

Root system size and precision in nutrient foraging: responses to spatial pattern of nutrient supply in six herbaceous species

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Summary

1 An experiment was carried out to test the hypotheses that in heterogeneous environments: (i) the size of species' root systems will be negatively correlated with their ability to place roots precisely in nutrient-rich patches; (ii) precision of root placement will be less affected by distance to nutrient patches in species with large root systems; (iii) species with greater precision in root placement will show greater variation in biomass (sensitivity) in response to heterogeneity in nutrient supply; and (iv) plants will be less precise in root placement, and will invest more biomass in above-ground structures or in fitness-related attributes, when in association with mycorrhizas.

2 Single plants of six herbaceous species (*Arrhenatherum elatius*, *Festuca ovina*, *Plantago lanceolata*, *Campanula rotundifolia*, *Papaver rhoeas* and *Sonchus oleraceus*) were grown in pots with mycorrhizas either present or absent. The same amount of nutrients was supplied either homogeneously or heterogeneously at different distances from the plants. Pots received the same quantity of nutrients in all treatments.

3 There was a significant negative correlation between species' root system biomass and precision. Several species, including some with large root systems, showed small but highly significant differences in precision between the various treatments. Only the high-precision species *Papaver* and the low-precision species *Campanula* exhibited sensitivity in biomass produced in response to different patterns of heterogeneity.

4 The precision with which roots were placed in nutrient-rich patches was affected by distance from patches in *Papaver*, the smallest-rooted species used in the experiment, and in *Plantago*, one of the larger-rooted species. There was no evidence to support the hypothesis that precision would be affected more by distance from nutrient patches in small-rooted species than in large-rooted species.

5 The presence of mycorrhizas did not affect precision of root placement in any species. However, allocation of biomass to roots was significantly lower in *Arrhenatherum*, and allocation to reproductive structures was significantly higher in *Campanula*, when mycorrhizas were present.

6 This study confirms that there are differences between species in precision of nutrient foraging that are related to root system size. It also shows that there is variation in precision *within* species in response to the location of nutrient-rich patches, and that the ability of a species to display precision in nutrient foraging is dependent on its environmental setting.

Key-words: environmental heterogeneity, morphological plasticity, nutrient acquisition, root distribution

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Introduction

The availability of essential resources for plant growth is spatially and temporally patchy in natural environments (e.g. Gupta & Rorison 1975; Lechowicz & Bell 1991; Jackson & Caldwell 1993; Kleb & Wilson 1997; Cain *et al.* 1999). Patches can differ in scale, concentration and contrast in resource supply, and in duration (Stuefer 1996). There are three primary aspects to the responses of plants to heterogeneity in resource supply. First, plant performance may be enhanced by selective placement of resource-acquiring structures (foraging, *sensu* Hutchings & de Kroon 1994) such as roots and leaves, and/or localized increases in resource uptake rates by these structures, in higher quality patches (Jackson *et al.* 1991; Robinson 1994). Secondly, biomass allocation to different structures, and the architecture of these structures, can change in response to local conditions (Fitter 1994; Wijesinghe & Hutchings 1997). Such localized morphological plasticity can also enhance resource acquisition.

The third aspect involves the ability of plants to perceive environmental heterogeneity. Species can detect some forms of heterogeneity and make morphological responses that match resource-acquiring activities to local resource availability. In other situations such matching is not possible because heterogeneity cannot be detected or responses cannot be made. Recent evidence suggests that morphological attributes such as plant size determine the forms of heterogeneity to which different species can respond (Crick & Grime 1987; Wijesinghe & Hutchings 1997, 1999; Einsmann *et al.* 1999).

Campbell *et al.* (1991) proposed that in nutritionally heterogeneous conditions, species with large root systems are less selective in placing their roots in nutrient-rich patches than species with smaller root systems. The former species were termed 'high scale' foragers and the latter 'high precision' foragers (Campbell *et al.* 1991), and it was suggested that these categories reflect an evolutionary trade-off between scale (size of root system) and precision (the selective placement of resource-acquiring structures in resource-rich patches of habitat) in resource foraging. High scale and high precision were described as 'genetically different types of foraging' behaviour (Campbell *et al.* 1991), implying that they are mutually exclusive and that their expression is independent of scale of heterogeneity and other environmental attributes. However, recent studies suggest that the foraging responses of plants to spatial heterogeneity are more complex than this (Wijesinghe & Hutchings 1997, 1999).

Rather than being genetically fixed traits, foraging responses appear to be plastic and dependent on the relationship between morphological scale and environmental scale. A species that is unable to select high quality habitat patches effectively at one scale of heterogeneity may be able to do so at other scales (Wijesinghe & Hutchings 1997, 1999). The term 'scale' as used

by Campbell *et al.* (1991) refers specifically to the size of species and not to the scale of environmental patchiness. More work is needed to assess the generality of the scale/precision trade-off, and to examine how it is affected by the interaction between plant size and scale of heterogeneity. In particular, plasticity in root placement patterns should be compared by exposing species of different size to a range of heterogeneous conditions.

It might also be predicted that plant responses to variation in the location of nutrient patches would differ between species of different size. For example, a plant with a root system large enough to explore both good patches and poor patches in a heterogeneous environment may not display variation in precision of root placement in response to its distance from nutrient patches. At the same environmental scale, a plant with a small root system, and therefore a more limited capacity for soil exploration, might show greater variation in precision of root placement in response to its distance from nutrient patches. Demonstration of such differences would refine our understanding of foraging considerably, by linking plant size and environmental scale. It would also indicate the importance of the location of resource patches in relation to the position of the plant.

The ability to forage precisely should enable plants to acquire resources more efficiently (e.g. Hutchings & de Kroon 1994). If this is true, plants that forage precisely in a given environment should exhibit enhanced growth or fitness resulting from gains in efficiency. Einsmann *et al.* (1999) tested the prediction that high precision foragers would exhibit greater sensitivity (measured as variation in biomass) than low precision foragers in response to different patterns of heterogeneity. Although there was not a correlation between precision and sensitivity among the species they studied, this hypothesis is worthy of further investigation.

