

TOWARD UNDERSTANDING THE CONSEQUENCES OF SOIL HETEROGENEITY FOR PLANT POPULATIONS AND COMMUNITIES

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Abstract. Several recent studies demonstrate that yield of individual plants, and their allocation of biomass between roots and shoots, can be profoundly affected by the pattern of supply of soil-based resources. Patchy provision of soil-based resources can affect the location of root biomass, as roots often proliferate in nutrient-rich patches. Root system size is important in determining whether plants access nutrient-rich patches, and the proportion of root systems located within such patches. This proportion will alter as growth proceeds. Species with small root systems have a limited ability to place roots in nutrient-rich patches even when they are very close. Of four species with different root system sizes, the growth of the species with the smallest root system was significantly limited by being located in nutrient-poor substrate even when nutrient-rich substrate was only 3.5 cm away, whereas three species with larger root systems were not disadvantaged. Both in the laboratory and in the field, root density is higher in nutrient-rich patches, and such patches can contain roots of many plants. Recent work showing that plants can respond to non-self roots sharing the same nutrient supply suggests that competition will be more severe in nutritionally patchy substrates than in homogeneous environments with the same overall nutrient supply. Taken together, these facts lead to the prediction that inter- and intraspecific plant interactions will be influenced by patterns of nutrient supply. We present evidence supporting this prediction, and indicating that population and community structure are also affected by patterns of nutrient supply. Significant differences in population yield, plant size distribution, and mortality have been recorded between populations growing under patchy and uniform conditions. Plant communities grown from identical seed inocula, with the same overall nutrient supply, provided in different spatial and temporal patterns, differed by up to 44% in total biomass, up to 70% in root biomass, and differed in species composition. These significant effects of heterogeneous resource supply on plants merit further detailed study.

We present a framework of predictions of the impacts of different types of spatial heterogeneity in nutrient supply on the performance of single plants, and on plant interactions, plant populations, and plant communities.

Key words: belowground competition; nutrient heterogeneity; patch scale; plant competition; plant growth; root proliferation; soil heterogeneity.

INTRODUCTION

A number of ecological investigations carried out in recent years have established that spatial heterogeneity in the availability of soil-based resources can strongly influence the growth and patterns of biomass allocation of single plants. Heterogeneity in supply might improve resource uptake by purely passive means, but many species also exhibit strong physiological and/or morphological responses to soil-based heterogeneity (e.g., Jackson et al. 1990, Jackson and Caldwell 1996, Einsmann et al. 1999, and Robinson 1994 for a review). For plants to respond to heterogeneity, its scale must either match or be less than the spatial scale over which the root systems of individual plants spread. Importantly in the context of the present paper, heterogeneity can elicit both localized and plant-wide responses.

Consequently we focus on the morphological responses of plants when patches of different quality are smaller than, or of a similar size to, the root systems of individual plants.

We begin our examination of this subject, and of the effects of heterogeneity on the interactions between plants, by reviewing some of the relevant behavior of single plants. A good understanding of individual plant responses to soil resource heterogeneity is essential if we are to make realistic predictions about the impact of heterogeneity on plant interactions. We then develop the argument that plant interactions will differ under heterogeneous and homogeneous conditions, using evidence from studies on competing plants, plant populations, and plant communities. We propose that our current limited knowledge of the effects of heterogeneity on plant behavior significantly hinders our understanding of plant competition, and community composition.

Our attention in this contribution focuses almost entirely upon spatial heterogeneity in the distribution of

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soil-based resources. With a few exceptions, we discuss studies in which the same total quantity of resources is provided in homogeneous and heterogeneous patterns, so that the effects of supplying nutrients in patches are not confounded with the effect of supplying different amounts of nutrients. This approach to the study of heterogeneity has not always been adopted, some authors preferring experimental designs in which nutrient patches are provided by adding nutrients (e.g., Robinson 1994) to an otherwise homogeneous background supply.

THE EFFECTS OF SPATIAL HETEROGENEITY ON PLANTS

Proliferation responses within root systems

There is evidence that many plant species can preferentially select nutrient-rich soil patches for root placement when grown in heterogeneous conditions (reviewed in Robinson 1994). Although most of the early work on this topic examined the proliferation responses of crop species, we now know that noncrop species with a wide range of life histories and ecological preferences also proliferate roots in nutrient-rich patches. For example, Einsmann et al. (1999) measured precision of root placement in 10 species with a range of life forms. Precision was measured as the difference in fine root mass in fertilized and unfertilized patches in heterogeneous substrate and in equivalent substrate patches in homogeneous conditions. Values were converted to relative precision measurements by dividing by the total fine root mass produced by plants in each treatment. Accurate measures of precision require that root growth is not constrained by pot size, and care was taken to ensure that this was the case. Several species exhibited a high degree of precision. In a study on eight herbaceous species, Campbell et al. (1991) also observed selectivity in placement of new root biomass in nutrient-rich patches in a heterogeneous substrate, and reported a significant negative relationship between root system size, measured as root mass, and the level of precision, measured as the proportion of new roots placed in nutrient-rich patches of habitat. Einsmann et al. (1999) failed to confirm this relationship using their measure of precision. Wijesinghe et al. (2001) observed a significant negative relationship between root system mass and precision (calculated as root biomass in enriched patches/total root biomass) in six herbaceous species, but also showed that precision was not constant for any species. It was affected both by the location of the plant with respect to nutrient-rich patches and by the spatial arrangement of those patches. Although at first sight the benefits of root proliferation in nutrient-rich patches seem obvious, several authors (Robinson 1996, Leyser and Fitter 1998) have pointed out that proliferation of roots in ephemeral nutrient-rich patches may not be an energetically efficient way of acquiring resources. This response to patchily

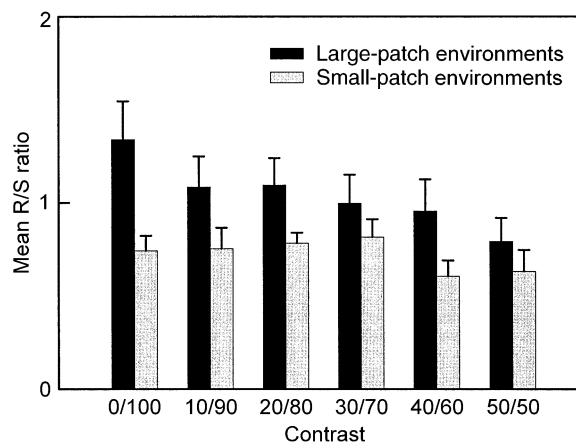


FIG. 1. Mean (± 1 SE) root/shoot ratio of clones of *Glechoma hederacea* grown in large- and small-patch environments with different degrees of contrast between patches. Patch scale had a significant effect on root/shoot ratio ($F_{1,48} = 14.75$, $P = 0.0004$), whereas neither contrast ($F_{5,48} = 1.23$, $P = 0.3078$) nor the interaction between scale and contrast ($F_{5,48} = 0.56$, $P = 0.7305$) significantly affected root/shoot ratio. Data are from Wijesinghe and Hutchings (1999).

distributed resources may be more easily explained as a response to competition for a finite resource, an idea to which we return below.

