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Patch–background contrast and patch density have limited effects on root proliferation and plant performance in *Abutilon theophrasti*

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Summary

1. We examined biomass and root proliferation responses of *Abutilon theophrasti* Medic. to the density of high nutrient patches and the patch–background contrast. Contrast in nutrient content between a patch and the background soil, as well as patch density, are important features of heterogeneous soil environments that have received little research attention.

2. Plants were grown in pots with no, one or two organic nutrient patches, and the equivalent nutrition of no, one or two patches in the background soil in a factorial design. Plant performance (root and shoot biomass) and root proliferation (root length inside and outside high-nutrient patches) were measured.

3. Root and shoot biomass increased with increasing nutrient heterogeneity, and root biomass declined with increased background soil nutrient availability. Patch–background contrast did not alter root or shoot biomass, nor allocation to roots. Biomass responses appeared to be driven by heterogeneity, as plants with access to the same total nutrients were larger when nutrients were concentrated in patches. The root proliferation response was not affected by either the density of patches or the degree of contrast.

4. A conceptual model is presented describing how a plant's overall nutrient status could respond to changes in the patch–background contrast. The model predicts that nutrient-sufficient plants should not respond to patches, but nutrient-limited plants should proliferate roots proportionally to the contrast. The proliferation response should saturate when the total nutrients in both patch and background are no longer limiting.

Key-words: nutrient patches, plasticity, root foraging, soil heterogeneity

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Introduction

Small-scale spatial variation in nutrient availability (nutrient heterogeneity) is a common feature of soils (Jackson & Caldwell 1993; Gross, Pregitzer & Burton 1995; Cain *et al*. 1999; Farley & Fitter 1999). Species possess several strategies to increase nutrient capture in heterogeneous soils, including root proliferation into nutrient patches, and increased uptake kinetics by roots within patches (Jackson, Manwaring & Caldwell 1990; Robinson 1994; Jackson & Caldwell 1996; Fitter, Hodge, & Robinson 2000). Responding to a patch carries an immediate energetic cost, as well as potential long-term costs such as irreversible changes in root architecture that, under some conditions, could raise the total costs of responding above the benefits gained (Fransen & de Kroon 2001; Robinson 2001; Alpert & Simms 2002). Strong or rapid responses may benefit plants in the short term, but for long-lived plants there may be no long-term benefits (Fransen & de Kroon 2001). Strategies to reduce net costs may include limiting responses to only 'high-value' patches, such that benefits will always tend to outweigh costs. One indicator of patch value may be the degree of contrast, or the difference in nutrient availability between the patch and the background soil (Kotliar & Weins 1990).

The effects of contrast on a plant's foraging response have received little attention compared to other aspects of soil heterogeneity. Models examining nutrient uptake from heterogeneous soils suggest that as contrast increases, the proportion of a plant's total nutrient uptake taken from the rich patch should increase more quickly than the rate of increase in contrast (Jackson & Caldwell 1996). The increase in uptake in a patch

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should be due to both the plant response, and the increased nutrient availability that occurs because more nutrient ions must compete for limited binding sites on the soil particles (Anghinoni & Barber 1980, 1988). This increased nutrient availability should benefit plants even in the absence of root proliferation, but the relative benefits of a patch that arise from proliferation *vs* increased nutrient availability are unknown. Models suggest that the biomass of plants that do not proliferate roots in nutrient-rich patches should not increase with an increase in contrast, but that of species that do proliferate should (Fransen *et al*. 1999). Experimental testing of this theory is limited to the clonal herb *Glechoma hederacea*, a species that benefits strongly from heterogeneous soil (Birch & Hutchings 1994). *Glechoma* increasingly concentrates root biomass in rich patches as contrast increases, while total shoot biomass is similar between contrast treatments (Wijesinghe & Hutchings 1999). The lack of a shoot response by *Glechoma* to changes in contrast suggests that, while a response to nutrient patches is adaptive, fine-scale distinctions between patches of slightly different value may not be important.

