

Nutrient foraging traits in 10 co-occurring plant species of contrasting life forms

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Summary

1 Responses to spatial heterogeneity of soil nutrients were tested in 10 plant species that differ in life form and successional status, but which co-occur in the South Carolina coastal plain. The morphological responses of the root system were tested by assessing scale (represented by root mass and root length densities), precision (preferential proliferation of roots in nutrient-rich patches compared with less fertile patches) and discrimination (ability to detect and proliferate within the richest patches when patches vary in nutrient concentration). We also investigated sensitivity (growth benefits gained as spatial heterogeneity of nutrients increases, measured as total biomass).

2 Ten individuals of each species were grown in pots under four treatments that had differing nutrient distribution but the same overall nutrient addition. Plants were harvested when roots reached pot edge.

3 We observed high variation between species in scale, precision and sensitivity. No significant discrimination responses were observed, although greatest root mass density occurred at intermediate fertility levels for all species.

4 We rejected the hypothesis that scale and precision are negatively correlated. Indeed, in herbaceous species alone, scale and precision were positively correlated.

5 Sensitivity was not closely related to precision, indicating that proliferation of roots in fertile patches does not always yield growth benefits in heterogeneous soils. Further, some sensitive species had very low precision, suggesting that a positive growth response in heterogeneous environments may be related to plasticity in physiology or root life span, rather than morphology.

6 Plant life form was not correlated with precision or sensitivity. However, scale of response was greater in herbs than in woody plants, possibly because the two life forms develop root systems at different rates.

Keywords: morphological plasticity, nutrient heterogeneity, root distribution, root proliferation, South Carolina

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Introduction

The availability of soil nutrients varies both in space and time (Nye & Tinker 1977; Fitter & Hay 1987; Fitter 1994). Heterogeneity of soil resources can occur at many scales, including those detectable by indi-

vidual plants (Jackson & Caldwell 1993). Consequently, ecologists have paid much attention to natural heterogeneity in soil resource availability and to the response of plants to such variation (Gross *et al.* 1995; Humphrey & Pyke 1997).

The term 'foraging' has been used to describe the process by which root systems grow in the soil and thus capture nutrients (Bray 1954). Plasticity can, presumably, increase the efficiency of resource foraging, and one of the most commonly reported plastic responses is the proliferation of roots in regions of

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high nutrient density (Passioura & Wetselaar 1972; Granato & Raper 1989). Most studies of root response to fertilizer patches have examined agricultural species known to have particularly high growth rates and large demands for nutrients (Drew 1975; Fitter 1994; Robinson 1994). More recently, plant root foraging responses in natural communities have been studied to determine whether they influence competitive interactions and succession (Crick & Grime 1987; Jackson & Caldwell 1989; Campbell *et al.* 1991; Mou *et al.* 1997).

Three plastic responses that may be important to below-ground resource foraging are variations in scale, precision and discrimination, which depend on the morphology of root systems with respect to nutrient location. Scale (which allows nutrient capture to be monopolized by the development of an extensive root system) and precision (the tendency to proliferate roots in resource-rich patches) were negatively correlated for eight herbaceous plant species (Campbell *et al.* 1991). Discrimination (the ability, when patches vary in fertility, to identify and to proliferate roots in patches of higher nutrient concentrations) has, to our knowledge, not yet been explicitly studied, although Jackson & Caldwell (1989) observed that some species differ in root proliferation depending on the concentration of resources within a patch.

A fourth plastic trait, sensitivity, focuses on total biomass responses to different levels of heterogeneity. A sensitive plant is one that displays increased biomass as a given amount of nutrients becomes more patchily distributed within the soil matrix. Sensitivity has been demonstrated experimentally for at least one clonal plant species (*Glechoma hederacea* L.); however, if enriched nutrient patches became too small, the plant responded as if the entire area was homogeneously poor (Birch & Hutchings 1994; Wijesinghe & Hutchings 1997). We believe that understanding sensitivity may be essential for predicting whether or not plants gain fitness benefits from an increased concentration of roots in fertile patches.

Nutrient foraging patterns and individual species' responses may be a key to competitive ability and dominance during various stages of succession. For example, Campbell *et al.* (1991) found that those species with the most extensive root systems (i.e. having the highest scale) were superior competitors in homogeneously fertile environments. They also found that stress tolerators had greater precision, suggesting a strategic trade-off between scale and precision. Thus, in an environment where nutrient distribution is heterogeneous, species that are highly responsive to nutrient heterogeneity may have an enhanced ability to tolerate stress or to compete with less sensitive neighbours. During a successional sequence it is possible that the relative advantage of precise foraging will change. Initially, growth will not depend on precise foraging due to low competitor density and high resource availability. However, as succession pro-

ceeds and space becomes more partitioned, greater benefits may be afforded to plants that are precise foragers.

These predictions concerning nutrient foraging effects on growth, competitive outcomes, and succession are only tentative. For instance, it is not known whether the scale vs. precision trade-off is general for plants in different communities (Campbell *et al.* 1991), nor is it clear whether consistent patterns of plasticity or resource foraging strategies are associated with specific types of plants, such as early vs. late successional species or herbaceous vs. woody species (Robinson 1994). Extrapolation from data sources such as the eight species used by Campbell *et al.* (1991), which were all herbaceous and came from several communities, should therefore be cautious. Investigations of root foraging using species from the same community will provide greater insight into within-community interactions. Even then, arguments about the ecological significance and evolution of root foraging traits (Grime *et al.* 1991; Jackson & Caldwell 1996; Gleeson & Fry 1997) depend on the important but often untested underlying assumption that precision leads to fitness gains in heterogeneous soil environments.