Plant responses to nutrient heterogeneity may be modified by symbiosis with arbuscular mycorrhizal fungi because mycorrhizas can extend the potential foraging range of roots by hyphal proliferation (Cui & Caldwell 1996b; Tibbett 2000). Mycorrhizas enhance the ability of plants to acquire nutrients, particularly those that are less mobile in soil, such as phosphate (Koide & Elliot 1989; Peat & Fitter 1993). They can also enhance nutrient acquisition in heterogeneous environments (Koide & Li 1990; Braunberger *et al.* 1991; Cui & Caldwell 1996a,b), and may therefore reduce the extent to which colonized plants engage in nutrient foraging. Consequently, the presence of mycorrhizas may result in a colonized plant of a given species exhibiting less precision in root placement at a given scale of heterogeneity than an uncolonized plant. Moreover, plants with mycorrhizal associates may invest less biomass in roots, and more in above-ground structures or fitness-related activities, than those without.

This paper reports an experiment designed to examine these facets of the relationship between morphological

scale and precision in foraging for nutrients in six herbaceous species, and to investigate the effects of this relationship on their growth. A range of heterogeneous environments was established to determine the effects of the size (measured as biomass) of different species' root systems, and distance from nutrient patches, on the precision with which roots are located in nutrient patches. Plants were grown both in the presence and absence of mycorrhizas. The same quantity of nutrients was supplied to plants in all treatments, and the pattern of heterogeneity was manipulated by providing either four identical nutrient patches or two high- and two low-concentration nutrient patches, at various distances from the plant. The following hypotheses were tested:

- Hypothesis 1. In nutritionally heterogeneous environments there is a negative correlation between the size of a species' root system and its ability to place its roots precisely in nutrient-rich patches (Campbell *et al.* 1991).
- Hypothesis 2. Precision of root placement is less responsive to variation in distance from nutrient patches in large-rooted species than in small-rooted species.
- Hypothesis 3. Species which forage precisely are also more sensitive to heterogeneity, in terms of biomass produced, than less precise foragers.
- Hypothesis 4. (a) The presence of mycorrhizal associates will reduce plant responsiveness (i.e. precision of root placement in nutrient-rich patches) to the pattern of nutrient supply. (b) Moreover, if mycorrhizas promote nutrient acquisition, plants with mycorrhizal associates will invest more biomass in above-ground structures, or in fitness-related attributes, and less in roots, than plants without mycorrhizal associates.

Materials and methods

SPECIES

To make the tests of these hypotheses as general as possible, we selected six common herbaceous species with a range of growth forms, relative growth rates (RGR) and sizes of root system. *Arrhenatherum elatius* and *Festuca ovina* are grasses with high and low RGR, respectively, *Plantago lanceolata* and *Campanula rotundifolia* are perennial forbs, also with high and low RGR respectively, and *Papaver rhoeas* and *Sonchus oleraceus* are annual forbs that, like most such species, have high RGRs (Grime & Hunt 1975).

METHODS

In August 1997, seeds of all six species were sown in trays of moist vermiculite. At the two-leaf stage, seedlings of equal size were selected and a single seedling was transplanted into the centre of each of 840 15 cm-diameter plastic pots containing sterile potting sand. The pots were placed in a glasshouse with a 12-h day/

night cycle and a temperature of 20–25 °C. After a 5-day establishment period, 40 mL of nutrient solution was applied to each pot every 3 weeks. This solution consisted of 500 mg of the granular fertiliser Sangral 3 : 1 : 6 (William Sinclair Horticulture Ltd, Lincoln, UK) per litre of distilled water, giving a solution containing N (as NO_3^- and NH_4^+), P_2O_5 , K_2O and MgO at concentrations of 80, 25, 160 and 10 p.p.m., respectively.

The experiment had a fully randomized 2×7 factorial design, with the presence or absence of mycorrhizas as one factor and pattern of nutrient supply as the other. Each treatment was replicated 10 times. Half of the pots (70 per species) received an inoculum of 8 g of the commercially available mycorrhizal formulation Vaminoc® (MicroBio Ltd, Hemel Hempstead, UK), placed in the pot directly around the roots of the seedling at the time of transplanting. The formulation contained propagules of three native mycorrhizal endophytes (*Glomus mosseae*, *G. caledonium* and *G. fasciculatum*) incorporated into inert clay granules. The pots in the non-mycorrhizal treatment each received 8 g of inert clay granules without the mycorrhizal endophytes.

There were seven patterns of nutrient application. The method of application was designed to maintain differences in nutrient concentrations in the heterogeneous treatments and to produce diffuse rather than precise patch borders, as in natural habitats. Preliminary studies using aliquots of different sizes (results not shown) demonstrated that this could be achieved by applying 40 mL of nutrient solution to each pot in the appropriate pattern every 3 weeks, together with supplementary watering to prevent plants from wilting.

The surface of each pot was divided into four quadrants for nutrient application. There were no partitions between these quadrants. In three treatments, all four quadrants were given 10 mL aliquots of the nutrient solution at each feeding, at distances of 7.5, 3.25 and 0 cm from the plant (treatments 4F, 4I and 4N, respectively). Nutrients were applied along the radius originating at the base of the plant and terminating at the centre of the arc forming the edge of each quadrant (Fig. 1). In three further treatments, two opposing quadrants each received 20 mL aliquots of nutrient solution at the same distances from the plants (treatments 2F, 2I and 2N, respectively, Fig. 1). In a seventh treatment (homogeneous, H) 40 mL of nutrient solution was evenly applied to the surface of the pot. All pots were watered as necessary with distilled water between feedings. All pots received the same amounts of nutrients and water throughout the experiment. Although treatments in which all four quadrants were enriched were considered less heterogeneous than those in which only two quadrants were enriched, it was expected that diffusion would cause nutrient patches to merge in 2N and 4N, making these treatments very similar in nutrient distribution.