In addition to contrast, the density of nutrient patches may have important consequences for foraging responses. The pattern of root proliferation when more than one patch is available to a plant is poorly understood (Crick & Grime 1987; Einsmann *et al*. 1999). Plants may proliferate equally in each patch, or they may allocate more resources to one or a few patches. Gersani, Abramsky & Falik (1998) found that when the conditions in each pot were similar, split-root plants invested equally in each pot. In competition studies of plant competition, a plant's root proliferation response is often measured in several patches – some of which are exclusive and some of which are shared with a competitor (Day, John, & Hutchings 2003). Plants may allocate more resources to patches to which they have exclusive access than to patches where a competitor is present (Day *et al*. 2003), or they may proliferate extensively in the shared patch (Gersani *et al*. 2001). When competitors are not present, plants proliferate more strongly in patches that are closer to the stem (Day *et al*. 2003).

Finally, the duration that a nutrient patch remains detectable to the plant may influence the root proliferation response (Robinson 1994; Hutchings, John & Wijesinghe 2003). Considerable temporal heterogeneity in nutrient availability occurs in natural soils (Taylor, de-Felice & Havill 1982; Cain *et al*. 1999; Farley & Fitter 1999), and leaching of mobile nutrients such as nitrate from the patch into and from the surrounding soil will reduce the potential value of a patch to a plant (Marschner 1995). In experimental systems using organic nutrient-rich patches, knowing how nutrient availability changes during an experiment can be important for the interpretation of results (Fransen & de Kroon 2001).

In this study we examined the effects of patch–background contrast and the density of patches on the root proliferation and growth responses of the annual weed *Abutilon theophrasti* Medic. Specifically, we investigated whether (a) plant performance (root and shoot biomass) and (b) root proliferation into nutrient-rich patches (root length inside and outside nutrient patches) were affected by the patch–background contrast and the number of high-nutrient patches available to the plant. We also examined the longevity of the nutrient patches used in the experiment.

Materials and methods

STUDY SPECIES

Abutilon theophrasti, an annual weed native to Asia but introduced in agricultural areas throughout the western hemisphere (Spencer 1984), was used as the study species for this experiment. We chose *Abutilon* because prior studies of *Abutilon* populations on heterogeneous soils provide a broad context in which the results of the present study could be evaluated. Casper & Cahill (1996, 1998) found that, in heterogeneous soil, populations of *Abutilon* proliferated roots extensively into nutrient-rich patches, but neither the overall shoot biomass of the population nor the distribution of shoot biomass among plants in the population was strongly affected by the heterogeneity. Finally, the nutrient foraging patterns of individual *Abutilon* plants in a population have been studied directly using nutrient analogue tracers (Casper, Schenk & Jackson 2003).

EXPERIMENTAL DESIGN

A 3×3 factorial design (background soil nutrient availability × number of nutrient patches per pot) with 10 replicates per treatment was used to examine the effects of soil heterogeneity and patch–background contrast on root proliferation and whole-plant performance (Fig. 1). The experiment was carried out in 12×12 cm square pots each filled 10 cm deep with background soil (3 : 1 mixture of sand and topsoil). The basic background soil, without the addition of any nutrients, is referred to as 'zero background soil' throughout this paper. No, one or two discrete nutrient patches were added to each pot, and the background soil in each pot had either no, one or two nutrient patch-equivalents added. A single nutrient patch (or patch equivalent) consisted of a 1 : 1 mixture of zero background soil and commercial cattle manure fertilizer (0·5–0·5–1) placed in a column, 2·7 cm^2 in area at the soil surface, extending from the base of the pot to the soil surface (27 cm^3 total volume). Nutrient-enriched background soil was created by homogeneously mixing either 27 cm^3 (+1 background) or 54 cm^3 (+2 background) of the patch soil throughout the background soil in the pot. A single *Abutilon* seedling <1 week old was bare-root transplanted into the centre of each pot.