Nutrients and other resources are unevenly distributed in soils (e.g., Jackson and Caldwell 1996, Cain et al. 1999, Farley and Fitter 1999, Lister et al. 2000), and proliferation of roots in nutrient-rich patches has been recorded in several natural environments (e.g., Caldwell et al. 1991, Mou et al. 1995). For instance, Mordelet et al. (1996) report a strong correlation between palm tree root density and soil nutrient status, with root density up to 10 times higher in areas of nutrient-rich soil than in the surrounding nutrient-poor savannah. Thus, it is clear that both nutrients and roots are unevenly distributed in natural environments, and that roots tend to be concentrated in areas of nutrient enrichment. This will inevitably create hot spots for plant interactions.

Root and shoot biomass

An illustration of the impacts of soil-based heterogeneity on plant production and allocation to roots and shoots is provided by the stoloniferous clonal herb *Glechoma hederacea* (Lamiaceae). This plant has a remarkable ability to match the placement of its roots in different soil patches to the relative resource level in each patch. Growth of *G. hederacea* was examined in several treatments that provided the same total quantity of nutrients in environments consisting of high and low quality patches. There were different levels of contrast in nutrient supply between high and low quality patches and two patch scales (Wijesinghe and Hutchings 1999). In the treatment labeled 50/50 (see Fig. 1) there was no contrast; all of the substrate was a mixture of 50%

sand and 50% compost (i.e., the environment was homogeneous). In treatment 0/100, the substrate in poor and good patches was respectively either 100% sand or 100% compost. Other treatments were made up of patches with intermediate contrast (e.g., patches in treatment 10/90 were either 90% sand, 10% compost or 10% sand, 90% compost). When contrast was higher, the total biomass of roots produced by the clone was greater, and the proportion of them located in nutrient-rich patches was greater. The plants also responded to patch size; although the total area and volume of all of the high quality patches was the same in treatments with patches of different sizes, more root biomass was produced when patches were larger. These root growth and root placement responses resulted in significant impacts on total clone growth. Growth was greater in treatments with large, highly contrasting patches than in homogeneous conditions with the same nutrient supply, but less when patches were small and highly contrasting.

The size of patches provided in this experiment also altered the pattern of allocation of biomass to roots and shoots. Whole clone root/shoot (R/S) ratio was significantly affected by patch size (see Fig. 1, showing previously unpublished results from the experiment of Wijesinghe and Hutchings 1999). In an earlier experiment (Birch and Hutchings 1994), *G. hederacea* clones were provided with the same total nutrient supply either homogeneously or heterogeneously, with half of the nutrients confined to a patch occupying only 10% of the area available for growth. Whole-clone R/S ratio was nearly twice as high in the heterogeneous treatment as in the homogeneous treatment (Birch and Hutchings 1994), because of earlier and far greater root growth by the ramets in the nutrient-rich patch.

We do not currently know enough to generalize across species about the impact of heterogeneity in soil resources on R/S ratio; many studies on the impact of heterogeneity on plant growth have not measured whole plant R/S ratio. It is clear, however, that heterogeneity can have substantial effects. Change in the allocation of resources between roots and shoots could have profound implications for competition, and ultimately for fitness, between plants in situations where above- or belowground resources are limiting. The sensitivity of R/S ratio to patchiness in soil resources must also change our view of R/S ratio as a measure of plant response to limiting resources. The normally accepted view in physiology and ecophysiology is that when light is limiting, a higher proportion of biomass is allocated to photosynthetic machinery, reducing R/S ratio, whereas when soil-based resources are scarce, more biomass is allocated to roots, increasing R/S ratio (Aung 1974, Hunt and Nicholls 1986). This may not reflect the situation in heterogeneous environments (Fitter and Hay 1987, Müller et al. 2000). More importantly in the context of the current discussion, generalizations about the influence of environmental con-

ditions on allocation to roots and shoots are far more difficult to make when plants experience heterogeneity. Furthermore, for clonal plants, several studies (e.g., Stuefer et al. 1994, 1996) show that plants grown under heterogeneous conditions exhibit important variations in R/S ratio at levels below that of the whole plant. When the scale of heterogeneity is smaller than that of the whole plant, clonal species not only locate a higher proportion of their roots in nutrient-rich patches, but they also develop higher R/S ratios locally in these patches (e.g., Birch and Hutchings 1994). This behavior (reviewed by Alpert and Stuefer [1997] and Hutchings and Wijesinghe [1997]) is the opposite of that reported at the whole plant level for many nonclonal and clonal species in homogeneous conditions. It indicates strong functional rather than allometric shifts in resource partitioning. Whether such functional shifts occur in nonclonal plants does not appear to have been investigated.

In addition to affecting the spatial distribution of plant biomass and allocation of biomass to different plant parts, the studies reviewed above, and others, show that total plant biomass can be significantly increased or even decreased, when only the pattern of resource delivery, rather than the quantity of resources, is changed. For example, Einsmann et al. (1999) demonstrated significant effects of patch scale on the yield of several species, and Wijesinghe et al. (2001) showed that distance to nutrient patches can affect yield. Cahill and Casper (1999) report a significant effect of heterogeneity on above ground yield of *Phytolacca americana*.

