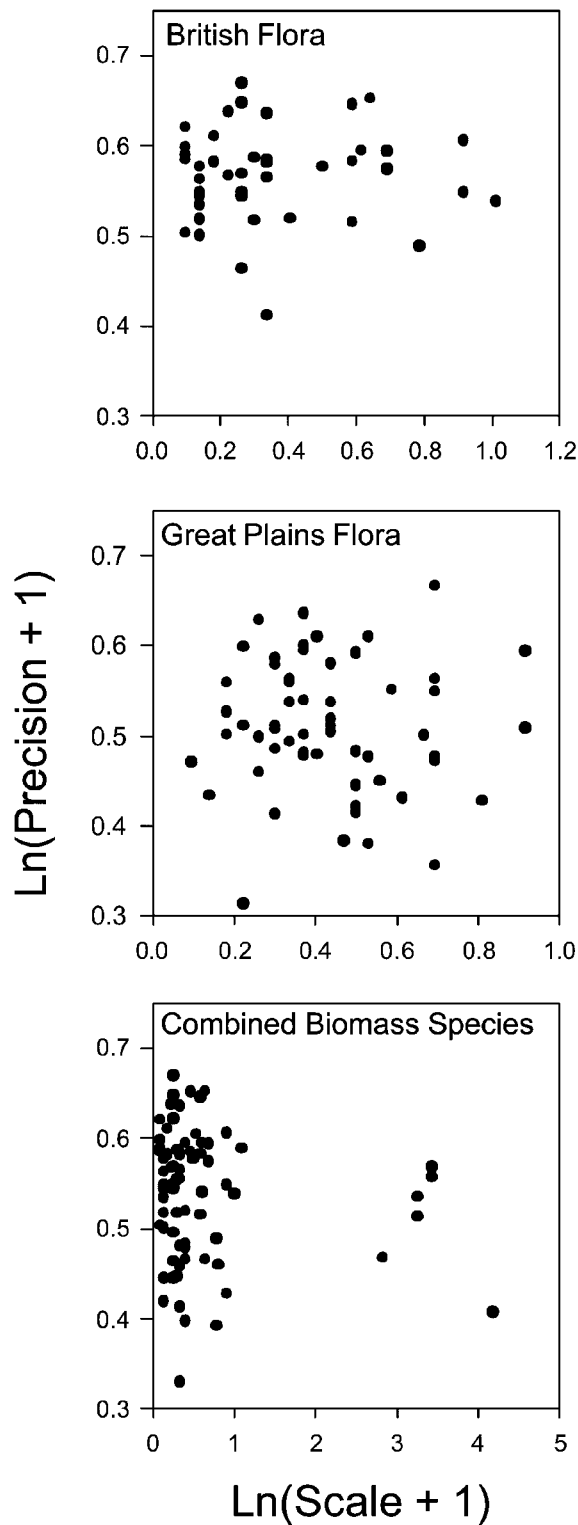


Figure 2: Ahistorical relationships (data points represent species) between root foraging precision and foraging scale for species whose response to

not due to low statistical power because the CB data set contains slightly more species than the GPF data set. Similarly, it is unlikely because of variation in study duration obscuring an underlying RGR-precision relationship as all species within the BF data set grew for the same duration, and yet no relationship was found. Additionally, there was no relationship between RGR and study duration in the CB data set (table 1), and controlling for variation in study duration did not change the significance of RGR-precision relationships (table 3). This study does not provide convincing support for the RGR-precision hypothesis as a general phenomenon, though clearly, the significant result in the GPF data set is intriguing. It is particularly noteworthy that of all the data sets, the GPF was the only one in which foraging response was measured as root surface area rather than biomass and also the only one in which the species all came from a single plant community type. The relevance of these two methodological details is unclear, though further investigation is warranted.

Some authors have previously suggested that tests for scale-precision trade-offs are often confounded by variation in RGR among species (e.g., Fransen et al. 1999a; Aanderud et al. 2003) primarily because two plants with equal ability to proliferate roots in response to nutrient availability will have different measured amounts of foraging precision if they are harvested at the same time and if there is substantial variation in growth rates among species (Fransen et al. 1999a). Plants that grow faster will have added more biomass per unit time and thus will have expressed their foraging precision to a greater degree than slower-growing plants. There is empirical support for this idea where interspecific differences in foraging precision were found when plants were harvested at a common time but not at a common size (Aanderud et al. 2003). Although conceptually elegant, these ideas had not been previously tested on large numbers of species, and there is only limited support found here.