A separate study indicated that *Abutilon* growth in the zero background soil was nitrogen limited, as plants

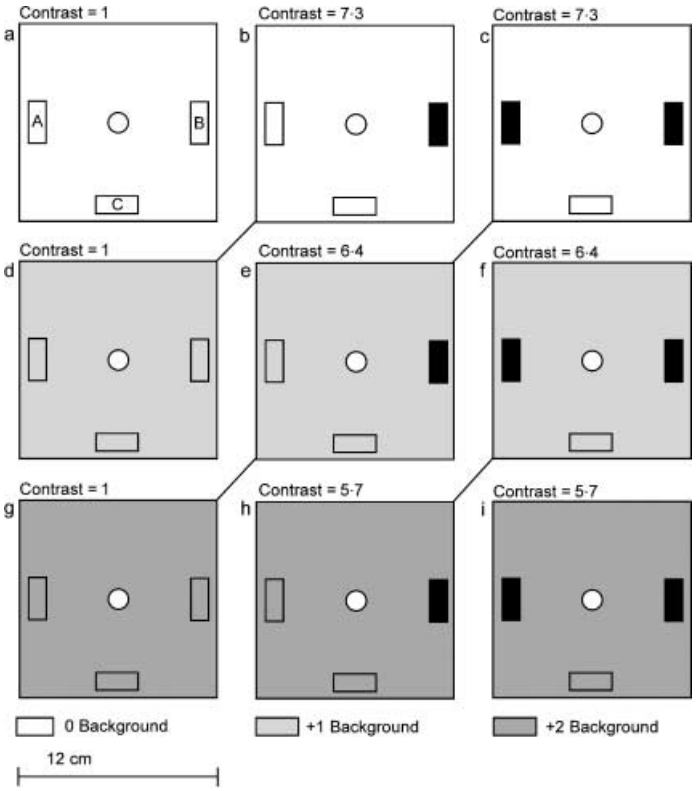

Fig. 1. Experimental layout. A single *Abutilon* was planted at the centre of each pot. The three locations for soil cores (A, B, C) are indicated for treatment a. Core locations shaded black contained a high-nutrient patch. Contrasts (patch nutrient level/background nutrient level) are indicated above each treatment. Diagonal lines connect treatments with the same total nutrient availability.

grown in pots supplemented with nitrogen fertilizer were ≈25% larger ($F_{2,26} = 9{\cdot}163$; $P = 0{\cdot}001$) than those in control pots or pots with added phosphate. Available nitrogen (NO_3^- and NH_4^+) in the patch and background soil of each treatment were estimated from the initial nitrogen concentrations (μg cm^{-3}) measured in the zero background soil and patch soil of the patch longevity experiment (see below). These data were used to estimate the contrast, or inorganic nitrogen concentration in the patch in excess of that in the background soil (Fig. 1).

Pots were randomly arranged in a growth chamber (18 h light, 24 °C, 65% humidity), watered every 2–3 days, and periodically rearranged to prevent biases resulting from spatial lighting or temperature differences. The experiment was harvested after 8 weeks; at that time some of the plants in high-nutrient conditions had begun to flower. In each pot a soil core of the same volume as the nutrient patch (27 cm^3) was extracted from three locations (Fig. 1). Two of the cores (locations A and B) contained nutrient patches in some treatments. The third, control core (location C) was taken at the same distance from the target plant as the nutrient patches. The roots from the cores were manually separated from the soil and scanned. Image analysis software (WinRhizo, Régent Instruments Inc., Quebec, Canada) was used to determine the total root length in each sample. Total root and shoot dry biomass were determined for each plant.

A second experiment was set up to determine patch longevity. Forty pots with zero background soil and a single nutrient patch (equivalent to treatment b in Fig. 1) were assigned to one of five planting/harvesting treatments. Two treatments had a single *Abutilon* seedling planted in the centre of the pot, while pots in the other three treatments had no plants. These pots were randomly arranged in the growth chamber used for the main experiment, watered every 2–3 days, and periodically rearranged. One no-plant treatment was harvested immediately, allowing determination of initial NH_4^+ and NO_3^- concentrations. Additional harvests of both ± plant treatments were done at 3 and 8 weeks. At each harvest a soil core was taken from the location of the nutrient patch and from the opposite side of the pot. Available NH_4^+ and NO_3^- in the cores were determined using KCl extraction and an automated continuous flow analyser (Technicon AutoAnalyzer II).