Both scale of heterogeneity and contrast in patch quality affected yield of *Glechoma hederacea* (Wijesinghe and Hutchings 1997, 1999). Different types of heterogeneity either increased or decreased growth compared with that achieved under homogeneous conditions with the same supply of resources. Lower growth under heterogeneous conditions could be caused by inability to match root distribution to pattern of resource supply, or by high or low resource concentrations limiting growth more than moderate concentrations. If the pattern of root distribution can be matched to soil resource supply, and biomass allocation to roots and root growth enhanced where soil-based resources are more abundant, more resources may be acquired and total growth may be greater. As indicated above, Birch and Hutchings (1994) also demonstrated that the onset of growth of the root initials on different ramets of *Glechoma hederacea* was extremely sensitive to local soil conditions, occurring far earlier in ramet development where nutrient supply was high, and later where it was low. This allows earlier and greater resource acquisition from resource-rich patches, and results in lower investment in resource-poor patches. Altogether, therefore, the plant acquires resources more efficiently, and achieves greater growth in appropriately scaled heterogeneous conditions. It should also

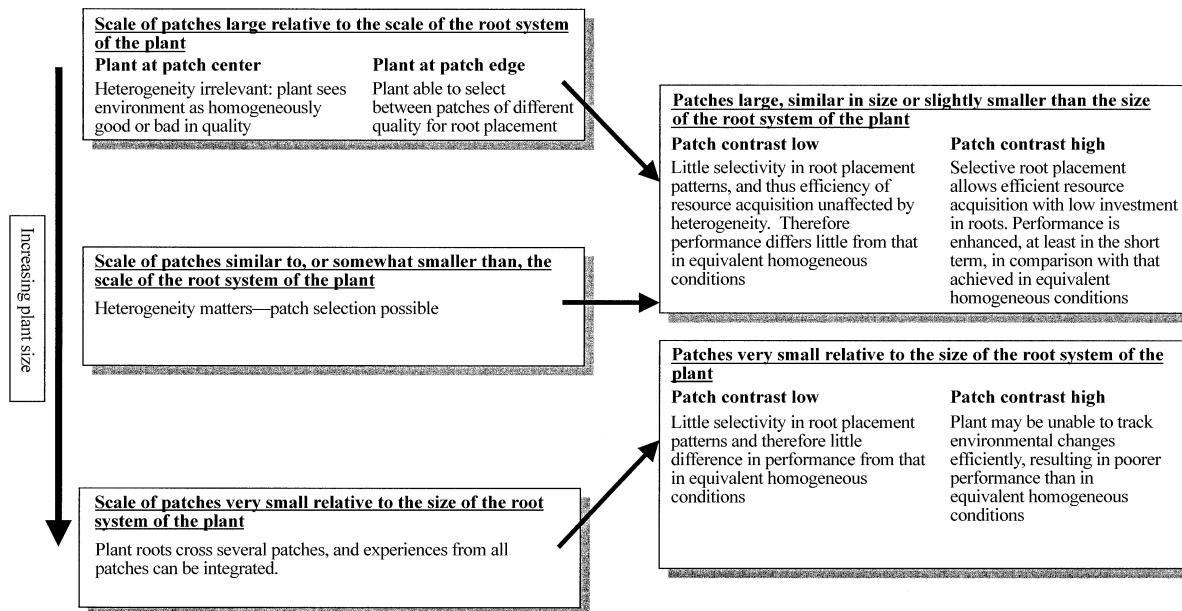


FIG. 2. Effects of spatial scale of heterogeneity in relation to the size of plant root systems, and contrast in patch quality, on the performance of individual plants. It is assumed that, in the boxes at the right of the figure, the overall level of resource supply is the same under both levels of contrast.

be recognized, however, that such benefits of heterogeneity may be transient. For example, plants may grow faster in heterogeneous than homogeneous conditions because of more efficient resource acquisition. However, growth may ultimately be no greater under either condition when resource supply is exhausted and differential uptake from patches of different quality has rendered the environment more homogeneous. A recent study has even indicated that a species that begins growth at an advantage under heterogeneous conditions can ultimately be suppressed by a competitor with slower initial growth that continues to accumulate biomass over a longer period (Fransen and de Kroon 2001).

The evidence presented so far demonstrates that both scale of patches and contrast in nutrient supply between patches can profoundly affect plant responses to heterogeneity (Fig. 2). We propose that changes in biomass and patterns of biomass allocation caused by heterogeneity in resource supply will inevitably affect interactions between plants, particularly as evidence suggests that responses to heterogeneity depend both on species characteristics and plant size, and on the form and scale of heterogeneity (Fig. 2, Box 1). Species-specific responses to heterogeneity reflect evolutionary history, and imply that there must have been variable selection in the past for particular responses to specific kinds of heterogeneity (Oborny 1994, Alpert and Simms 2002).

ACCESS TO NUTRIENT-RICH PATCHES

Plant roots initially tend to grow somewhat radially, although probably far from symmetrically under het-

erogeneous conditions (Casper et al. 2003), from a point source. Consequently, unless a plant germinates within a resource-rich patch, or is immediately next to one, none of its root system will initially be in resource-rich conditions. As growth proceeds, some roots may access resource-rich patches and the plant may begin to display precision in locating its roots in such patches. Precision therefore depends on plant size and on the plant's initial distance from resource-rich patches. Plants that can access a nutrient-rich patch from an early stage of growth may initially show strong precision in locating their roots in the patch, but as they grow, and perhaps deplete the patch of nutrients, root distribution throughout the substrate is likely to become more even.

Species of plants with widely spreading root systems, and roots with rapid lateral extension, are more likely than species with smaller or slower growing root systems to access laterally distant nutrient patches. That the initial location of a plant can have lasting consequences for its subsequent ability to access patchily distributed resources was shown by a previously unpublished experiment conducted on four herbaceous species with root systems of different masses (*Arrhenatherum elatius*, *Campanula rotundifolia*, *Papaver rhoeas*, and *Plantago lanceolata*). Circular pots 15 cm in diameter were set up containing substrate arranged as two opposing quadrants of nutrient-rich soil separated by two opposing quadrants of nutrient-poor soil. There were no barriers between the quadrants, allowing roots to grow freely between them. A single seedling of one of the species was grown in each pot, planted in either a nutrient-rich or nutrient-poor quadrant, 3.75

Box 1. Known and predicted effects of small- and large-scale spatial heterogeneity in the availability of soil-based resources, on pairwise competition between plants, on plant populations, and on plant communities. It is assumed that (i) within each habitat considered the sizes of patches are relatively constant, (ii) at least one patchily distributed resource is limiting to growth, and (iii) overall resource supply is the same in the different habitat types at each of the three levels of complexity. Predicted effects are set in italics.