High RGR is often considered as a mechanism that enhances ecological traits such as competitive ability (Keddy 2001). We suggest that instead of RGR being viewed as a confounding effect related to plant foraging, it may itself be a mechanism by which plants are able to rapidly exploit nutrient patches. This idea is supported by recent work showing that nutrient patches can be very short lived

nutrient heterogeneity was measured as proportion of root system surface area (Great Plains flora) or biomass (British flora; combined biomass) in high- versus low-nutrient patches. Ahistorical and phylogenetically independent contrast correlations (not shown) between foraging precision and scale were nonsignificant ($P > .05$). For the combined biomass species, correlation analyses were repeated after excluding the six tree species with $\ln(\text{scale} + 1) > 2$; the correlations remained nonsignificant.

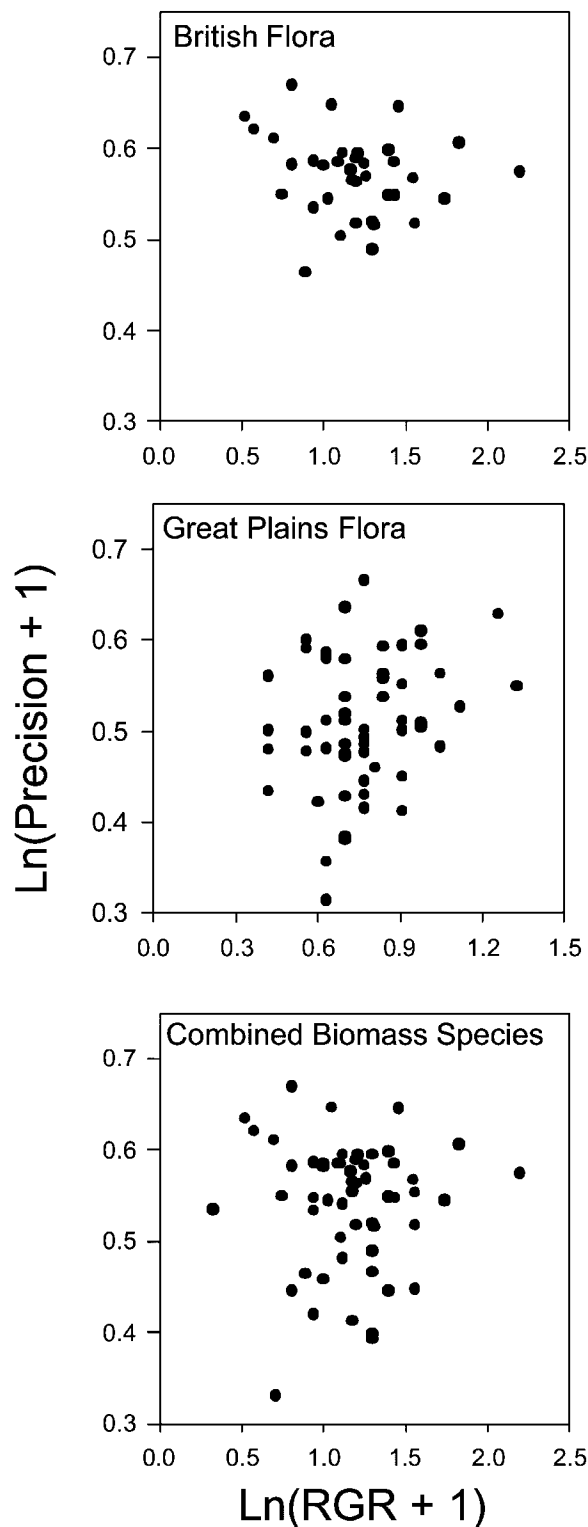


Figure 3: Ahistorical relationships (data points represent species) between root foraging precision and relative growth rate (RGR [week^{-1}]) for spe-

(Lamb et al 2004), and thus only those plants able to respond quickly to ephemeral patches will be able to accrue any advantage. This is further supported by our findings of a clear negative relationship between study duration and precision (fig. 4; table 1). We argue that it makes biological sense to find lower foraging precision after extended periods of growth because nutrients in old patches are probably depleted, and thus patches will have little value relative to the background soil. We argue that given short-lived nutrient patches in natural systems, what ultimately affects plant fitness is whether a plant is able to exploit those resources and not whether it does so through higher growth rates or variation in foraging precision. If the ephemeral nature of patches does influence their relative value to a plant, then the method of patch creation used by an experiment (press vs. pulse) may have significant consequences for the outcome of the study.