DATA ANALYSIS

To determine how the nutrient levels of the patches changed through the experiment, nitrate and ammonium concentrations were analysed using ANOVA: four separate tests (NO_3^- concentrations in patch and background, and NH_4^+ concentrations in patch and background) with time (0, 3, 8 weeks) and plant (± plant in pot) as fixed factors. *Post hoc* Tukey tests were used to distinguish between the time treatments. Data were ln-transformed to correct for non-normality.

To determine whether the number of nutrient patches and the patch–background contrast altered plant performance, above- and below-ground biomass were analysed using multivariate ANOVA. Data were ln- and arcsine-transformed as appropriate to correct for non-normality. Above- and below-ground biomass were first examined using a MANOVA with background soil inorganic nitrogen concentration and nutrient patch number as fixed factors. A significant patch number–background interaction would indicate that plant performance had been influenced by the patch–background contrast. Changes in allocation between roots and shoots were tested using an ANCOVA with shoot biomass as the dependent variable, background nutrients and patch number as fixed effects, and root biomass as a covariate (*sensu* Cahill 2003).

Root proliferation between contrast treatments was examined using the ratio of root length in nutrient patches (mean of root length in cores A and B when two patches present; or root length in core B when only one patch present) to the root length in the background soil (length from location C). When no patches were present (treatments a, d, g) the ratio of mean root length at locations A and B to the length at location C was used. This approach is similar to the relative fine root mass difference used by Mou, Mitchell & Jones (1997), except that in the latter approach the mass difference is relativized to the total root mass of the plant. To determine whether the number of nutrient patches

and the patch–background contrast affected root proliferation, the ln-root length ratio was compared using ANOVA with background soil inorganic nitrogen concentration and patch number as fixed factors.

Results

PATCH LONGEVITY

Nutrient patches initially contained higher concentrations of nitrate and ammonium relative to background levels (Fig. 2), with 90% of the available nitrogen in the background soil (99% in patches) present as NO_3^-. Nitrate concentrations declined with time (patch: $F_{2,35} = 38{\cdot}342$, $P < 0{\cdot}001$; background: $F_{2,35} = 20{\cdot}310$, $P < 0{\cdot}001$), and were smaller when plants were present (patch: $F_{1,35} = 69{\cdot}987$, $P < 0{\cdot}001$; background: $F_{1,35} = 38{\cdot}582$, $P < 0{\cdot}001$). The time–plant interaction was significant (patch: $F_{1,35} = 14{\cdot}428$; $P = 0{\cdot}001$; background: $F_{1,35} = 23{\cdot}477$, $P < 0{\cdot}001$) indicating that the plants had drawn down inorganic nitrogen more quickly than leaching losses. By the end of the experiment, plants had drawn nitrate concentrations nearly to zero in both patches ($0{\cdot}44\ \mu g\ g^{-1} \pm 0{\cdot}54$ SD) and background soil ($0{\cdot}27\ \mu g\ g^{-1} \pm 0{\cdot}25$ SD); they were slightly greater without plants. Ammonium concentrations in patches declined with time ($F_{2,35} = 7{\cdot}748$, $P = 0{\cdot}002$), but the presence of plants had no effect on this trend ($F_{1,35} = 0{\cdot}081$, $P = 0{\cdot}778$). There were no significant changes ($P > 0{\cdot}05$) in ammonium concentrations in the background soil. In treatments without plants, 91% of the available nitrogen in the background soil (87% in patches) was present as NO_3^- at the end of the experiment, while in treatments with plants only 30% of the available nitrogen in the background soil (27% in patches) was present as NO_3^-.