Pairwise competition—Small scale, high contrast:

Roots of both plants cross patch boundaries. Higher quality patches selected for root placement by both plants, resulting in more intense competition than in equivalent homogeneous environments. Small patches rapidly dominated by fast-growing plants, *denying resources to slower-growing neighbors. Competitive asymmetry greater than in homogeneous environments. Selection favors plants that respond rapidly to resource-rich patches. Location of each competitor with respect to patch quality is critical for success. These effects are increasingly important as the limiting resource is confined to smaller patches, and as patch contrast increases.*

Populations—Small patches, high contrast:

Resource-rich patches can become occupied by roots of plants located in both rich and poor patches. This will produce intensified competition involving many plants. There will be mortality in both rich and poor patches. However, overall mortality may be less than in equivalent homogeneous environments, as the intensity of competition is not as spatially uniform and the probability of survival will be higher in resource-poor patches. *Resource-poor patches will be little utilized by roots, but plants in these patches may suffer from competition for light from large plants growing nearby in resource-rich patches.*

Communities—Small patches, high contrast:

Fast-growing species with high resource demands access many resource-rich patches by growing across resource-poor patches, eliminating slow-growing species. *Overall, species richness lower, and the community more uniform, than in heterogeneous habitat with large patches. Communities less diverse than in equivalent homogeneous habitats, because resource-rich patches favor fast-growing species, increasing the intensity of competition throughout the community. Colonization by new species less likely than in large scale or homogeneous habitats, as there are few refuges from intense competition for young seedlings.*

Pairwise competition—Large scale, high contrast:

The environment is perceived as uniformly good or bad, except when plants are located at patch edges. Under such conditions, plants will select the higher quality patch for root placement, resulting in intensified local root competition. *Selection for rapid root proliferation in resource-rich patches will be less intense than at smaller scales of heterogeneity, because it is less likely that the root system of a single plant can completely dominate a resource-rich patch.*

Populations—Large patches, high contrast:

For plants with roots located wholly within a single patch, population processes will operate as they would in a homogeneous environment of the same quality. Rates of growth and mortality, and intensity of competition and biomass accumulation will differ dramatically between patches. *However, plants at patch boundaries will mainly place their roots in the more resource-rich patch, resulting in more intense competition in resource-rich locations near patch boundaries than in equivalent parts of homogeneous environments.*

Communities—Large patches, high contrast:

Little effect of heterogeneity on plant interactions except at patch boundaries where *large species with fast root proliferation eliminate slow-growing species.* Intensity of competition greater in resource-rich patches, and fast-growing species eliminate slow-growing species. *Rich patches support lower plant density and diversity and a different sub-community than poor patches. Few fast-growing species survive in poor patches. In poor patches, plant density and diversity are greater, and slow-growing species dominate. Overall diversity higher than in equivalent homogeneous habitats. Colonization by new species more common in resource-poor patches.*

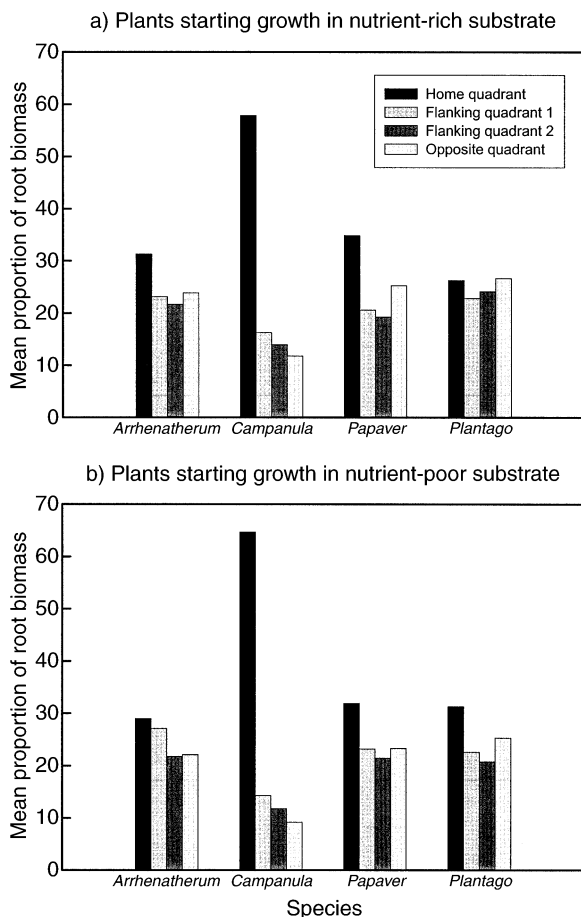


FIG. 3. The mean proportion of total root biomass distributed in the four quadrants within pots for each of the species *Arrhenatherum elatius*, *Papaver rhoeas*, *Plantago lanceolata*, and *Campanula rotundifolia*. The quadrant into which each plant was transplanted at the beginning of the experiment is designated as "home." The home and opposite quadrants were of similar quality. In (a) the home quadrant was nutrient rich; in (b) the home quadrant was nutrient poor.

cm from the intersection of the four quadrants. The total quantity of nutrients in each pot was the same in each treatment. After 12 weeks of growth, aboveground biomass was dried and weighed, and roots were extracted separately from each quadrant, dried, and weighed.

Analyses were carried out to determine whether the species displayed selectivity in placement of roots between the four quadrants (described as home, opposite, and flanking quadrants). Nonparametric Friedman tests (with chi-square approximation with $df = 3$) were carried out for each species, to compare the proportions of the total root biomass recovered from the four quadrants. The null hypothesis, that roots are evenly distributed, would be supported if the median root distributions were the same for all quadrants. Two (or more) quadrants having different median values would indicate uneven root distribution. Separate tests were carried out for plants starting growth in rich and poor home quadrants. Differences between species in the degree of selectivity of the four quadrants for root placement were analyzed by fixed-model multivariate analysis of variance of the proportion of root biomass located in each quadrant. Data were angular transformed before analysis.