The annual species, *Papaver* and *Sonchus*, were harvested 4 months after the first feeding, by which time all *Papaver* plants had completed flowering. The other

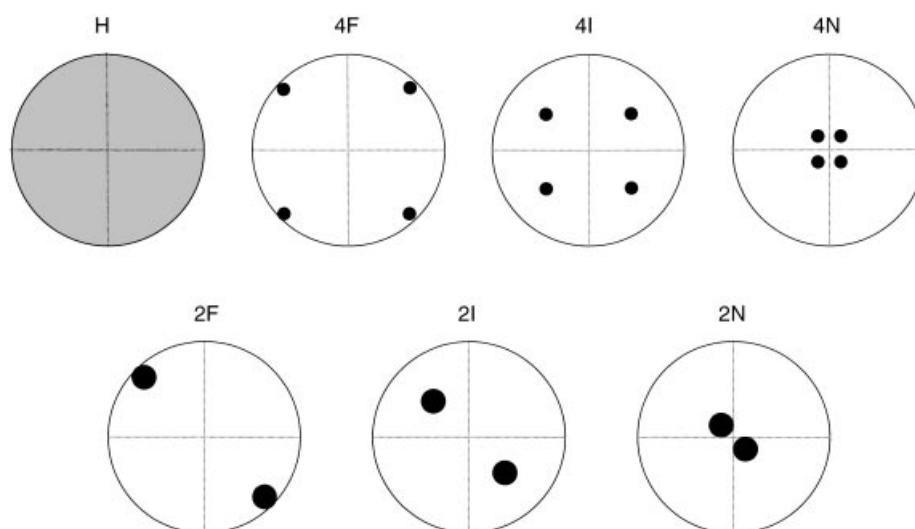


Fig. 1 The experimental design. Pots were 15 cm in diameter and in all treatments a single plant was placed at the centre of the pot. Dotted lines indicate quadrants used to define positions for nutrient application (except in treatment H), and for dividing the substrate when roots were harvested. There were no partitions in the substrate between these quadrants. The filled circles indicate positions at which nutrients were applied. Twice as much nutrient solution (represented by larger circles) was applied at each position in treatments 2F, 2I and 2N as in treatments 4F, 4I and 4N. Nutrients were applied evenly over the surface of the pots in treatment H. All treatments received the same quantity of nutrients. See Methods for further details.

species were harvested after 6 months. Above- and below-ground parts were harvested separately. The number of flowers produced by *Papaver* was recorded in each treatment. *Campanula* produces upright shoots arising from basal rosettes, and prostrate clonal shoots. All upright shoots eventually flower, but few flowers had been produced by harvest. Therefore, flowers were included with the upright shoots for analysis. Rosettes and clonal shoots were harvested separately. *Arrhenatherum*, *Festuca*, *Plantago* and *Sonchus* did not flower. No species produced storage roots during the experiment. Root biomass was used, as in Campbell *et al.* (1991), as a measure of the size of the root system and the area over which it foraged. Root topology (Fitter 1987) was not measured, because obtaining enough measurements for reliability in each treatment would have been logistically impossible given the scale of the experiment. Roots were harvested separately from each of the four quadrants of the pots by inserting metal partitions vertically into the sand and removing sand and roots together before washing the sand away. All plant parts were dried separately at 80 °C and weighed.

Root samples from each species were examined for mycorrhizal colonization. For half of the replicate plants from each treatment, nine 10-mm root sections from two adjacent quadrants (i.e. from two enriched quadrants in treatments 4F, 4I and 4N, from a nutrient-rich and a nutrient-poor quadrant in treatments 2F, 2I and 2N and from two identical quadrants in H) were mounted in water on a microscope slide. These sections were examined under an epifluorescence microscope fitted with an ultraviolet lamp, following the method of Gange *et al.* (1999). The presence or absence of arbuscules was recorded in each root sample (Gange *et al.* 1999).

DATA ANALYSIS

Data for each species were analysed using fixed-model, two-way analyses of variance (ANOVA), with presence or absence of mycorrhizas and pattern of nutrient supply as main factors. Data were corrected for non-normality and heteroscedasticity by logarithmic or angular transformations. Univariate ANOVAs were used to examine the effects of treatment on total plant biomass, above-ground and root biomass, root : shoot (R : S) ratio and percentage biomass allocation to above-ground parts. Multivariate ANOVAs were used to examine the effect of treatment on above-ground and root biomass, and on percentage biomass allocation to all recorded structures in *Papaver* and *Campanula*. Precision of root placement in nutrient-rich patches was also examined by ANOVA for each species. In treatments 2F, 2I and 2N, precision was calculated as (biomass of roots recovered from the two enriched quadrants/total root biomass). Similar calculations were made for treatments H, 4F, 4I and 4N by selecting the two opposite quadrants in the same position as the enriched quadrants in 2F, 2I and 2N, and dividing the weight of roots in these quadrants by total root biomass. After a significant ANOVA, the Bonferroni method was used to compare means.

The analyses described above were used to examine hypothesis 3 concerning the relationship between precision and sensitivity (variation in total biomass produced in different heterogeneous treatments), and hypotheses 4a and 4b concerning the effects of presence or absence of mycorrhizas on precision of root placement and biomass allocation patterns in each species. Significant interactions between nutrient supply and mycorrhizas would indicate effects of mycorrhizal colonization on foraging ability. Hypothesis 1, concerning

Table 1 Mean mycorrhizal colonization rates for the six species used in the experiment, calculated as the percentage of root fragments examined that contained arbuscules. Eighteen fragments were examined per replicate. Thirty-two replicates per species were examined, by sampling roots equally from rich and poor quadrants of the pots

Species	Mean colonization (%)	Standard deviation	Range (%)
<i>Arrhenatherum elatius</i>	6.42	8.68	0–38.89
<i>Campanula rotundifolia</i>	28.41	25.88	0–88.98
<i>Festuca ovina</i>	13.02	15.60	0–61.11
<i>Papaver rhoeas</i>	4.52	11.31	0–50.00
<i>Plantago lanceolata</i>	6.67	10.85	0–55.56
<i>Sonchus oleraceus</i>	No arbuscules seen		

the relationship between root system size and precision of root placement (Campbell *et al.* 1991), was tested by examining the correlation between mean total root biomass of each species, calculated across all treatments, and precision of root placement in treatment 2F, using the Spearman rank correlation test; 2F was the treatment in which nutrient patches of different quality were expected to be most distinct (i.e. the most heterogeneous treatment).

The response of each species to distance from nutrient patches was examined by comparing mean precision in 2F and 2N. These treatments differed only in the distance of nutrient supply from the plant. Hypothesis 2 predicts that species with small root systems would show greater differences in precision between treatments 2F and 2N than species with large root systems.

Results

MYCORRHIZAL COLONIZATION

Examination of sections of roots from plants in the mycorrhizal treatment showed the presence of arbuscules in five of the six species (Table 1). The apparent absence of arbuscules in *Sonchus* (and the low level in *Papaver*) may have been caused by masking by latex, which fluoresces under UV light, in the roots. Arbuscules were not recorded in the roots of any plants in the non-mycorrhizal treatment.