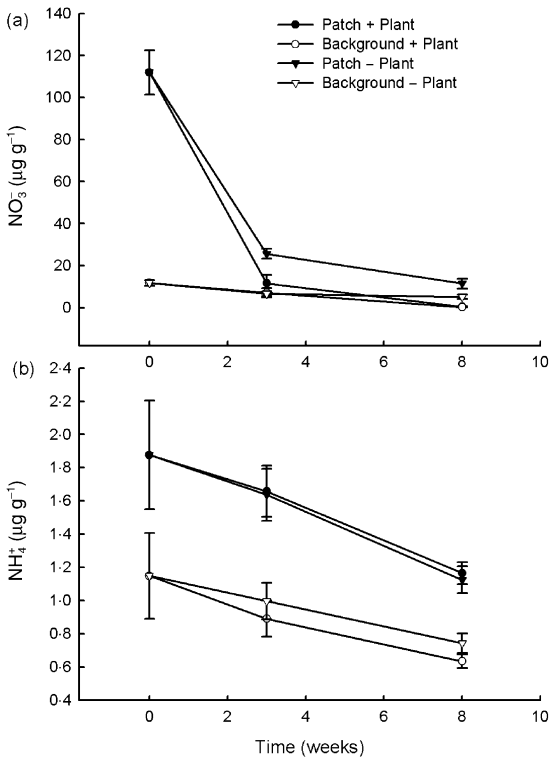

Fig. 2. Available nitrate (a) and ammonium (b) concentrations in a nutrient patch and in zero background soil over the course of the experiment. Patches remained distinct during the experiment when no plants were present, but the presence of a plant drew nitrate concentrations down similarly in both patches and background soil. Error bars are 1 SD.

WHOLE-PLANT PERFORMANCE

Root and shoot biomass increased with the numbers of nutrient patches (Table 1; Fig. 3). Background soil nutrient availability did not affect shoot biomass, but root biomass in the zero background soil exceeded that in the +1 and +2 background soils. The patch–background contrast did not alter root or shoot biomass (interaction $P > 0{\cdot}05$). Root biomass declined as contrast declines in Fig. 3, but the same pattern was also found in the treatments with homogeneous soil. This indicates that the greater root biomass at higher contrast is due to the low nutrient content of the zero background soil, rather than to changes in contrast.

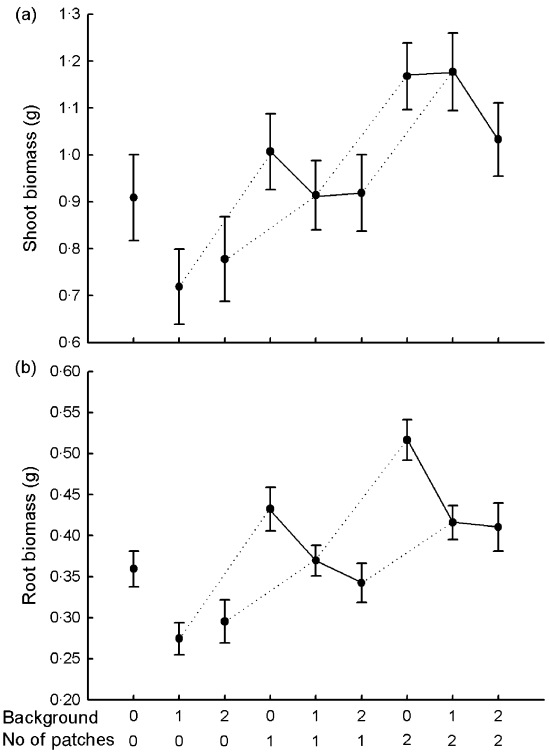

Fig. 3. Total shoot (a) and total root (b) biomass in each of the patch and background treatments. Dotted lines join treatments with equal amounts of nutrients, but differing in nutrient heterogeneity (proportion of nutrients concentrated in patches). Solid lines join treatments that have equal numbers of nutrient patches but differ in background nutrients, resulting in a series of decreasing contrasts (7·4–6·4–5·7). Both shoot and root biomass were significantly different ($P < 0{\cdot}05$) between each of the three groups of patch number treatments. Only root biomass was significantly different ($P < 0{\cdot}05$) between background treatments (zero background was higher than +1 and +2 background treatments). Error bars are 1 SD.