All species tended to place roots unevenly between the four quadrants (Fig. 3, Table 1). A significantly greater proportion of roots was recovered from the rich home quadrant, irrespective of its quality, than from other quadrants in all cases except for *P. lanceolata* in rich home quadrants. The overall pattern of root distribution between the quadrants did not differ significantly between *A. elatius*, *P. rhoeas*, and *P. lanceolata*, but for all of these species the pattern differed significantly from that of *C. rotundifolia* (Bonferroni multiple means comparison test at $P < 0.05$). Roots of *C. rotundifolia* were significantly more confined to the home quadrant than were the roots of the other species. About 60% of *C. rotundifolia* roots were located in the home quadrant, regardless of its quality (Fig. 3), whereas only 30–35% of the root biomass of the other three

TABLE 1. Analyses of selectivity of root placement patterns in four pot quadrants of either high or low nutrient content, for four species, when originally planted in either a nutrient-rich or nutrient-poor quadrant.

Species	Plant in rich/poor quadrant	F_r	P
<i>Arrhenatherum elatius</i>	rich	26.43	<0.0001
	poor	19.48	<0.001
<i>Plantago lanceolata</i>	rich	5.88	not significant
	poor	17.88	<0.001
<i>Papaver rhoeas</i>	rich	36.85	<0.0001
	poor	27.40	<0.0001
<i>Campanula rotundifolia</i>	rich	49.77	<0.0001
	poor	55.83	<0.0001

Notes: Analysis was by the Friedman test. The values tabulated are the test statistic (F_r) and the probability of accepting the null hypothesis of equality of root distribution among the four quadrants of the pot. $n = 20$ per species for plants in both rich and poor quadrants.

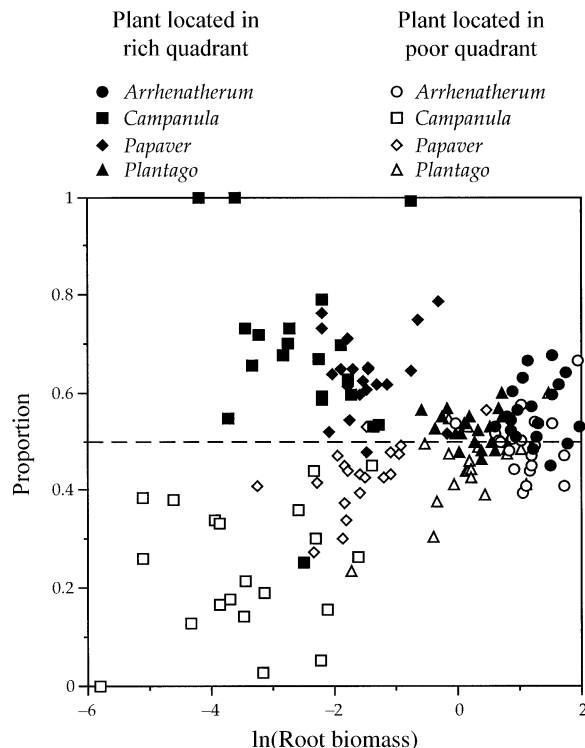


FIG. 4. The relationship between total root biomass (natural log transformed) and the proportion of total root biomass distributed in nutrient-rich quadrants for species grown in isolation. Correlations between these variables were as follows: for plants that began growth in rich quadrants, Pearson product-moment correlation $r = -0.48$, $P < 0.0001$, $n = 80$; for plants that began growth in poor quadrants, $r = 0.70$, $P < 0.0001$, $n = 80$. Data were pooled across species for each correlation.

species was located in the home quadrants. The more extensive exploration of the substrate observed in the species with larger root systems would enable them to access nutrients from non-home quadrants to a considerable extent, whereas greater confinement to its home quadrant would be more likely to cause a small species such as *C. rotundifolia* to deplete accessible resources quickly to levels that limit further growth. Species with larger root systems may avoid local resource depletion.

Strikingly, there were strong correlations between the biomass of individual plant root systems and the proportion of roots in nutrient-rich quadrants (Fig. 4). In rich home quadrants, those plants with the smallest root systems (mostly *C. rotundifolia*) tended to be strongly confined to their home quadrant, whereas those with larger root systems projected a high proportion of their roots into other quadrants including the nutrient-rich quadrant opposite. In poor home quadrants, plants with large root systems also projected a large proportion of their roots into other quadrants, whereas the roots of most *C. rotundifolia* plants were once again mostly confined to their home quadrant (Fig. 4). There was a large (45%) and significant reduction in yield of *C. rotundifolia* caused by beginning life in poor rather than rich home quadrants (Table 2), but no such decrease for the other species. Thus the impact of soil heterogeneity on plant performance was crucially dependent both on whether a plant began growth in a rich or poor patch and on the size of the plant. It is clear that, particularly for species of small stature, starting life in a poor patch in a heterogeneous environment can significantly limit performance, even when nutrient-rich conditions are close by, and, as in this experiment, even in the absence of competition. Adding competition to this handicap might be expected to result in greater suppression of the growth of such plants, or even in their death, because plants that acquire access to resource-rich patches faster than their neighbors are advantaged in competition (Box 1; Hodge et al. 1999).

Few studies of the effects of heterogeneity on plants have directly examined the impact on plant performance of the distance to nutrient patches. Although the outcome of such experiments may be affected by the size of plant root systems and the amount of growth prior to harvest, Wijesinghe et al. (2001) found significant effects of distance to nutrient patches on precision of root placement in two out of six species, and smaller (nonsignificant) effects on another two species. Some roots of some plants may gain access to nutrient patches a considerable distance away, having bypassed numerous intervening plants to reach these patches (Casper et al. 2000). Thus, for some species, distance

TABLE 2. Mean (± 1 SE, $n = 20$) plant mass and results of t tests comparing mass of plants beginning life in nutrient-rich or nutrient-poor patches within 15 cm diameter pots containing the same overall supply of nutrients in each treatment.