Whole Plant Responses to Nutrient Heterogeneity and Community-Level Implications

For individually grown plants, the magnitude of root proliferation response to nutrient heterogeneity is not a predictor of the accrued growth benefit in heterogeneous soils (fig. 5; table 1). This result is in contrast to an analytical model of root foraging that predicts a relationship between foraging precision and response to heterogeneity (Fransen et al. 1999a) and could be caused by a variety of factors. Although root proliferation can increase nutrient uptake from patches (Jackson and Caldwell 1996), proliferation does not always result in increased N uptake (Fransen et al. 1998; Hodge et al. 1998), and it is possible that the main benefit of soil heterogeneity is that a given soil volume has limited binding capacity, and thus a greater proportion of nutrients are available when presented as patches (Anghinoni and Barber 1980b). All plants whose growth is nutrient limited should benefit from this simple fact of soil chemistry, regardless of their proliferation ability. Alternatively, although root proliferation is the most visually obvious response to nutrient patches, physiological shifts in uptake kinetics (Jackson et al. 1990) could be more important in determining growth responses to soil heterogeneity (Hodge 2004).

cies whose response to nutrient heterogeneity was measured as proportion of root system surface area (Great Plains flora) or biomass (British flora; combined biomass) in high- versus low-nutrient patches. Ahistorical and phylogenetically independent contrast correlations (not shown) between foraging precision and scale were nonsignificant ($P > .05$) for British flora and combined biomass species, and positive for Great Plains flora species (ahistorical: $r = 0.24$, $P = .0758$; phylogenetically independent contrast: $r = 0.33$, $P = .0282$).

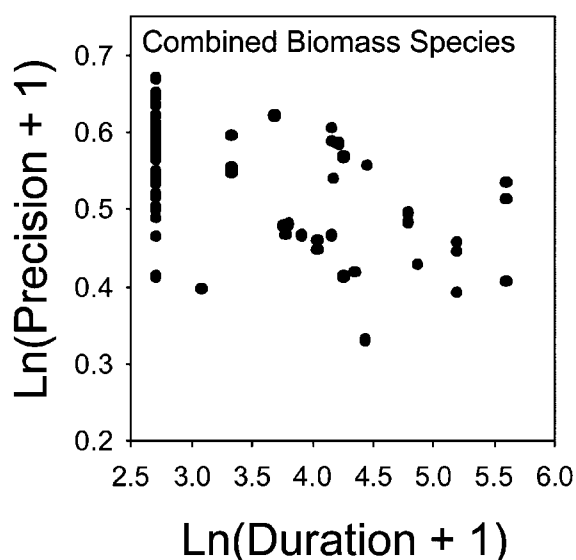


Figure 4: Ahistorical relationships (data points represent species) between root foraging precision and study duration for species whose response to nutrient heterogeneity was measured as proportion of root system biomass in high- versus low-nutrient patches (combined biomass data set). The negative correlation between foraging precision and study duration remained significant when the British flora species (duration = 14 days) were removed from the analysis.

Even in the absence of a foraging scale-precision trade-off, nutrient heterogeneity could influence community composition if it changes the nature of competition. Soil heterogeneity can alter belowground neighborhood structure (Casper et al. 2000, 2003), competitive interactions (Fransen et al. 2001), and relative abundances of species (Wijesinghe et al. 2005). Additionally, if nutrient heterogeneity changes the symmetry of competition (Schwinning and Weiner 1998; Fransen et al. 2001), it would have a variety of significant consequences for community composition (Rajaniemi 2003) even if foraging ability is unrelated to competitive ability (Larigauderie and Richards 1994). Ultimately, the response of isolated plants to heterogeneity under artificial conditions may not be a good indicator of the importance of nutrient heterogeneity or foraging ability in natural populations. Even simple species mixtures can result in different effects of heterogeneity on growth compared with isolated plants (Cahill and Casper 1999). Alternatively, soil heterogeneity may be important to individuals, but these impacts do not necessarily scale up to the community (Tilman and Pacala 1993).

What is clear from this study is that proliferation is not essential for increased growth in heterogeneous soils. These findings raise the question posed earlier by Robinson (1996) of why plants bother to proliferate roots.

Although root proliferation is a widespread phenomenon found in many plant taxa, this does not necessarily mean it has adaptive value under natural growing conditions. A standard argument has been that differences in root proliferation ability among species may have fitness consequences when plants are grown with neighbors, even if such a pattern does not occur among individually grown plants (fig. 5). Despite the intuitive appeal of this argument, some studies have found a relationship between competition and proliferation ability (e.g., Robinson et al.