The objective of this study was to quantify root system plasticity in response to various levels of soil heterogeneity using 10 species from the same community. Scale, precision, discrimination and sensitivity were measured and analysed to answer the following questions. (i) Do these co-occurring species differ in root foraging behaviour? (ii) Are root foraging traits correlated? (iii) Does increased root proliferation within nutrient patches confer growth benefits on species? (iv) Is foraging ability related to life form?

Materials and methods

EXPERIMENTAL SET-UP

A study was undertaken with potted plants during the 1997 growing season in glasshouses located at Virginia Tech, Blacksburg, Virginia, USA. The 10 plant species used are native to warm temperate forests of the coastal plain of South Carolina (Table 1; Radford *et al.* 1968; Tucker 1996). We chose three annuals, three perennial herbs and four woody species to test for correlation between foraging ability and life form. All of these species co-occur on uplands with sandy, nutrient-poor soils subject to periodic summer droughts. In the autumn and winter of 1996–97, seeds were gathered from pine forests of different successional stages at the Savannah River Site, Aiken and Barnwell Counties, South Carolina, USA. During March through May, seeds were germinated on wet filter paper in a growth chamber and then planted into a nutrient-rich potting soil upon the emergence of cotyledons.

Table 1 Co-occurring species from South Carolina used in the study, and dates during 1997 when plants were subject to treatments

Species [family]	Successional status*	Life form	Transplant date	Harvest date	Days of growth
<i>Chamaecrista nictitans</i> (L.) Moench [Fabaceae]	1	Annual	27 June	4–6 August	39
<i>Erigeron canadensis</i> L. [Asteraceae]	1	Annual	4–5 June	22–24 July	49
<i>Hypericum gentianoides</i> L. [Hypericaceae]	1	Annual	27–28 May	31 July	65
<i>Desmodium strictum</i> (Pursh) DC. [Fabaceae]	2–3	Perennial herb	3 June	16–17 July	43
<i>Solidago nemoralis</i> Aiton. [Asteraceae]	2–3	Perennial herb	16 June	30–31 July	44
<i>Diospyros virginiana</i> L. [Ebenaceae]	5–15	Deciduous tree	1 July	2 September	64
<i>Liquidambar styraciflua</i> L. [Hamamelidaceae]	5–100	Deciduous tree	17 June	26 August	70
<i>Pinus taeda</i> L. [Pinaceae]	5–100	Evergreen tree	14 July	6–8 October	85
<i>Elephantopus tomentosus</i> L. [Asteraceae]	> 30	Perennial herb	20–22 May	2–4 July	42
<i>Euonymus americanus</i> L. [Celastraceae]	> 30	Deciduous shrub	13 June	20–22 October	130

*Years during secondary succession when species is most abundant, based on field observations.

Plants were allowed to grow until large enough (2–4 cm tall) to survive transplanting (one plant per pot) into 30-cm diameter by 28-cm deep pots. Because the species germinated and grew at different rates, transplanting took place between 20 May and 14 July, with the majority of species being transplanted in June (Table 1). Within a species, however, all individuals were transplanted either on the same day or over 2 or 3 consecutive days. We used construction grade sand as a growth medium because it is naturally low in nutrient content, and the soils where the seeds were collected have sandy surface horizons. Before transplanting to sand, plant roots were gently rinsed with tap water to remove adhering potting soil. Each transplant was watered in with a small amount of fertilizer solution (30 ml of Peter's General Purpose Fertilizer, The Scotts Co., Marysville, OH: 200 mg l⁻¹ N, 87 mg l⁻¹ P, 166 mg l⁻¹ K) to promote seedling establishment. Five grams of sandy soil, collected from one location at the Savannah River Site, was added to each pot to provide a source of indigenous microbes. Plants were misted for 30 s twice daily for 2 weeks and then once daily in the early morning for the rest of the study.

Six grams of general purpose, slow-release fertilizer (15-10-10, N-P-K plus minors, 8.3% ammoniacal-N, 6.7% nitrate-N; The Scotts Co., Marysville, OH) was added to each pot as described below. This amount was chosen to provide N mineralization rates similar to those we have measured in natural coastal plain pine forests. All of the elements in this fertilizer are formulated to release slowly and consistently over a period of several months. This is somewhat artificial because nutrients are probably more pulsed in the natural environment.

The 6 g of nutrients was arranged in different spatial patterns to create four treatments. In the first, fertilizer was broadcast evenly over the surface of the pot (homogeneous treatment = H). In the second, all of the fertilizer was concentrated on the surface of

just one quarter of the pot (quarter treatment = Q) following a method outlined by Mou *et al.* (1997). In the third and fourth treatments, fertilizer was mixed into three plugs (diameter 2.5 cm, depth 15 cm) of sand equally spaced from one another and each 5 cm from the plant. In the 'plugs equal' treatment (PE) each plug had the same amount of fertilizer (2 g) and in the 'plugs unequal' treatment (PU) each plug had a different amount of fertilizer varying by a constant factor of approximately four (0.30, 1.15 and 4.55 g).