Table 1. Multivariate ANOVA on the effects of patch number and patch–background contrast on *Abutilon* shoot and root biomass: (a) multivariate test statistics; (b) corresponding univariate test statistics for patch number and contrast and the interaction term

(a) Source	Wilkes Lambda	df	*F* ratio	*P*
Patch number	0·617	4,158	10·773	<0·001
Background	0·731	4,158	6·688	<0·001
Patch number × background	0·923	8,158	0·807	0·597

(b) Source	Variable	df	MS	*F* ratio	*P*
Patch number	Shoot	2	0·213	12·298	<0·001
	Root	2	0·073	24·612	<0·001
Background	Shoot	2	0·031	1·808	0·171
	Root	2	0·036	12·135	<0·001
Patch number × background	Shoot	4	0·009	0·544	0·704
	Root	4	0·001	0·362	0·835
Error	Shoot	80	0·017		
	Root	80	0·003		

Table 2. Analysis of covariance on effects of patch number and patch–background contrast on shoot biomass with root biomass as a covariate

Source	df	MS	*F*	*P*
Patch	2	0·009	0·962	0·387
Background	2	0·001	0·129	0·880
Root Biomass	1	0·646	69·383	<0·001
Patch × background	4	0·002	0·185	0·945
Patch × biomass	2	0·010	1·045	0·357
Background × biomass	2	0·003	0·334	0·717
Patch × background × biomass	4	0·002	0·274	0·894
Error	71	0·009		

Table 3. ANOVA on effects of patch number and patch–background contrast on *Abutilon* root length ratio (root length in patch/root length in background soil)

Source	df	MS	*F*	*P*
Patch number	2	3·461	23·770	<0·001
Background	2	0·159	1·090	0·341
Patch number × background	4	0·005	0·308	0·872
Error	80	0·146		

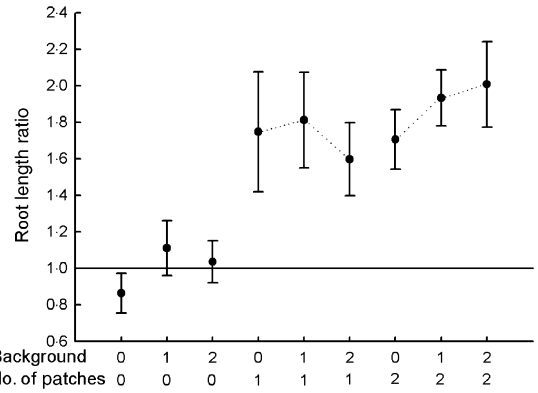

Fig. 4. Root length ratios (root length in patch/root length in background) for each of the patch and background treatments. The one- and two-patch treatments were not significantly different from each other ($P = 0{\cdot}323$), but they were significantly different from the no-patch treatments ($P < 0{\cdot}001$). Dotted lines join treatments that have equal numbers of nutrient patches but differ in background nutrients, resulting in a series of decreasing contrasts (7·4–6·4–5·7). Error bars are 1 SD.

Root and shoot growth were strongly correlated, and biomass allocation between roots and shoots did not change as a function of either background nutrients or patch number (Table 2). Overall, the biomass responses were driven by heterogeneity rather than total nutrient supply. Plants with access to the same total nutrients produced more root and shoot biomass when the nutrients were concentrated in a discrete patch (Fig. 3).