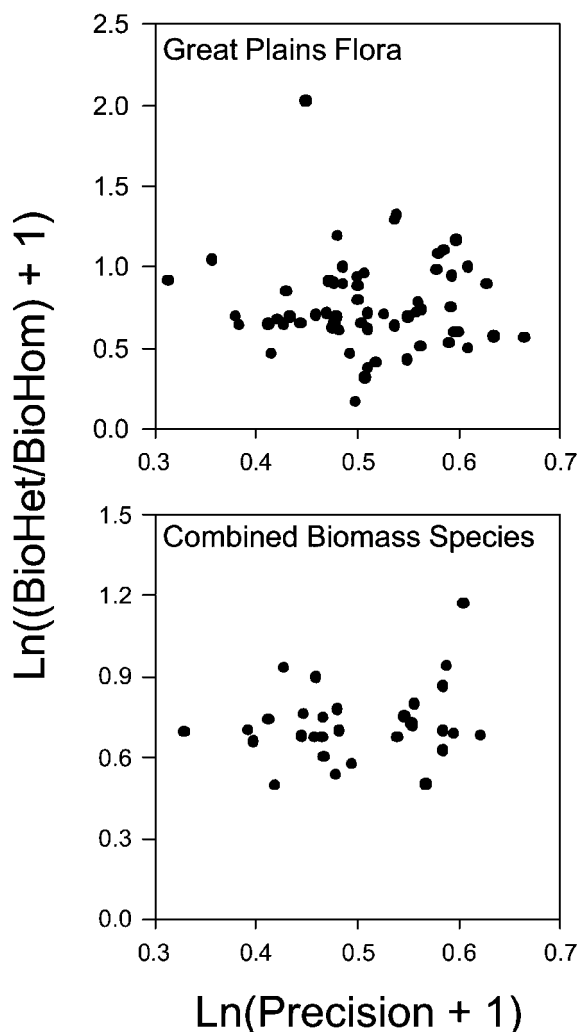


Figure 5: Ahistorical relationships (data points represent species) between root foraging precision and response to nutrient heterogeneity (biomass in heterogeneous soil/biomass in homogenous soil) for species whose response to nutrient heterogeneity was measured as proportion of root system surface area (Great Plains flora) or biomass (combined biomass) in high- versus low-nutrient patches. Ahistorical and phylogenetically independent contrast correlations (not shown) between foraging precision and response were nonsignificant ($P > .05$).

Table 3: Partial correlations (ahistorical and phylogenetically independent contrasts [PIC]) among root foraging traits controlling for a covariate

Variable 1	Variable 2	Covariate	<i>N</i>	Ahistorical correlation (<i>r</i>)	<i>P</i> value	PIC correlation (<i>r</i>)	<i>P</i> value
Combined biomass species (multiple studies):							
Precision	Scale (height)	RGR	56	-.02	.9050	-.13	.3440
Precision	Scale (height)	Study duration	78	.16	.1550	-.04	.7300
Precision	RGR	Study duration	56	-.19	.1640	-.18	.2060
British flora (Grime and Mackey 2002):							
Precision	Scale (height)	RGR	36	.12	.5060	.03	.8640
Great Plains flora (Johnson and Biondini 2001):							
Precision	Scale (height)	RGR	54	-.09	.5120	-.05	.7060

Note: PIC partial correlation *P* values based on comparison of observed partial correlations with partial correlations obtained for 1,000 random trees generated by shuffling species across the tree. All partial correlations calculated using $\ln(x + 1)$ transformed data. PIC partial correlations and *P* values represent the means from analyses of 100 trees generated by randomly resolving all polytomies in the original phylogeny; in all cases, results from these randomly generated trees were comparable (i.e., trait partial correlations were nonsignificant for >90% of randomly resolved trees). *N* = number of species, RGR = relative growth rates.

1999; Fransen et al. 2001), and others have not (e.g., Cahill and Casper 1999). Equally contradictory results are also found at the population (e.g., Casper and Cahill 1996; Day et al. 2003a) and community levels (e.g., Collins and Wein 1998; Wijesinghe et al. 2005). A significant problem in identifying whether small-scale heterogeneity consistently alters population and community level processes is that few studies have been conducted, and individual studies have tended to focus on a limited number of species. More emphasis on experimental designs representative of natural conditions would greatly improve our ability to address this most basic question. At this point, there are not enough data available to determine whether Tilman and Pacala (1993) were correct in their argument that this scale of nutrient heterogeneity is unimportant for plant communities.

Conclusions

This is the first large synthetic study of root foraging ability in vascular plants. At a most basic level, there was evidence in some groups of species that root phenotypic plasticity is a phylogenetically and taxonomically conserved trait, mainly at deep levels in the angiosperm phylogeny, with most clades generally containing both precise and imprecise foragers. From an ecological perspective, it appears that long-standing theories of the controls of interspecific variation in root foraging are incorrect. We found no empirical support for a trade-off between foraging scale and precision, nor was there widespread support for an RGR-precision relationship. The fact that foraging precision was

not related to the growth benefit accrued from growing in heterogeneous soil is particularly surprising. This latter finding raises significant questions about the ecological relevance of small-scale nutrient heterogeneity in natural systems, as well as our ability to draw conclusions about community-level effects of foraging ability and nutrient heterogeneity on the basis of plants grown in isolation. The functional ecology of roots is still very poorly understood (Pregitzer et al. 2002), and we agree with Hodge (2004) that ecological research must move beyond the study of root responses of isolated plants and focus on the functional consequences of root foraging ability under more natural conditions in multispecies communities.

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