For each species, 10 pots per treatment were laid out in a completely randomized design, and up to five additional H treatment pots were included. Periodically, some of the extra pots were harvested to determine progress of root system development. For two species there were extra H pots remaining at the end of the experiment and these were included in the final harvest and analysis of treatment effects. For *Diospyros virginiana* L., PE and PU treatments were not included due to a shortage of seedlings for transplant.

HARVEST

All plants of each species were harvested when roots of that species had reached pot edge (determined by periodic harvest of the extra H treatment plants). At this time the plants' root systems had filled the pots both horizontally and vertically. Harvest dates occurred between 16 July and 22 October, and total time between transplanting and harvest ranged between 39 and 130 days, depending on species (Table 1). At harvest, above-ground portions were removed and then roots from each nutrient patch within the pot were collected. To obtain roots in the Q and H treatments, soil in the pots was divided into four equal quarters. In the Q treatment, one of the quarters was the fertilized patch, the location of which fixed the boundaries for the remaining three quarters. In the H treatment, the location of quarters was chosen at random. One of the H treatment quarters

was chosen at random, and a plug of 2.5 cm diameter by 15 cm deep and located 5 cm from the plant was removed to compare this treatment to same-sized plugs harvested in the PE and PU treatments. Roots from each soil volume were separated from the sand by washing over a 2-mm mesh screen, washed again, and then divided into three fractions: where present, the central or 'taproot' was separated (although it did not belong to any particular quarter) before coarse roots (> 1 mm diameter) were separated from fine roots. The taproot was not present for all species, and in these cases the roots in all zones were separated into only two groups. The washing removed virtually all mineral soil. Tests using two species revealed that the root samples had a 7–8% ash content. Following processing, all plant parts were dried to a constant mass at 60 °C and weighed.

ION EXCHANGE TEST

Ion exchange membranes (Abrams & Jarrell 1992; Subler 1996) were used to assess whether nutrients diffused laterally out of fertilized patches into non-fertilized regions. We tested for nitrate because it is more mobile in the soil than ammonium or phosphate and therefore more likely to move within the pot. Pieces of membrane (each 2.5 by 5.0 cm) were placed at two depths (9 cm and 18 cm) in each of seven quarterly fertilized pots with no plants in them. Four locations were tested: patch centre, the boundary between the patch and the non-fertilized region, and 2.5 cm and 5 cm into the non-fertilized region. Pots were misted once in early morning to mimic the treatment of the pots with plants. Membranes were left in the pot for 10 days, before removal from soil, and extraction with 0.5 M NaCl. Extracts were analysed using a QuikChem AE flow injection analyser (Zellweger/Lachat, Milwaukee, WI). The Lachat QuikChem method 12-107-04-1B (nitrate in 2 M KCl soil extracts) was used with 0.5 M NaCl for the carrier and standard diluent.

DATA ANALYSIS

Nitrate concentrations for the ion exchange membranes were log transformed to correct for heteroscedastic variance and then analysed using two-factor ANOVA, with location and depth of membranes as the main effects.

Two parameters were used to estimate scale: root mass density and root length density. Each was calculated for whole pots. Root mass density was calculated by dividing the total root mass in the pot by total soil volume in the pot. To determine root length density, specific root length (SRL) was first estimated for each species. At least 15 samples of fresh roots (c. 0.01–0.05 g dry mass each) were selected randomly from patches of different fertility across the four treatments. The length of all roots in each sample was

estimated using the grid method (adapted from Böhm 1979). The roots were then pooled before weighing to estimate a single SRL (cm roots g⁻¹ dry root mass) for each species. Root length density for a whole pot was then estimated by multiplying dry root mass density in that pot by SRL for the species concerned. Results for each measure of scale were compared using one way ANOVA with species as the main effect. We did not compare treatments because scale is a measure of total allocation to roots, rather than root placement within heterogeneous environments. For root mass density, we used data from the homogeneous treatment only. For root length density, we used data from all treatments combined because each estimate of SRL was derived from a sample collected from all treatments and then pooled.

Precision was tested by comparing the relative fine root mass difference (RFRMD) between two randomly selected, opposite quarters in the H treatment to the RFRMD between the fertilized and opposite quarters in the Q treatment. RFRMD is calculated by dividing the fine root dry mass difference between two quarters by the total pot fine root dry mass (Mou *et al.* 1997). Division by the total pot fine root dry mass makes this a relative measure by correcting for differences in plant size. Differences in RFRMD were analysed using two-way ANOVA with treatment and species as main effects.

Plants that are able to discriminate between patch fertility levels were expected to exhibit more root biomass variability between plugs in the PU treatment than in the PE treatment. We tested for this by a homogeneity of variance *F*-test using percentage of the total root system in each plug as the response variable.