EFFECTS OF PATTERN OF NUTRIENT SUPPLY AND MYCORRHIZAS

Precision

All species except *Arrhenatherum* and *Campanula* showed significant effects of pattern of nutrient supply on precision of root placement (Fig. 2, Table 2). *Festuca*, *Papaver*, *Plantago* and *Sonchus* placed a higher proportion of their roots in nutrient-rich than nutrient-poor quadrants in the more heterogeneous treatments (i.e. 2F and 2I). Precision was significantly lower in these four species in the less heterogeneous treatment 4F than in the more heterogeneous treatment 2F, in which nutrients were supplied at the same distance from the plant. *Papaver* and *Plantago* also exhibited an

effect of distance from nutrient patches on pattern of root placement (i.e. mean values in 2F and 2N were significantly different, Fig. 2, Table 2). Effects of distance to nutrient supply were less pronounced for *Festuca* and *Sonchus*. The mycorrhizal treatment had no effect on precision in any species (Table 2).

R : S ratio and biomass allocation

R : S ratios varied between species: mean ($\pm$ SE) values across all treatments were as follows: *Arrhenatherum*, 2.54 ± 0.06 ; *Festuca*, 1.50 ± 0.04 ; *Plantago*, 1.22 ± 0.03 ; *Campanula*, 0.96 ± 0.03 ; *Sonchus*, 0.64 ± 0.02 ; *Papaver*, 0.56 ± 0.04 . Mycorrhizas only affected R : S ratio significantly in *Arrhenatherum* (2.31 ± 0.07 when mycorrhizas were present vs. 2.77 ± 0.10 when they were absent, Table 2). Pattern of nutrient supply affected R : S ratio only in *Papaver* (Table 2, highest value in the homogeneous treatment (0.98 ± 0.21), and lowest in 4N and 2N (0.36 ± 0.06 and 0.32 ± 0.05 , respectively), where nutrients were closest to the plants).

Pattern of nutrient supply affected biomass allocation to different structures only in *Papaver* (MANOVA of allocation to shoots, flowers and roots: Wilks' lambda = 0.72, $F_{18,348} = 2.35$, $P < 0.01$). Allocation to flowers was highest in 2N ($26.1 \pm 3.3\%$) and lowest in H ($10.5 \pm 2.7\%$; univariate ANOVA: $F_{6,125} = 3.52$, $P < 0.01$), whereas allocation to roots was highest in H ($42.8 \pm 3.7\%$) and lowest in 2N ($22.4 \pm 2.5\%$; univariate ANOVA: $F_{6,125} = 5.45$, $P < 0.001$), suggesting a trade-off between these variables. This was confirmed by a significant negative correlation between root biomass and number of flowers produced ($r = -0.685$, $P < 0.001$, $n = 139$).

Mycorrhizas affected biomass allocation in *Arrhenatherum*, *Campanula* and *Papaver*. *Arrhenatherum* allocated $72 \pm 0.7\%$ of its biomass to roots in the absence of mycorrhizas and $69 \pm 0.7\%$ in their presence (univariate ANOVA: $F_{6,125} = 12.71$, $P < 0.001$). In *Campanula*, the allocation of biomass to flowering and clonal shoots, rosettes and roots was significantly affected by mycorrhizas (MANOVA: Wilks' lambda = 0.91, $F_{4,123} = 3.19$, $P < 0.05$), mainly because of greater allocation to flowering shoots in their presence ($23 \pm 2.0\%$ vs. $15 \pm 2.0\%$; univariate ANOVA: $F_{1,126} = 7.23$, $P < 0.01$). In *Papaver*, biomass allocation

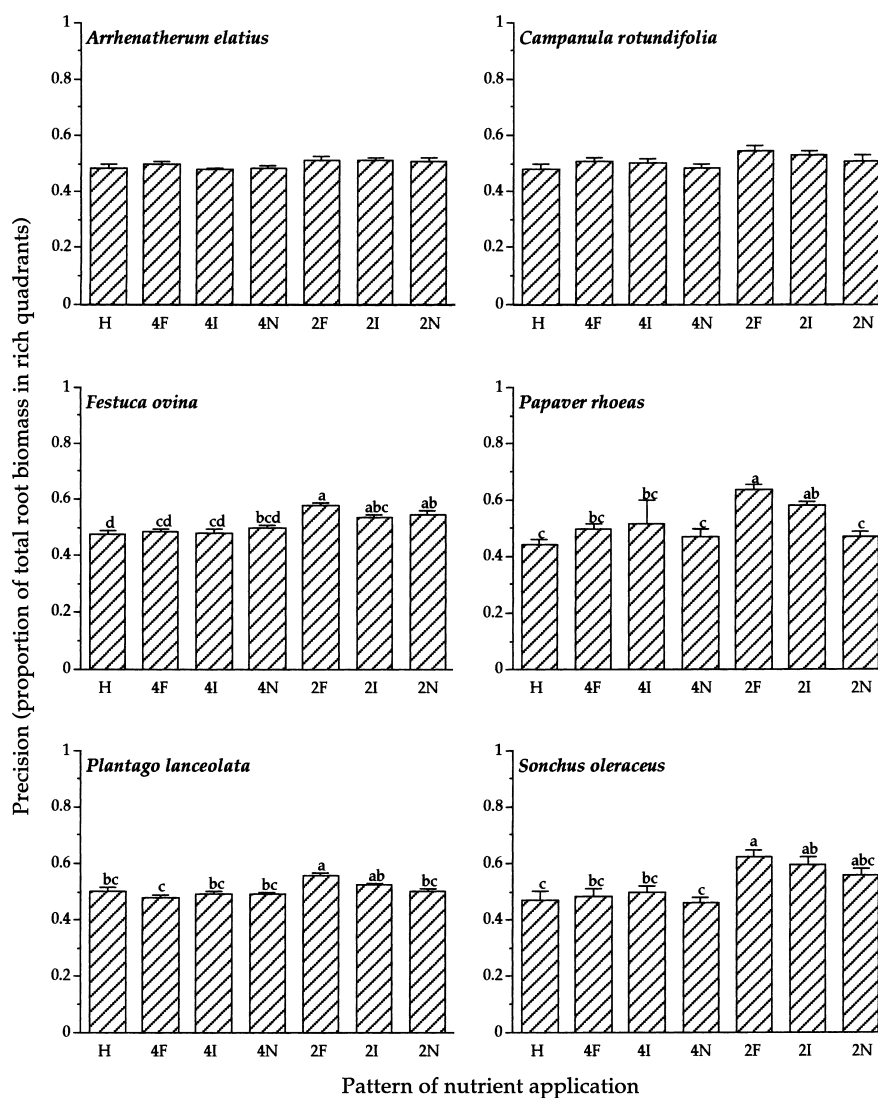


Fig. 2 Mean (+ SE) precision of root placement in rich patches in the seven nutrient treatments (see Methods and Fig. 1). Statistical analyses are given in Table 2. Means with different letters above the error bars differ significantly (Bonferroni multiple means comparison test, $P < 0.05$).