Species	Mean (± 1 SE) plant mass (g)		t	df	P (two-tailed)
	Nutrient-rich quadrants	Nutrient-poor quadrants			
<i>Arrhenatherum elatius</i>	4.75 \pm 0.33	4.18 \pm 0.32	1.383	38	0.175
<i>Campanula rotundifolia</i>	0.28 \pm 0.05	0.15 \pm 0.04	2.499	38	0.008
<i>Papaver rhoeas</i>	1.10 \pm 0.05	1.07 \pm 0.09	0.654	38	0.516
<i>Plantago lanceolata</i>	2.40 \pm 0.15	2.45 \pm 0.26	0.358	38	0.722

Notes: The t tests were performed on ln-transformed data. The means presented here are untransformed.

from nutrient patches may limit growth less than expected. Casper et al. also found that many different plants may place roots in, and acquire resources from, the same patch of soil, and suggested that the number of plants interacting in this way might be greater in nutrient-rich patches in heterogeneous soils than in equivalent volumes of homogeneous soils, a prediction supported by a limited amount of data from natural environments (Caldwell et al. 1991, Mordelet et al. 1996). This leads to the prediction that heterogeneity would fundamentally change competitive interactions between plants, with greater intensity of competition being experienced within nutrient-rich patches (Box 1). We now address this prediction.

MODE AND INTENSITY OF COMPETITION IN HETEROGENEOUS CONDITIONS

The ability of plants to locate roots in resource-rich soil patches with precision, the greater root biomass found in these patches, and the possibility that larger numbers of plants access such patches, suggest that competitive interactions may differ in uniform and heterogeneous soils with the same overall nutrient supply. It has been predicted (Schwinning and Weiner 1998) that whereas belowground competition is size symmetric when soil-based resources are homogeneously distributed, spatial heterogeneity may produce size-asymmetric competition, with the plants that reach resource-rich patches first gaining an advantage over their competitors that is disproportionate to the difference in their sizes (see also Casper and Jackson 1997). Despite the intuitive appeal of the prediction that competition will differ under homogeneous and heterogeneous conditions, the relevant information is conflicting, and in some cases difficult to interpret. Cahill and Casper (1999) grew the herbs *Phytolacca americanum* and *Ambrosia artemisiifolia* alone and together, in homogeneous and heterogeneous conditions. When grown alone, both species produced more shoot biomass (significantly more for *P. americanum*) under heterogeneous conditions. The presence of neighbors did not reduce mean shoot biomass of either species significantly in any treatment. Casper et al. (2000) have cited this study as providing no evidence for an effect of heterogeneity on the interaction between plants. However, when grown alone, the mean shoot weight of *P. americanum* was significantly greater (by ~56%) in heterogeneous conditions than in homogeneous conditions. With neighbors, there was no difference between shoot weights in heterogeneous and homogeneous conditions (their Fig. 2). This suggests that *P. americanum* suffered greater competitive suppression under heterogeneous than homogeneous conditions. Results were less clear cut for *A. artemisiifolia*.

Blair (2001) looked for evidence of greater shoot size variation among competing plants of *Ipomoea tri-color* under heterogeneous conditions than under homogeneous conditions with the same total level of re-

source supply. The absence of a significant difference was regarded as evidence that competitive interactions were unaffected by the pattern of nutrient supply, although such a difference would only provide indirect evidence for size-asymmetric competition under heterogeneous conditions (Schwinning and Weiner 1998). Fransen et al. (2001) studied the impact of the spatial pattern of nutrient supply on plant competition between the grasses *Festuca rubra* and *Anthoxanthum odoratum*. Two different heterogeneous treatments and one homogeneous treatment were used. All treatments provided the same total nutrient supply. The two grasses were sown in monocultures or as 50:50 mixtures. Plant density was the same in all treatments.

Under homogeneous conditions, the relative competitive ability of *F. rubra* exceeded that of *A. odoratum*, but both species were equally competitive under heterogeneous conditions. In the heterogeneous treatment with small, concentrated patches of nutrients, both species produced more root biomass in the enriched patches, but the extent of this proliferation was the same for both (neither showed such proliferation in the treatment with larger, less concentrated patches). Whereas root activity (estimated by measuring uptake of strontium, a calcium analogue) of *F. rubra* was higher than that of *A. odoratum* under homogeneous conditions, both species had similar root activities under heterogeneous conditions. Thus, the change in relative competitiveness under heterogeneous conditions appeared to have been caused by greater physiological responsiveness of *A. odoratum* to the pattern of nutrient provision.

It would be predicted that plants with the ability to forage with precision for resources would be at a competitive advantage under heterogeneous conditions. Bliss et al. (2002) found that precise foragers were advantaged in competition with less precise foragers when growing in heterogeneous environments, although this was only significant for 2 out of 6 species pairs tested. Clearly this prediction merits further investigation. Other studies indicate that the ability of plants to exploit nutrient-rich patches depends on whether or not interspecific neighbors are also sharing the patch (Huante et al. 1998, Hodge et al. 1999). Huante et al. (1998) demonstrated that for a fast growing tropical tree, the presence of a competitor of a different species reduced its ability to place its roots in a nutrient-rich patch.

A recent study by Day (2001) is one of the first to demonstrate that the intensity of competition is increased by heterogeneity. He examined the impact of competitors on the growth of the grass *Briza media* under heterogeneous and homogeneous conditions in which the total supply of nutrients was the same. Single target plants of *B. media* were either grown alone, or with a single conspecific neighbor, or a neighbor of the grass *Festuca ovina*. In the heterogeneous treatment the plants were placed in nutrient-poor locations within

pots containing small cores of nutrient-rich soil, including one directly between, and equidistant from, the neighbor and the target plant. The impact of competition in each treatment was estimated by calculating the mean reduction in growth of target plants under competition compared with their mean growth when grown alone with the same nutrient supply.

The biomass of *B. media* was significantly reduced by competition in the heterogeneous treatment, but was not significantly reduced by either intra- or interspecific competition in the homogeneous treatment. This constitutes strong direct evidence for a difference in the intensity of plant competition under heterogeneous and homogeneous conditions when nutrient supply remains the same. Both intra- and interspecific competitors caused similar reductions in the growth of *B. media* in heterogeneous conditions. Contrast between rich and poor patches was high in this experiment, and the size of the nutrient-rich patches was very small compared with the size of the nutrient-poor patches. This rather marked form of heterogeneity would be very likely to affect the intensity of competition (Box 1), because roots are competing for a resource that is highly restricted in its spatial distribution.