Total biomass was used to detect sensitivity to different levels of nutrient heterogeneity. We assumed that heterogeneity increases along the treatment gradient H < Q < PE < PU. Further, we assumed that the H and Q treatments were a coarser scale of heterogeneity (large patches relative to pot size) than the PE and PU treatments, although the reverse would be true if plants were unable to detect the small patches in the PE and PU treatments (Wijesinghe & Hutchings 1997). Four comparisons were made to test for sensitivity: H vs. Q, PE vs. PU, H vs. Q vs. PE vs. PU, and (H + Q) vs. (PE + PU). It could be argued that H is not a heterogeneous treatment and therefore the last comparison of coarse- vs. fine-scale heterogeneity ought to be Q vs. (PE + PU)/2. We analysed the data in both ways and found no qualitative differences in the results, so we present only (H + Q) vs. (PE + PU). Comparisons were made by two-way ANOVA in which species and treatment were the main effects. Linear contrasts were used in the (H + Q) vs. (PE + PU) comparison.

Pearson's correlation coefficients were calculated to test for the strength of the relationships among and between three sets of traits: (i) nutrient foraging traits

such as scale and precision; (ii) sensitivity; and (iii) two standard root system morphology measurements, specific root length and root to shoot ratio. Because the root to shoot ratio changes as plants grow in size, we used estimates derived from linear regressions (of natural log of root mass regressed on natural log of shoot mass) to calculate a ratio for each species at the mean shoot mass across all treatments. All statistical analyses were conducted using SAS (SAS Institute Inc. 1996). Extra H pots and transplant mortality led to an unbalanced data set (Table 2) and the mixed procedure (PROC MIXED) was therefore used in the analysis of scale, precision and sensitivity. Species were dropped from analysis in cases when $n < 5$ for any treatment being compared. Least-squares means were used for *post hoc* tests (SAS Institute Inc. 1996).

Results

Analysis of the ion exchange extracts revealed significant location effects on nitrate concentration ($P = 0.0001$); however, depth and interaction effects were not significant ($P > 0.05$). In pots without plants, nutrients leached downwards with little lateral movement (Fig. 1), although nutrient patterns might

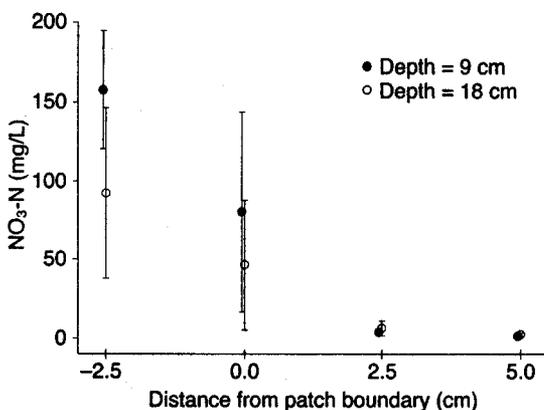


Fig. 1 Nitrate concentrations at different depths and locations (negative distances represent points within the fertilized patch) in a quarterly treatment pot. Values were obtained after a 10-day incubation of ion exchange membranes in seven pots. Mean \pm SD.

have been different in pots with plants where nutrients were not measured.

At harvest, ectomycorrhizal development was observed in *Pinus taeda*, and root nodules were observed on both legume species (*Chamaecrista nictitans* and *Desmodium strictum* (Pursh) DC). Roots were not dissected to determine if endomycorrhizae were present; however, we assume that all but *P. taeda* form endomycorrhizae in natural soils.

INDICES OF ROOT TRAITS

Both measures of scale revealed significant species differences ($P < 0.05$) that were as large as 30-fold for root length density and sevenfold for root mass density (Table 3).

Patchy nutrient availability caused a shift in root mass allocation in some species but not in others (Fig. 2). Significant treatment (H vs. Q; ANOVA; d.f. = 1169; $P = 0.016$), species (d.f. = 9169; $P = 0.0001$) and interaction (d.f. = 9169; $P = 0.028$) effects on RFRMD were detected. The absence of any differences from zero for RFRMD in the H treatment indicated that root systems developed symmetrically. In the Q treatment, seven species had an RFRMD that was statistically different from zero, and of these the four with the greatest RFRMD were also statistically different from the homogeneous pots (Fig. 2). The RFRMD in quarterly fertilized pots was used as an index of precision in our analysis of correlations between root system traits and whole plant responses (see below).

Evidence of discrimination was weak. The mean root mass (as a percentage of pot total) in the individual PE and PU plugs varied between 1% and 8% of the total pot root dry mass depending on species (data not shown). Significant heterogeneity of variance in these percentages (PE vs. PU) was detected in only one species, *Pinus taeda* ($P < 0.05$). In this species, however, the higher variance in the PU treatment was due to a single pot, which had an unusually large root mass in the plug with the lowest fertility level. Transplant mortality meant that only six other species could be tested. Although differences within these

Table 2 Number of individuals harvested for each species, by treatment

Treatment	Species									
	Cn	Ds	Dv	Ea	Ec	Et	Hg	Ls	Pt	Sn
Homogeneous	10	9	10	12	10	10	10	10	11	8
Quarterly	10	9	9	5	10	10	7	9	10	9
Plugs equal	10	9		4	9	10	7	8	10	9
Plugs unequal	9	9		3	9	10		6	8	10

Species symbols are as follows: Cn, *Chamaecrista nictitans*; Ds, *Desmodium strictum*; Dv, *Diospyros virginiana*; Ea, *Euonymus americanus*; Ec, *Erigeron canadensis*; Et, *Elephantopus tomentosus*; Hg, *Hypericum gentianoides*; Ls, *Liquidambar styraciflua*; Pt, *Pinus taeda*; Sn, *Solidago nemoralis*.