to shoots, flowers and roots was significantly affected by the presence of mycorrhizas (MANOVA: Wilks' lambda = 0.88, $F_{3,123} = 5.68$, $P < 0.001$), mainly because of greater allocation to shoots in the mycorrhizal treatment ($53 \pm 1.0\%$ vs. $47 \pm 1.0\%$; univariate ANOVA: $F_{1,125} = 12.27$, $P < 0.001$). *Papaver* also produced fewer flowers per plant when mycorrhizas were present (3.09 ± 0.34 vs. 5.21 ± 0.58 ; univariate ANOVA: $F_{1,125} = 11.94$, $P < 0.001$).

Total biomass

Pattern of nutrient supply affected biomass production significantly only in *Campanula* and *Papaver* (Table 2), which show high and low precision, respectively (Table 2, Fig. 2). Thus, hypothesis 3, concerning the relationship between precision and sensitivity, was not supported. In *Campanula*, significantly less biomass was produced in 4F than in 4N and 2I, because of less above-ground production (Fig. 3, Table 2). Biomass of

Papaver was highest in the homogeneous treatment, mainly as a result of greater root biomass, and lowest in 2F (Fig. 3, Table 2). However, as stated above, *Papaver* plants with smaller root systems produced more flowers, and allocation to flowers was relatively low in the homogeneous treatment.

Mycorrhizal treatment affected biomass significantly in *Arrhenatherum*, *Festuca* and *Sonchus* (Fig. 4, Table 2); in all cases biomass was lower in treatments in which mycorrhizas were present. Root biomass was significantly lower in *Arrhenatherum* in the mycorrhizal treatment (univariate ANOVA: shoot biomass, $F_{1,125} = 0.95$, $P = \text{NS}$; root biomass, $F_{1,125} = 24.26$, $P < 0.0001$). Both shoot and root biomass were lower in *Festuca* and *Sonchus* when mycorrhizas were present (univariate ANOVA: for *Festuca*, shoot biomass, $F_{1,126} = 26.10$, $P < 0.0001$; root biomass, $F_{1,126} = 10.08$, $P < 0.01$; for *Sonchus*, shoot biomass, $F_{1,126} = 12.82$, $P < 0.0001$; root biomass, $F_{1,126} = 6.23$, $P < 0.05$; Fig. 4). For *Sonchus* there was a strong interaction

Table 2 Analyses of variance of the proportion of total root biomass placed in nutrient-rich quadrants of pots (precision), root : shoot (R : S) ratio and total biomass for each of the six species. The experiment was a two-way factorial, with the pattern of nutrient application (nutrients) and the presence or absence of mycorrhizas (mycorrhizas) as the main factors. Degrees of freedom, *F*-statistics and significance (at $P < 0.05$) are shown for each test. The data on precision were angular-transformed, and total biomass and R : S ratio of *Papaver*, and R : S ratio of *Festuca*, were log-transformed prior to analysis

Species	Source	d.f.	Precision		R : S ratio		Total biomass	
			<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
<i>Arrhenatherum</i>	Nutrients	6	1.772	NS	0.437	NS	0.578	NS
	Mycorrhizas	1	0.009	NS	13.896	< 0.001	22.569	< 0.0001
	Nutrients × mycorrhizas	6	2.197	< 0.05	1.508	NS	0.640	NS
	Error	125						
<i>Campanula</i>	Nutrients	6	1.970	NS	0.662	NS	2.648	< 0.05
	Mycorrhizas	1	0.816	NS	0.272	NS	3.011	NS
	Nutrients × mycorrhizas	6	0.951	NS	1.050	NS	1.326	NS
	Error	126						
<i>Festuca</i>	Nutrients	6	9.352	< 0.0001	1.353	NS	0.363	NS
	Mycorrhizas	1	1.198	NS	2.062	NS	18.593	< 0.0001
	Nutrients × mycorrhizas	6	0.594	NS	0.887	NS	0.582	NS
	Error	126						
<i>Papaver</i>	Nutrients	6	13.246	< 0.0001	5.515	< 0.0001	2.134	< 0.05
	Mycorrhizas	1	0.037	NS	0.007	NS	0.107	NS
	Nutrients × mycorrhizas	6	0.499	NS	0.953	NS	0.495	NS
	Error	125						
<i>Plantago</i>	Nutrients	6	7.077	< 0.0001	1.387	NS	1.309	NS
	Mycorrhizas	1	0.021	NS	0.409	NS	0.276	NS
	Nutrients × mycorrhizas	6	1.306	NS	1.089	NS	0.424	NS
	Error	126						
<i>Sonchus</i>	Nutrients	6	5.553	< 0.0001	0.970	NS	1.277	NS
	Mycorrhizas	1	3.262	NS	0.245	NS	10.595	< 0.01
	Nutrients × mycorrhizas	6	0.477	NS	2.129	< 0.05	3.971	< 0.001
	Error	126						

between pattern of nutrient supply and mycorrhizal treatment (univariate ANOVA: shoot biomass, $F_{6,126} = 3.81$, $P < 0.01$, root biomass, $F_{6,126} = 3.77$, $P < 0.01$). Non-mycorrhizal plants produced significantly more biomass than plants with mycorrhizas in 2N ($F_{6,126} = 3.97$, $P < 0.001$). Whereas total yield of *Campanula* was not significantly affected by presence of mycorrhizas, yield of its components was affected (MANOVA of log-transformed data: Wilks' lambda = 0.92; $F_{4,123} = 2.52$, $P < 0.05$): plants produced significantly more flowering shoot biomass (0.61 ± 0.07 g vs. 0.46 ± 0.07 g; univariate ANOVA: $F_{1,126} = 3.90$, $P < 0.05$) and significantly less clonal shoot biomass when mycorrhizas were present (0.18 ± 0.03 g vs. 0.35 ± 0.06 g; univariate ANOVA: $F_{1,126} = 6.61$, $P < 0.01$).