ROOT PROLIFERATION

The root length ratio (root length in patch/root length in background soil) was greater when one or two patches were present, but was not affected by background nutrient availability (Table 3; Fig. 4). The root length ratio of the treatments with a contrast of 1 were not significantly different from 1 (a: $t_8 = -1{\cdot}254$, $P = 0{\cdot}245$; d: $t_9 = 0{\cdot}733$, $P = 0{\cdot}482$; g: $t_9 = 0{\cdot}305$, $P = 0{\cdot}767$), indicating that in homogeneous soil, root distributions were similar throughout the pot. The ratios of the one-patch and two-patch treatments were significantly higher than in the no-patch treatments, but those in the one- and two-patch treatments did not differ from each other (Fig. 4). This indicates that roots proliferated in patches, but the proliferation response did not differ depending on the number of patches available. The patch–background contrast did not alter the root length ratio.

Discussion

PATCH–BACKGROUND CONTRAST

Neither root and shoot biomass nor root proliferation was affected by patch/background contrast. The ratio of root length in patches/background soil increased from the treatments with homogeneous soil (contrast = 1) to treatments with patches (contrast = 5·7–7·4). *Abutilon* had a clear root proliferation response in the patches, but the plants did not respond to the differences in contrast among heterogeneous soils. Three explanations for the lack of response are possible: (a) the relative differences between the ratios of nutrients in patches and background soil contrasts were too small to be detected by *Abutilon*; (b) there was an upper limit to the proliferation response in *Abutilon* and the plants were incapable of more proliferation; or (c) there is some threshold value necessary to trigger an increased response (possibly a combination of factors such as patch value and overall nutrient status) that was not reached. If the third explanation is correct, these threshold values should indicate to the plant that a patch is

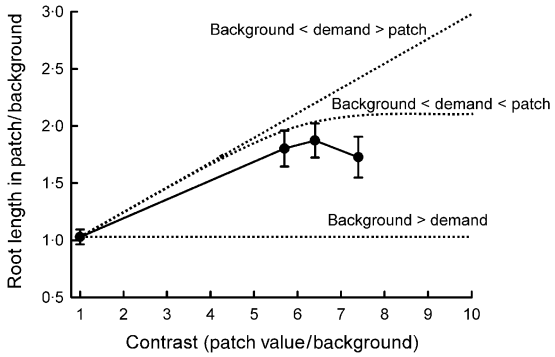

Fig. 5. Conceptual model of how plants should respond to varying contrast under different levels of background nutrients. Solid line shows how the ratio of root length in the patches changed relative to root length in the background soil over the range of contrasts used in this study. Error bars are 1 SD. Dotted lines show how the degree of root proliferation should change with the nutrient demand of the plant relative to the amount of nutrients available in the background soil.

sufficiently valuable for a plastic response to be likely to increase fitness (Alpert & Simms 2002).

Given that the overall nutrient status of a plant influences root proliferation responses (Robinson 1994), we propose the following conceptual model (Fig. 5). We assume in this model that nutrient availability in the patch never reaches toxic levels, and that there is no inherent upper limit to root proliferation responses. This model shows how a plant could respond to changes in the patch–background contrast, depending on whether the nutrients available meet demand (non-limiting nutrients). When the value of the nutrients available in the background soil alone is greater than plant demand, there should be little response to increasing contrast. When nutrients in the background are less than demand, then root proliferation into a patch should increase with increasing contrast. The response should become saturated once the total value of the patch and background soil exceeds demand, but the data from this experiment are insufficient to test this. The responses of *Abutilon* in this experiment appear to lie along the middle curve in Fig. 5. Similarly, the proportion of the roots of *Glechoma hederacea* clones found in rich patches also increased with increasing contrast, but appeared to saturate at higher contrast values (Wijesinghe & Hutchings 1999). Without treatments with a wider range of nutrient availability at the same levels of contrast, we are unable to separate a saturating response following the model from one simply caused by *Abutilon* reaching an upper limit of root proliferation.