Table 3 Root foraging and root morphology traits for 10 species of co-occurring plants from South Carolina, listed in order of greatest to least root mass density. Means (values with \pm standard error) within columns with different letters are significantly different ($P < 0.05$) according to Tukey's test (SAS Institute Inc. 1996). Root mass density is based on the heterogeneous nutrient treatment only; all other parameters are based on all harvested plants. See text for methods to calculate the sensitivity index and root to shoot ratio

Species	Root mass density (kg dry mass m ⁻³ soil)	Root length density (km m ⁻³)	SRL (km roots kg ⁻¹ dry mass)	Sensitivity index	Root to shoot ratio
<i>S. nemoralis</i>	0.116 \pm 0.030 ^a	36.6 \pm 3.9 ^a	392	-0.14	0.18
<i>C. nictitans</i>	0.087 \pm 0.009 ^{a,b}	35.6 \pm 2.4 ^a	483	-0.02	0.19
<i>H. gentianoides</i>	0.069 \pm 0.015 ^{a,b,c}	34.1 \pm 4.1 ^a	478	0.39	0.23
<i>E. canadensis</i>	0.057 \pm 0.008 ^{b,c,d}	28.5 \pm 2.1 ^a	411	0.45	0.41
<i>D. virginiana</i>	0.034 \pm 0.010 ^{c,d}	2.8 \pm 0.6 ^b	92	*	0.44
<i>E. tomentosus</i>	0.027 \pm 0.005 ^{c,d}	12.8 \pm 1.2 ^b	564	0.21	0.19
<i>L. styraciflua</i>	0.024 \pm 0.004 ^{c,d}	4.6 \pm 0.5 ^b	184	0.53	0.28
<i>D. strictum</i>	0.022 \pm 0.007 ^{c,d}	13.2 \pm 1.4 ^b	470	0.54	0.31
<i>E. americanus</i>	0.017 \pm 0.004 ^d	1.9 \pm 0.4 ^b	88	0.26	0.30
<i>P. taeda</i>	0.016 \pm 0.003 ^d	1.2 \pm 0.1 ^b	65	-0.19	0.23

*Not measured due to inadequate sample size.

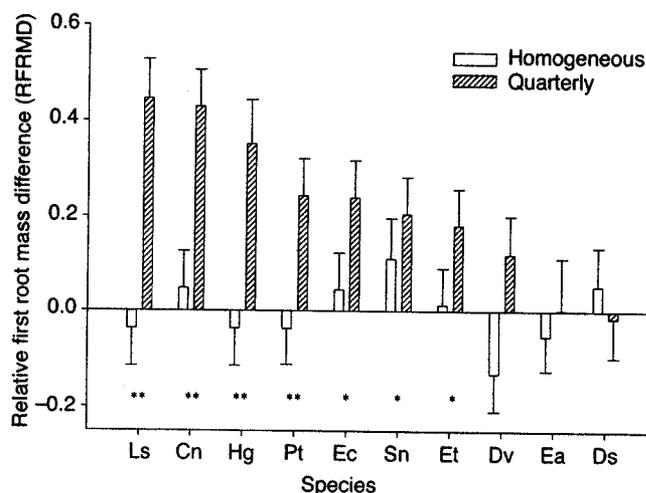


Fig. 2 Precision of root growth in nutrient-rich patches for 10 plant species. Precision (RFRMD) is expressed as: fine root mass density in one quarter of a pot minus that in the opposite quarter divided by total root mass in the pot. For Q pots, this corresponds to fertilized and opposite unfertilized quarters; for H pots, this is two equally fertilized opposite quarters. In no case was the H RFRMD different from zero (i.e. no random preferential proliferation in any particular patch) at $P = 0.05$. **Q RFRMD is significantly different from both zero and H RFRMD ($P < 0.05$). *Q RFRMD is different from zero but no significant treatment effects are detected. Bars are least squares means \pm SEM. Species symbols are as in Table 2.

species were not significant, at least two of the PU plug types (i.e. low, intermediate and high fertility) within a species differed by 1.5- to fivefold (data not shown) which suggests that some discrimination may have occurred. No index of discrimination was calculated.

Many species showed a slight increase in the percentage of roots located in the plugs between the low and intermediate levels, and a large decrease between the intermediate and high levels of fertility in the PU treatment (data not shown). To examine this relationship further, we compared root mass in patches as a percentage of total root mass in the pot at the various fertilizer densities used in the experiment. Five of the seven patches (single plug collected in H, mean of

three plugs for PE, and three unique plugs in PU treatments) in this comparison were the same size, but the two patches from the Q treatment were larger. To correct for these differences in size, we created a root mass density index: root mass in patch as percentage of mass in total pot divided by the volume of soil in the patch. For all eight species, the maximum root mass density index occurred at an intermediate fertility level (Fig. 3). Some species differences were apparent; two had maximum rooting densities at around 8 kg of fertilizer m⁻³ soil, while three others had maximum rooting densities at less than 2 kg m⁻³ (Fig. 3).