Although pattern of nutrient supply affected precision of root placement in *Festuca*, *Papaver*, *Plantago* and *Sonchus*, no interaction between pattern of nutrient supply and presence of mycorrhizas on precision was found for any species. Thus, there was no support for the prediction that plant responsiveness to the pattern of nutrient supply would be lower in the presence of mycorrhizas (hypothesis 4a). In the presence of mycorrhizas, less biomass was allocated to roots in *Arrhenatherum*, and more biomass was allocated to flowering in *Campanula*. Although allocation to shoots increased in *Papaver* in the presence of mycorrhizas, allocation to flowering was not affected. However, fewer flowers

were produced in the mycorrhizal treatment. Thus, there was only partial support for the prediction that plants with mycorrhizal associates would invest more biomass in above-ground structures, or in fitness-related attributes, and less in roots, than plants without mycorrhizal associates (hypothesis 4b).

TESTS OF HYPOTHESES 1 AND 2

There was a significant negative correlation between the mean root biomass of each species and its precision of root placement in nutrient-rich patches (Fig. 5). This result supports hypothesis 1 that there is a correlation between size of root system and precision of root placement in nutrient-rich patches. However, only the relatively large-rooted *Plantago* and small-rooted *Papaver* demonstrated significant differences in precision between 2F and 2N. Thus, hypothesis 2 was not supported.

Discussion

Campbell *et al.* (1991) suggested that an important attribute in species that dominate plant communities is the development, particularly in the absence of disturbance, of extensive root systems and leaf canopies that monopolize resource capture over wide areas, regardless of variation in habitat quality within those

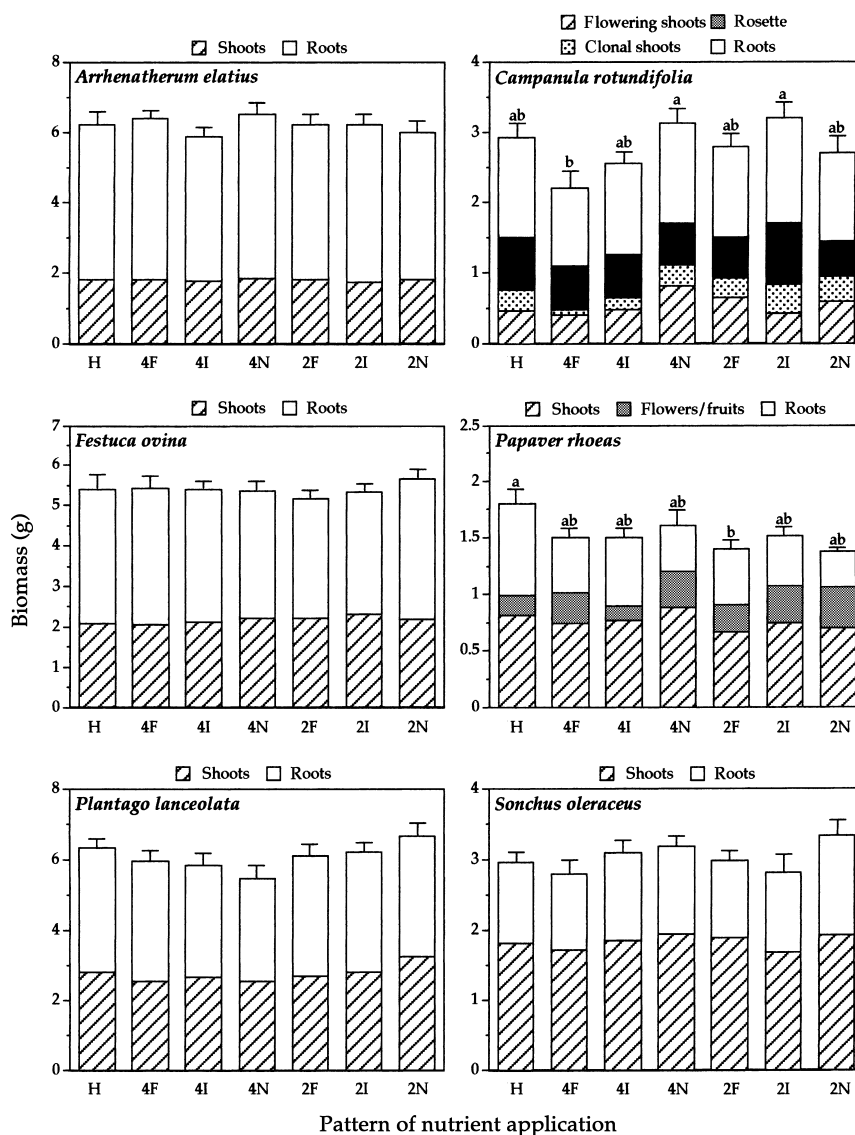


Fig. 3 Mean total, above-ground and root biomass of each species in the seven nutrient treatments. Error bars are shown for total biomass only. Note the differences in scale on the y-axes. Statistical analyses are given in Table 2, statistical conventions as in Fig. 2.

areas. In contrast, subordinate species produce much smaller root systems and leaf canopies, but place a high proportion of their roots and leaves in the more resource-rich parts of patchy habitats. This ability to efficiently exploit areas that have abundant resources promotes persistence in the face of competition from dominant species, particularly when disturbance limits the growth of the latter. The contention of Campbell *et al.* (1991) was that these are *alternative* strategies, i.e. large scale species cannot be precise foragers and *vice versa*. They regarded this proposed trade-off between scale (size) of plant and foraging precision as an important concept in need of independent testing, and called for further studies on the subject. The results presented here lend support to their proposal in that, at the scale of this experiment, species with smaller root systems showed more precision in placing roots in nutrient-rich patches (Fig. 5, hypothesis 1). In contrast, recent work by Einsmann *et al.* (1999), on a group of 10 species from vegetation types along a successional sequence, did not

support the proposal. Thus, the relationship between the scale of species' root systems and their precision in placing roots in high quality patches of soil is still open to question.