One other study has demonstrated changes in competitive interactions in response to supplying a soil-based resource in different heterogeneous patterns (Novoplansky and Goldberg 2001). Water, rather than nutrients, was provided in pulses to three perennial grass species, producing heterogeneity in time rather than space. The performance of single plants was affected more by the total quantity of water supplied than by pulse frequency, but pulse frequency had far greater effects on the relative performance of plants growing in competition. When pulses were frequent, the species characteristic of the most productive field conditions, which also had the fastest growth, caused the greatest suppression of competitors and was best at tolerating competition. When pulses were less frequent, the species from the least productive field conditions, which had the slowest growth, became better at both suppressing and withstanding the effects of competitors. Although this experiment did not compare growth under heterogeneous and homogeneous conditions, it indicates clearly that providing soil-based resources in different heterogeneous configurations changes competitive relations. As the authors state, these results add to the growing evidence that we need to analyze not only the effects of mean resource conditions on plants, but also the effects of spatial and temporal variation in resource availability.

Although limited in quantity, the available evidence supports the view that both the scale and pattern of heterogeneity in resource supply will have consequences for the way in which plants compete (Box 1). Moreover, it is clear that assessments of the relative competitive ability of species made under homogeneous conditions may be an inadequate basis from which to

predict the outcome of competition between the same species when grown under heterogeneous situations.

THE VALUE TO PLANTS OF ROOT PROLIFERATION IN RESOURCE-RICH PATCHES OF SOIL

Proliferation and selective placement of roots in nutrient-rich patches of soil is common, but by no means universally exhibited by plants (Robinson 1994). Robinson (1994, 1996) and others have calculated that, for many species, root proliferation may not occur until after most of the nutrients (particularly those with high mobility) in patches have been taken up. If this is the case, root proliferation would probably be an inefficient way of acquiring resources, being too slow and energetically costly for the resources gained to exceed the cost of the investment. Although nutrient-rich patches in natural soil are certainly transient (e.g., Farley and Fitter 1999), there is a shortage of data about their duration. Nutrient patches have remained detectable for rather long periods in several experimental studies, even when the concentration of mobile nutrients, such as nitrate ions, was measured. For example, nutrient patches were still detectable 6–10 wk after the start of glasshouse-based pot experiments involving competing plants (Casper and Cahill 1996, 1998, Cahill and Casper 1999).

Many observations of root proliferation in soil patches with a high nutrient content have involved plants growing in isolation. Under natural conditions, however, plants usually grow with competing neighbors. Robinson et al. (1999) have demonstrated that, under these conditions, a plant that increases root growth in a nutrient-rich patch more rapidly than its competitor gains a higher proportion of the nutrients from the patch and, consequently, also gains a competitive edge. Root proliferation may be a deeply embedded response to competition that can not be avoided even when plants grow alone. It may even be advantageous for plants growing in isolation, as they are likely to have to compete with the soil microbial community for available nutrients. However, there may be important costs associated with root proliferation in resource-rich patches. Recent research has shown that when plants compete intraspecifically for nutrients at a given concentration within a shared volume of soil, each plant produces more roots, but has a lower reproductive yield, than when given sole access to half as much soil containing nutrients at the same concentration (Gersani et al. 2001). Thus, although root proliferation denies resources to competitors, it imposes a cost in individual fitness. Although nutrient acquisition may be faster, it is less efficient, because more roots are produced than necessary to harvest the nutrients from the patch. Ultimately, however, the cost to each plant is lower than it would be if it ceded resources to its competitor (the “tragedy of the commons”; Hardin 1968). When a plant grows alone, speed of acquisition becomes less important, as there are no neighbors to capture the nu-

trients, and efficient nutrient harvesting can be achieved with less root, permitting greater biomass allocation to functions such as reproduction. The increase in root proliferation recorded by Gersani et al. (2001) when resources were contested by more than one plant indicates a highly developed capacity in plants to distinguish between their own roots and those of other plants.

Further studies should be undertaken to examine the generality of the results of Gersani et al. (2001). Their study suggests that plants display highly aggressive behavior when faced with the problem of acquiring resources from a shared space. This strengthens the prediction that competition will be more intense, and more asymmetric, when resources are concentrated in a smaller proportion of the rooting volume than when they are uniformly distributed.

One final consideration to bear in mind is that species with the most marked root proliferation responses in nutrient-rich soil may well be those that forage most extensively (Crick and Grime 1987, Hutchings and de Kroon 1994). Such species tend to inhabit resource-rich environments, where nutrient-rich patches can be frequently encountered in time and space. It would be predicted that these species will produce low-cost, short-lived roots for rapid exploration and exploitation of resource-rich substrate patches. Their roots will either be jettisoned quickly, after patches are depleted of resources, or used as bridgeheads to reach more distant patches. In such species, the costs and benefits of root proliferation cannot realistically be estimated on the basis of what happens in single patches, since proliferation serves both to increase resource acquisition in the plant's immediate vicinity and to enable wider exploration of the soil environment.

THE POPULATION-LEVEL CONSEQUENCES OF HETEROGENEITY IN NUTRIENT SUPPLY

Despite convincing demonstrations of the impact of heterogeneity on individual plants, to date, only four studies have directly examined the effects of spatial heterogeneity in nutrient supply on plant populations. Once again results are contradictory. When populations of *Abutilon theophrasti* were grown with a fixed quantity of nutrients supplied either uniformly or in a checkerboard pattern of high or low nutrient concentration patches, there were no significant differences in yield or size hierarchy (Casper and Cahill 1996, 1998). The effect of heterogeneity on the performance of individual plants growing at the same locations within populations was also examined. Plants at only two out of 10 randomly chosen locations were affected by pattern of nutrient supply (Casper and Cahill 1998). However, mortality was twice as high in populations under homogeneous conditions as under heterogeneous conditions, and this difference was significant (Casper and Cahill 1996).

In contrast, Day et al. (2001, 2003) found that the total yield, and yield of both below- and aboveground parts, of populations of *Cardamine hirsuta* was significantly higher under heterogeneous conditions with a range of patch scales, than under homogeneous conditions providing the same overall nutrient supply. Variation in shoot size was significantly greater in heterogeneous conditions, primarily because of large differences in the sizes of plants located in nutrient-rich and nutrient-poor soil patches, and increased (though not significantly) as the scale of patches increased. As would be expected in heterogeneous conditions, the proportion of the population's biomass in nutrient-rich patches (calculated from the biomass of roots in nutrient-rich patches plus shoot biomass supported by plants rooted in nutrient-rich patches), was significantly above 50%, although both rich and poor patches were equal in area and soil volume. Similar results are reported by Facelli and Facelli (2002), who found that size inequality and shoot biomass were both higher in environments in which phosphorus was supplied patchily than in otherwise identical environments where it was supplied homogeneously.