Comparisons of H vs. Q, PE vs. PU, and H vs. Q vs. PE vs. PU revealed no significant differences in

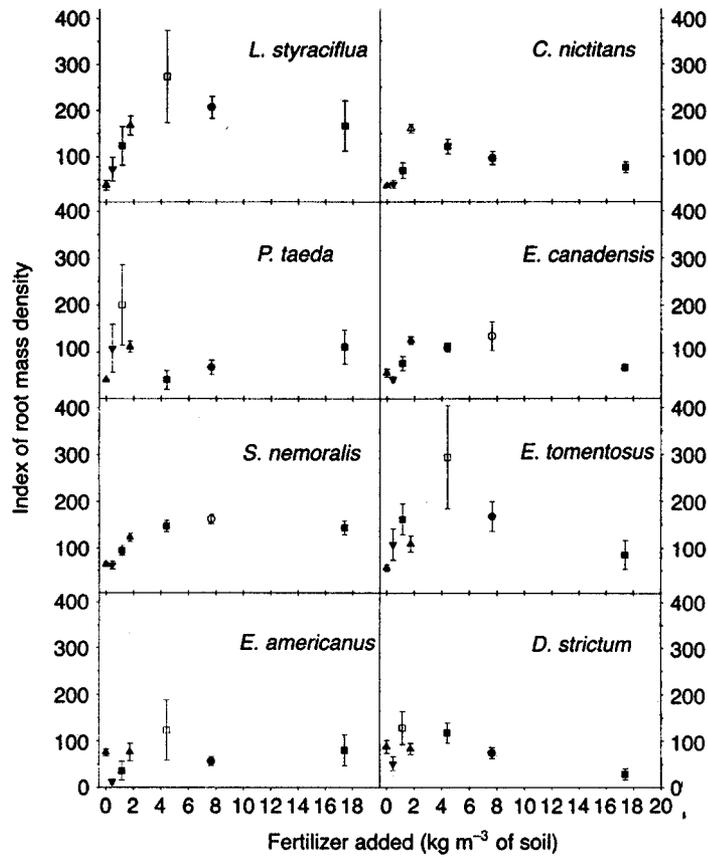


Fig. 3 Index of fine root mass density (roots in patch as percentage of total pot, scaled to a m³ of soil volume to control for patch volume differences) for different rates of fertilization. Symbols represent all fertilizer densities (including no fertilizer added) in homogeneous (▼) and quarterly (▲) treatments, plus fertilizer densities in the plugs for the plugs equal (●) and plugs unequal (■) treatments. Maximum root mass density index for each species is shown as an open symbol.

biomass within any species ($P > 0.05$). However, when data were grouped to consider coarse nutrient heterogeneity (H and Q treatments) vs. finer scale heterogeneity (PE and PU treatments), significant species (ANOVA; d.f. = 8308; $P = 0.0001$), treatment (d.f. = 1308; $P = 0.0001$) and species \times treatment (d.f. = 8308; $P = 0.0006$) effects were detected. Four

species produced significantly more biomass in the finer scale treatment ($P < 0.05$; Fig. 4). A sensitivity index was calculated for each species by taking the difference between total biomass in fine and coarse heterogeneity treatments, and dividing this difference by mean total biomass in the fine heterogeneity treatments (Table 3). Sensitivity scores ranged from 0.54

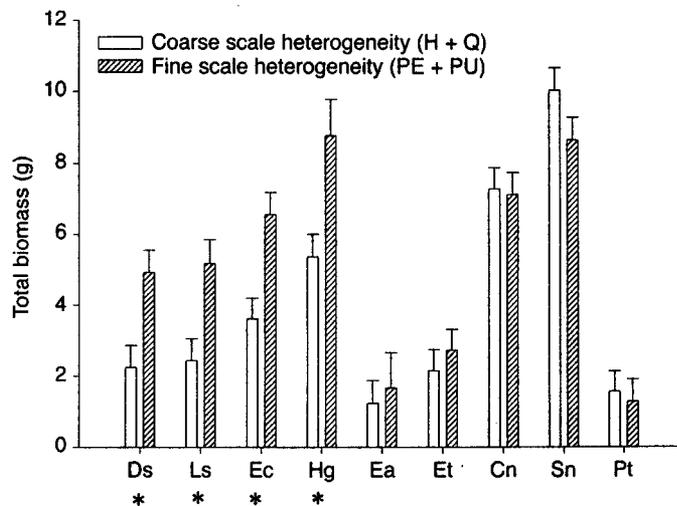


Fig. 4 Total plant biomass in pots with fine scale (PE and PU) vs. coarse scale (H and Q) heterogeneity (least squares mean \pm SE). Results were similar if PE and PU were compared to Q alone. *Significant treatment differences ($P < 0.05$). Species symbols are as in Table 2.

to -0.19 . Larger numbers represent greater stimulation of total biomass growth as soil heterogeneity becomes increasingly fine-scaled. The species with negative scores had less biomass when grown in pots with fine-scale heterogeneity than in pots with coarse-scale heterogeneity.

CORRELATION BETWEEN TRAITS

Scale and precision were not related as hypothesized. When all species were included in analysis, the only significant correlation among root foraging traits was between the two measures of scale (Table 4). Moreover, when woody species were excluded from analysis, we found positive correlations between both measures of scale and precision, and negative correlations between both measures of scale and sensitivity (Table 4). When the correlations between each of the root foraging traits (scale, precision, and sensitivity) were plotted (using the most strongly related measures of scale), broad differences were apparent between woody species (for which scale was very similar) and herbs (where scale was more variable; Fig. 5).