Differences in experimental procedures, and in methods of measuring the scales of root systems and precision of root placement patterns, probably contribute to the contrasting outcomes of these studies (Hutchings *et al.* 2000). Moreover, the results of the current experiment showing variation in precision between different treatments confirm our contention that precision is not a fixed property. Instead, the ability of a species to place resource-acquiring structures selectively in the higher quality patches of a heterogeneous habitat depends on the environmental context. Thus, the appearance of a cross-species trade-off between scale and precision will depend on the species chosen and the environments in which they are studied. The important point is that the scale of spatial heterogeneity affects the ability of species to respond to patch

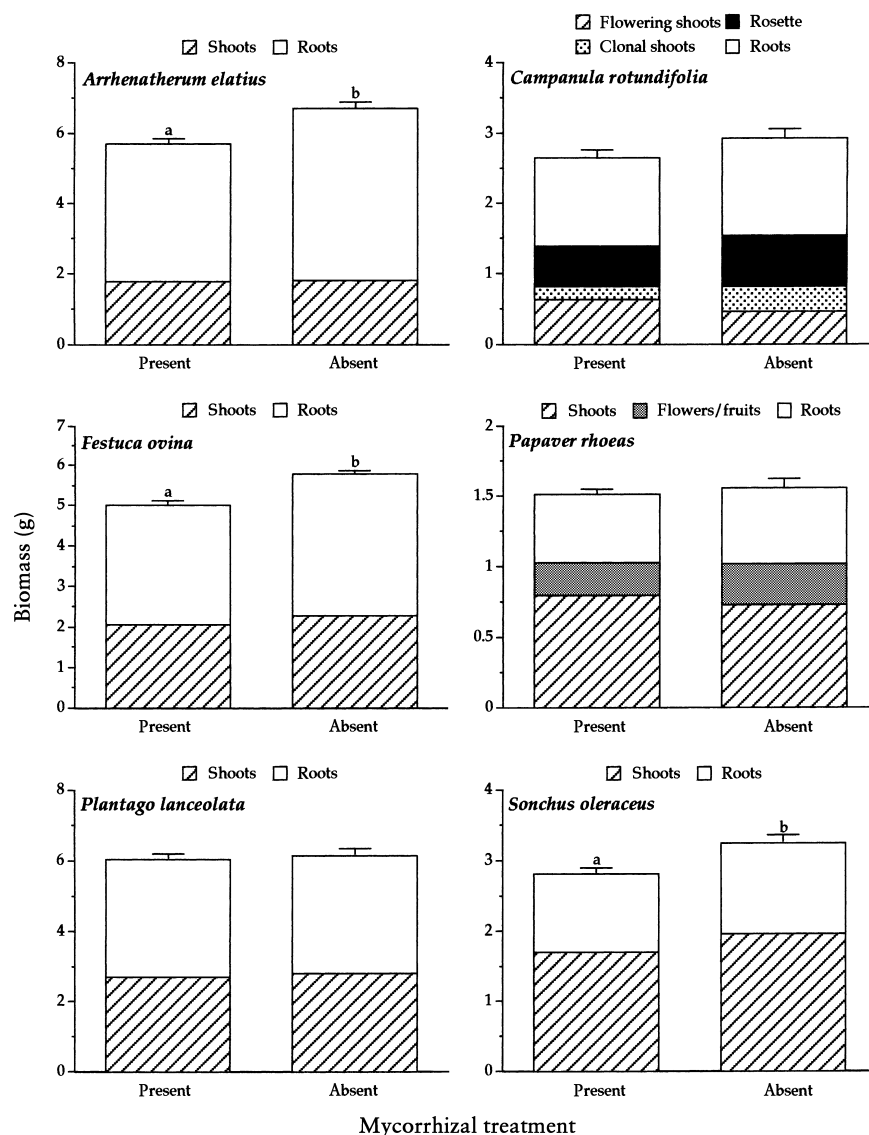


Fig. 4 Mean total, above-ground and root biomass of each species in the mycorrhizal treatments. Error bars are shown for total biomass only. Note the differences in scale on the y-axes. Statistical analyses are given in Table 2. Means with different letters above the error bars differ significantly (Bonferroni multiple means comparison test, $P < 0.05$).

quality (Wiens 2000). This has been confirmed both for animals (e.g. With 1994) and for clonal plant species (Wijesinghe & Hutchings 1997, 1999). Precision in selecting higher quality patches depends on the ability of a species to perceive the heterogeneity and respond to it. Evidence suggests that this can be achieved most effectively when there is a match between the scale of species' resource-acquiring structures and the scale of heterogeneity (Wijesinghe & Hutchings 1997, 1999).

Of the species studied by Campbell *et al.* (1991), *Campanula* had the highest precision. However, the very small amount of root produced by *Campanula* in their study, and the rather indirect method that they used to measure precision, would have made individual values highly susceptible to random variation and this would have lowered the reliability of the measurement. *Campanula* had a small root system in the present experiment, but did not display precision in root placement. *Papaver* and *Sonchus*, which had even smaller

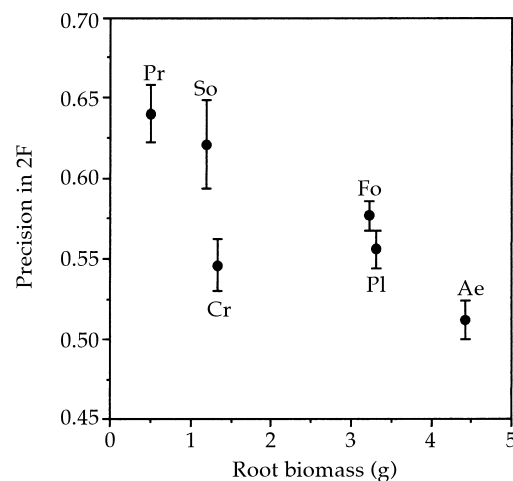


Fig. 5 The relationship between root biomass and precision of root placement in treatment 2F. Plotted values are means $\pm$ SE. The correlation is significant (Spearman rank correlation one-tailed test $r_s = -0.829$, $P = 0.05$, $n = 6$).