The concentration of biomass in nutrient rich locations reported by Day (2001) and Facelli and Facelli (2002) suggests that nutrient-poor patches could be refuges from severe competition in heterogeneous conditions. This conclusion is reinforced by Day's (2001) observation that, despite populations being planted at identical densities and in identical patterns, overall mortality was significantly greater in homogeneous conditions. Homogeneous conditions may generate greater mortality because there are no such refuges. The majority of the plants that died in populations in patchy substrates were in nutrient-rich patches (Day 2001).

The results of Day (2001) and Day et al. (2003) clearly demonstrate that, both at the level of individual patches, and at the level of the whole population, there are important differences in competitive processes and their outcome between populations growing under heterogeneous and homogeneous conditions. This is probably largely due to greater variation in growth and ensuing intensity of competition between plants in nutrient-rich and nutrient-poor soil patches in heterogeneous conditions. The differences observed by Day (2001) in mortality between populations in heterogeneous and homogeneous conditions parallel those reported by Casper and Cahill (1996). These studies of the impact of heterogeneity on populations lead to the conclusion that heterogeneity has major effects on several aspects of population performance (Box 1).

THE COMMUNITY-LEVEL CONSEQUENCES OF HETEROGENEITY IN NUTRIENT SUPPLY

To date, little quantitative information has been published about the effects on communities of supplying nutrients heterogeneously rather than homogeneously.

It is often assumed that, because heterogeneous environments possess much variation in quality between habitat patches, the diversity of the communities they support is also high, because different species preferentially occupy patches of different quality (Fitter 1982, Pacala and Tilman 1994, Huston 1999). However, data do not always support this prediction (Kleb and Wilson 1997, Collins and Wein 1998, Wilson 2000). When the scale of heterogeneity is small enough for parts of the root systems of single plants to occupy several different quality patches simultaneously, the relationship between the number of different types of patches in the environment and the number of species that can be supported might be far from simple (Box 1). If some species are particularly well adapted to dominate patchily distributed resources, then heterogeneity at some scales could lead to reductions in species richness compared to otherwise identical homogeneous environments. For this reason, experimental studies of the effects on community structure of small-scale soil-based heterogeneity are urgently required. A recent study by Wijesinghe et al. (*unpublished manuscript*) demonstrates some consequences of such heterogeneity.

The effect on community structure of providing the same quantity of nutrients in different spatial and temporal patterns was examined. A field experiment was carried out over two years in boxes into which a standard inoculum of seeds of 20 species was sown. The substrate in the boxes was divided into 64 patches of identical size, without partitions separating them, so that roots could grow freely between them, and each patch was either enriched by adding a single tablet of a slow-release fertilizer or left without nutrient addition. Two scales of heterogeneous treatments were established, in which either 32 or 16 of the 64 patches were fertilized at each of two or four prescribed dates, respectively, in both years of the experiment. These treatments were labeled HET50 and HET25 because either 50% or 25% of the patches were fertilized at each feeding. There was also a homogeneous treatment (HOM), in which all 64 patches were enriched with a single fertilizer tablet at the start of each of the two growing seasons. All treatments received the same total amount of nutrients over the course of each of the two years.

A destructive harvest of all above- and belowground plant parts, carried out at the end of the second year, showed that neither the Shannon Index of community diversity nor community evenness were affected at all by treatment. However, there was a 44% difference in biomass produced by the communities in the most (HET25) and least (HOM) productive of the treatments. Treatment affected root biomass more strongly (root biomass was 71% greater in the most productive than the least productive treatment) than aboveground biomass (there was a 20% difference in aboveground biomass between the most and least productive treatment).

The effects of treatment on both root and aboveground biomass were significant. Analysis of the effect of homogeneity vs. heterogeneity, and of the HET50 vs. the HET25 treatments showed significant effects on community biomass. Despite the lack of effects of treatment on community measures of diversity, there were effects of treatment on individual species. For instance, the biomass of *Rumex crispus* in the homogeneous treatment was at least twice that in any of the four heterogeneous treatments. Thus, this experiment demonstrates that heterogeneity in nutrient supply exerts important effects, both at the community level and at the level of individual species. However, this study was not able to distinguish between the effects of heterogeneity on individual species' performances or its effects on species interactions. One group of species that was differentially affected by the different treatments was those that colonized the communities despite not being in the sown mixture. Such species were significantly more abundant in the final community in the HOM and HET50 treatments than in the HET25 treatments. That some patterns of resource supply make a community more invasible than others has also been demonstrated recently by Davis and Pelsor (2001). It is not surprising that local variation in the intensity of competition, caused by spatial and temporal variation in resource supply, affects the ease of invasion by new species into plant communities (Davis and Pelsor 2001, Davis et al. 2000).

We are only at the beginnings of understanding the impact of patchiness in resource supply on community structure. However, we are confident in predicting that future research will confirm that heterogeneity can both increase and decrease diversity, depending on the scale of patches, and change community biomass, the distribution of biomass between below- and aboveground parts, and species composition. Our rationale is summarized in Box 1.

CONCLUSIONS

There is a growing body of ecological evidence indicating important effects of heterogeneity in the availability of soil-based resources on individual plants, on the interactions between plants, on plant populations and on plant communities. Our knowledge of these effects, and the level of agreement over what they are, is greatest at the individual plant level. We still know very little about population- and community-level effects. Even the question of whether heterogeneity in the supply of soil-based resources alters the mode and intensity of competition is still subject to some debate. Our progress in understanding the impacts of heterogeneity on plant interactions will in part depend on progress in related areas, such as the understanding of belowground plant-plant recognition mechanisms, and on our ability to describe belowground interactions accurately.

Homogeneous environments rarely exist outside the laboratory and glasshouse. Even in agriculture, spatial heterogeneity (and, just as importantly, temporal heterogeneity) abounds. The impacts of heterogeneity on plant growth can be so great that it seems almost unbelievable that plant physiologists and ecologists have given it so little attention until recently. There is still much to be learned and understood about many fundamental issues, such as how plants behave, how much they grow, how they interact, and how their populations and communities develop, when their resources are patchily configured, rather than spatially or temporally uniform in supply. Further research is urgently needed to fill the fundamental gaps that still remain in our knowledge in these areas.

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