For all species combined, specific root length was positively correlated with all measures of root foraging traits; however, only the correlation with root length density was significant (Table 4). Woody plants had much smaller values for SRL and one or both measures of scale than herbs did (Table 3). When woody plants were removed from the analysis, correlations between SRL and scale became negative, although not significant (Table 4). For the root to shoot ratio, the strongest correlation was with sensitivity, which was nearly significant for all species combined and for herbs alone (Table 4). Sensitive plants thus had greater proportional allocation to roots.

Discussion

The 10 plant species tested in this study exhibited a wide range of types of root morphological plasticity

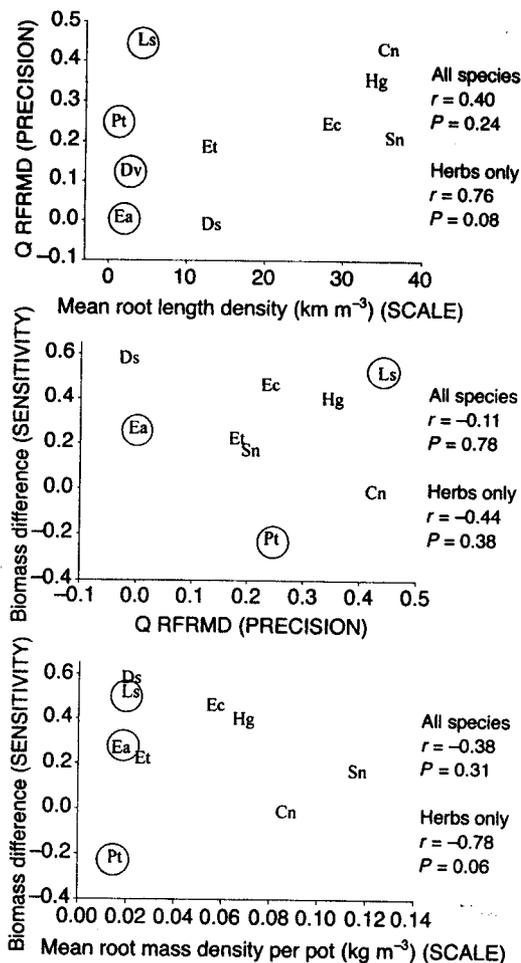


Fig. 5 Relationships between scale, precision and sensitivity with correlation coefficients and tests of their significance. Woody species are denoted by circles. Species codes are as in Table 2.

and a large degree of variation in expression of growth benefits obtained at different levels of heterogeneity. These findings and those of others clearly show that plant root responses to nutrient heterogeneity in soils are complex (Crick & Grime 1987; Hutchings 1988;

Table 4 Pearson's correlation coefficients (P -values for test of significance in parentheses) for relationships between foraging traits (scale, precision and sensitivity) and two other root system traits (SRL and root to shoot ratio)

	Root mass density (scale)	Root length density (scale)	Q RFRMD (precision)	Sensitivity index (sensitivity)	Specific root length
All species ($n = 10$ species except 9 for sensitivity)					
Root length density	0.91 (<0.01)				
Q RFRMD	0.39 (0.27)	0.40 (0.25)			
Sensitivity	-0.38 (0.31)	-0.14 (0.73)	-0.11 (0.78)		
Specific root length	0.47 (0.17)	0.73 (0.02)	0.17 (0.64)	0.21 (0.59)	
Root to shoot ratio	-0.37 (0.29)	-0.37 (0.30)	-0.35 (0.32)	0.65 (0.06)	-0.40 (0.25)
Herbaceous species only ($n = 9$ species)					
Root length density	0.92 (0.01)				
Q RFRMD	0.58 (0.23)	0.76 (0.08)			
Sensitivity	-0.78 (0.06)	-0.55 (0.25)	-0.44 (0.38)		
Specific root length	-0.62 (0.18)	-0.59 (0.21)	-0.59 (0.21)	0.01 (0.99)	
Root to shoot ratio	-0.40 (0.43)	-0.21 (0.69)	-0.32 (0.53)	0.74 (0.09)	-0.38 (0.46)

Jackson & Caldwell 1989, 1996; Campbell *et al.* 1991; Gleeson & Fry 1997; Mou *et al.* 1997).

We found significant differences in scale, precision and sensitivity between the species tested (Figs 2 and 4 and Table 3). Previous studies have reported differences for scale and precision (Campbell *et al.* 1991; Robinson 1994; Mou *et al.* 1997), although the techniques used to measure these characteristics are not always the same, and methodological differences can greatly influence conclusions drawn from such data (Robinson 1994).

To our knowledge, no other study has clearly tested the response of multiple species to different degrees of heterogeneity. However, the effects of spatial scale of nutrient heterogeneity on total growth have been measured for *Glechoma hederacea*, a clonal herb. This species was able to forage successfully in large patches (25 cm × 50 cm) but responded to soils with small patches (12.5 cm × 12.5 cm and smaller) as if they were homogeneously poor (Wijesinghe & Hutchings 1997). The surface area of the patch size when the plant could no longer detect nutrients was smaller than the size of the quarterly patch in our study.