root systems than *Campanula*, were the most precise species in locating roots in nutrient-rich patches (Fig. 5), although larger-rooted species also exhibited precision (Fig. 2). *Arrhenatherum* was the least precise forager in the experiment of Campbell *et al.* (1991). It also failed to respond to the pattern of nutrient supply in the present experiment, probably because the scale of heterogeneity was small relative to the size of its root system. At the scale at which this experiment was performed, the large root systems of *Arrhenatherum* (Fig. 5) occupied all of the sand and probably obtained the same amount of nutrients in all treatments. This could explain the lack of patch selection. However, Einsmann *et al.* (1999) harvested each species in their study when it occupied the whole pot, and some of their species exhibited quite striking precision in root placement. In the present experiment, species with small root systems had not occupied all of the sand by harvest, and while some of these species exhibited root proliferation in nutrient-rich patches, others such as *Campanula* did not. Whether species do or do not exhibit precision cannot therefore be dependent on whether their roots had occupied the whole pot volume.

Although the distances from plants to nutrient supply points were small (7.5 cm or less), they were enough to produce significant differences in precision in some species with both small (*Papaver*) and relatively large (*Plantago*) root systems (Fig. 2). The two smallest-rooted species exhibited the greatest precision (Fig. 5). However, relatively large-rooted species such as *Plantago* and *Festuca* also showed small but highly significant differences in precision between treatments in which nutrients were supplied at different distances (Table 2, Fig. 2), with large ANOVA *F*-ratios associated with the effects of pattern of nutrient supply on precision.

Whereas several species exhibited precision in root placement, only *Papaver*, which showed the greatest precision, exhibited significant plasticity in R : S ratio in response to pattern of nutrient supply. R : S ratio was highest in *Papaver* when nutrients were homogeneously distributed and lowest when nutrient patches were closest to the plant (treatments 4N and 2N). Although precision was similar for *Papaver* in all of these treatments (i.e. H, 4N and 2N, Fig. 2), suggesting that all appeared similar to the plant in terms of patchiness, differences in R : S ratio imply that *Papaver* responded to differences in nutrient accessibility. The greater proximity of nutrients in 4N and 2N apparently permitted greater economy (Bloom *et al.* 1985) in root production, and greater allocation to above-ground structures and to reproduction, than in the homogeneous treatment. Thus, distance to nutrient patches had a significant impact upon fitness in *Papaver*. The importance of patch location in relation to the position of the plant would be expected to increase if different plants were close enough to compete for nutrients in the same patch. Similar effects to those seen in *Papaver* might be

expected in species with larger root systems when the scale of heterogeneity is greater.

Of the four species that showed variation in precision in root placement, only *Papaver* exhibited sensitivity (i.e. exhibited significant variation in biomass) in response to pattern of nutrient supply. Although *Campanula* exhibited very low precision, its biomass was also sensitive to pattern of nutrient supply (Fig. 3). Thus, in agreement with the results of Einsmann *et al.* (1999), our data do not support hypothesis 3 that precision and sensitivity are correlated. This may be because the species studied could not respond to spatial heterogeneity at the scales at which these experiments were performed, but it may also be that, as Einsmann *et al.* (1999) suggest, yield is not always a good indicator of fitness in heterogeneous environments. This view is supported by the fact that at least one species in this study (*Papaver*) had higher fitness in environments where its total biomass was lower. Another possibility is that whereas some species (such as *Campanula*) are not morphologically plastic with respect to root placement patterns, they may be physiologically or architecturally responsive. We would not have recorded such responses in the current study.

The presence of arbuscules in the mycorrhizal treatment was confirmed in *Arrhenatherum*, *Campanula*, *Festuca*, *Papaver* and *Plantago*. This indicates functional associations between the plants and the endophyte (Gange *et al.* 1999).

Mycorrhizal associates did not enhance yield in any species by the time of harvest. These results add to the body of evidence reporting a continuum of plant yield responses to mycorrhizal colonization ranging from positive to negative, depending on the extent of colonization and environmental factors such as nutrient and light supply (Koide & Elliot 1989; Johnson *et al.* 1997; Lapointe & Molard 1997; Gange & Ayres 1999). Although arbuscules were not seen in *Sonchus*, this species produced less biomass in the treatment with mycorrhizas. Root, shoot and total biomass were all significantly lower in *Festuca* and *Sonchus* in the presence of mycorrhizas. Root biomass was also lower in *Arrhenatherum* in the mycorrhizal treatment. Without knowing the long-term impact of mycorrhizas on fitness, it is difficult to assess whether a reduction in plant yield due to mycorrhizal infection is actually detrimental to a plant. However, it is unlikely that the fairly low mycorrhizal colonization levels seen for most species in this study would lead to a high level of plant benefit (Gange & Ayres 1999). The exception to this was *Campanula*, which had the highest levels of mycorrhizal colonization and therefore might have been expected to benefit most from the mycorrhizal treatment. In this species flowering shoots were larger, and more biomass was allocated to sexual reproduction, when mycorrhizas were present.

This is the only species providing support for our hypothesis (4b) that allocation to fitness-related attributes would be greater in plants with mycorrhizal

associates. In contrast, *Papaver* suffered reduced fitness, as measured by flower production, when mycorrhizas were present.

There was no evidence from any species to support the prediction that mycorrhizal association leads to lower precision in root placement in heterogeneous conditions (hypothesis 4a, also see Tibbett 2000). However, in the mycorrhizal treatment *Arrhenatherum* allocated a lower proportion of its biomass to roots, while its shoot biomass remained the same as in non-mycorrhizal plants. This implies that the presence of mycorrhizas enabled *Arrhenatherum* to conserve resources that would otherwise have been used in nutrient acquisition, as predicted by hypothesis 4b.

In conclusion, this experiment provides some support for the hypothesis of Campbell *et al.* (1991) that there is a trade-off between root system size and precision of root placement in nutrient-rich patches in heterogeneous environments. It also shows that plant responses to heterogeneity are complex. Although smaller-rooted species tended to show greater precision than larger-rooted species, precision in some larger-rooted species was highly responsive to pattern of nutrient supply. The presence of mycorrhizas did not affect precision of root placement. Thus, further studies of the relationship between scale and precision must take into account the fact that there is variation in precision of root placement *within* species in addition to differences between species, and that the precision displayed by any species is dependent on its environmental setting.

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