We were unable to detect differences in discrimination between species, possibly because root proliferation was not stimulated at the highest fertility levels. All species in this experiment reached a peak rooting density at an intermediate fertilizer concentration, and proliferation dropped off at higher fertilizer concentrations (Fig. 3). The consistency among the species in this response is suggestive that roots do indeed discriminate between patches of differing richness, as has been predicted by simulation models (Gleeson & Fry 1997), but do not necessarily proliferate more at progressively higher levels.

Our data do not support the hypothesis that scale and precision are negatively correlated. When all species were compared, no measure of scale was negatively correlated with precision (Table 4). Furthermore, when just herbaceous plants were compared, relatively strong, positive relationships between scale and precision were detected (Table 4 and Fig. 5). These correlations all lack power because they compare a limited number of species ($n = 10$ overall, $n = 6$ herbs). None the less they are interesting, considering that Campbell *et al.* (1991) reported a negative relationship between scale and precision. The contrast in findings between our experiment and that of Campbell *et al.* (1991) suggests that relationships between root foraging traits may not be general across plant communities, or that the difference in methods used to measure scale and precision influences the results dramatically (Robinson 1994).

We expected that sensitivity to the soil heterogeneity would be greater for precise than for imprecise foragers, but no such effect was detected at the fertility levels of this experiment (Table 4 and Fig. 5). In fact, the species with the highest and lowest precision (*Liquidambar styraciflua* and *Desmodium*

strictum, respectively) were the two most sensitive species. Fransen *et al.* (1998) found that nitrogen acquisition by plants is sometimes enhanced in heterogeneous environments, but they concluded that the enhancement was not related to root proliferation. We did not assess nutrient uptake in our experiment. None the less, our findings, plus those of other studies, call into question the benefit that species obtain from investing carbon into proliferation of roots in nutrient-rich patches, and they suggest that other mechanisms result in high sensitivity to nutrient heterogeneity.

Two mechanisms that may result in enhanced nutrient uptake without root proliferation are plasticity in root uptake kinetics and plasticity in root demography (Jackson & Caldwell 1996; Eissenstat & Yanai 1997). Jackson *et al.* (1990) found that phosphate uptake rates were up to 82% greater for roots growing in nutrient-rich patches than for roots growing outside patches. Furthermore, Caldwell (1994) demonstrated that some plants increase phosphate uptake from enriched patches without significantly increasing rooting density in these patches. A field (Pregitzer *et al.* 1993) and a glasshouse (Gross *et al.* 1993) study provide evidence that some plants respond to nutrient patches with demographic plasticity, although the responses reported are not uniform. Pregitzer *et al.* (1993) reported an overall community response of increased root longevity in enriched patches compared with roots in control patches. Gross *et al.* (1993) found a decreased life span for roots of four herbaceous species growing in enriched patches. Together, these studies suggest that plasticity in uptake rates and root demography are also complex responses, and by measuring only total root biomass in nutrient patches we may be missing other important plastic responses.

Herbaceous plants with root systems that are small relative to other species but with large root to shoot ratios were best able to gain benefits from nutrient patches in soils. A strong negative correlation between sensitivity and scale and a strong positive correlation between sensitivity and root to shoot ratio were observed (Table 4 and Fig. 5). However, none of these correlations was statistically significant. Additional studies with greater numbers of test species are needed to determine whether our findings can be generalized to other plant communities.

Although they ranged widely in precision, woody plants exhibited the lowest scale (Fig. 5). Thus, life form may be a fair predictor of a root system's scale, but not of precision. For woody plants that have a lower growth rate than many herbs, it is likely that a longer experiment and larger pots would reveal greater variability in scale.

Our intent in this study was to determine if life forms differ in nutrient foraging behaviour, but since our test species also differed with respect to dominance during succession, we were able to examine

Table 5 Rank correlations between nutrient foraging traits and year of dominance during succession ($n = 10$ species, P -values given after correlation coefficients). A rank of 1 was given for species with the highest value for a trait, and for species with the earliest year of dominance during succession (see Table 1). Ties were assigned average ranks, and species that appear at year 30 or thereafter in succession were considered later successional species than those appearing during years 5–100

Trait	r (P)
Root mass density (scale)	0.58 (0.07)
Root length density (scale)	0.75 (0.01)
Sensitivity	0.15 (0.69)
Precision	0.33 (0.34)

relationships between foraging traits and successional status using rank correlation (Table 5). We found no relationship between successional status and sensitivity or precision, although early successional plants had greater scale (significantly so when measured by root length density; Table 5). This analysis is confounded by the fact that life form and successional status co-vary (Table 1).

Our data provide strong evidence that current theories about foraging behaviour and trade-offs between certain traits need more testing and perhaps some rethinking. We still believe that the ability of roots to respond to nutrient patches is a key to predicting competitive interactions between individual species. However, it may be difficult to group species according to their root foraging abilities due to an apparent lack of correlation between root foraging traits and plant groups (herbs, woody species; early and late successional species). Further, more work needs to be done before we are able to suggest which traits increase fitness in heterogeneous environments. In this study we assessed morphological root system responses only, and noted no clear pattern between them and growth benefits as heterogeneity increased. More comprehensive studies that examine demographic and physiological plasticity in addition to root system morphology may be needed to reveal patterns between plant response to heterogeneity and fitness benefits.

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