This model is similar to ideal free distribution (IFD) models in which density in a patch should be proportional to the resources available in that patch (Gersani *et al*. 1998). Increasing contrast is an indication of increasing local resource availability, linking the patterns in Fig. 5 to an IFD. The allocation of biomass to different parts of a split-root system in pea plants (*Pisum sativum*) was consistent with an IFD (Gersani *et al*. 1998). Our model suggests that the interaction between nutrient demand and the location of those nutrients (measured as the contrast between patch and background) may be an important component if plants are to maintain an optimal pattern of biomass allocation in heterogeneous soils. Validation of this model will require similar experiments using a much wider range of contrasts and total nutrient availability.

NUMBER OF NUTRIENT PATCHES

The root proliferation response into individual patches did not depend on the number of patches. Root proliferation responses are generally localized within an enriched patch (Robinson 1994), so separate parts of a root system should be equally capable of proliferating. These results support Gersani *et al*. (1998) who found that split-root plants exploited equivalent patches equally. It is likely that these responses change only when the spatial arrangement of patches changes. For example, the degree of proliferation of a lone plant into a patch can be smaller if another patch is directly between the plant and the further patch (Day *et al*. 2003), but it is likely that a plant is equally capable of detecting and exploiting numerous patches that are equidistant from the plant. Relatively little is known about the responses of lone plants to multiple patches, even though this response is the null model to which studies of competition using multiple patches should be compared. Studies involving competition have demonstrated a range of responses, from avoidance (Day *et al*. 2003) to aggressive proliferation (Gersani *et al*. 2001), in shared patches. The symmetrical proliferation by lone plants found in our study supports the suggestion that the varied proliferation responses of plants competing for patches are a consequence of the competition (Day *et al*. 2003), rather than simply an artefact of how a plant responds to multiple patches.

WHOLE-PLANT PERFORMANCE

At the whole-plant level, individual *Abutilon* plants performed better in heterogeneous than in homogeneous soil. More above- and below-ground biomass was produced when a given amount of added nutrients was concentrated in patches (Fig. 3). While the presence of patches had strong effects on biomass, only root biomass was affected by background soil nutrients. It is not clear why root biomass declined from the zero background soil to the +1 and +2 background soils. A possible explanation is that differences in biomass allocation within the root system occurred between the treatments. Total root length was not measured, but when it was estimated from pot volume and the root length per core volume, the effect of patch number was significant ($F = 3{\cdot}713$; $P = 0{\cdot}029$), but not the effect of background soil ($F = 1{\cdot}411$; $P = 0{\cdot}250$). These results suggest that the increase in root biomass in the zero background treatments was due not to increased root

length, but rather to increased allocation to the taproot and other major roots. If increased allocation to larger roots does occur, it may indicate that, in homogeneous soils, *Abutilon* uses a strategy of foraging for patches using larger roots and proliferates finer roots only when a patch is encountered. Alternatively, such shifts in allocation may not be caused by the optimal partitioning of biomass, but simply an allometric consequence of plant development. For example, in *Abutilon* grown in low-nutrient conditions, relative biomass allocation shifts from roots to shoots over the life of the plant (Gedroc, McConnaughay & Coleman 1996). If, in our experiment, the timing of the shift in allocation was delayed from the time observed by Gedroc *et al*. (1996) (≈3 weeks), this could explain the greater root biomass in our zero background treatments. Given the current lack of understanding of the functional ecology of roots (Pregitzer 2002), we cannot be certain why this apparent shift in allocation occurred.

The improved performance of individual *Abutilon* plants in heterogeneous soils conflicts with previous research on *Abutilon* populations (Casper & Cahill 1996, 1998; Casper *et al*. 2003). This disparity illustrates the importance of scale and community context when studying soil heterogeneity (Hutchings *et al*. 2003). Casper & Cahill (1996, 1998) grew *Abutilon* populations in homogeneous soil and heterogeneous soils containing large (8 × 8 cm) nutrient-rich patches. Root biomass in rich patches was greater than in poor patches, indicating a strong proliferation response, but there were few differences in above-ground biomass between homogeneous and heterogeneous treatments. *Abutilon* plants can forage up to 32 cm away from the stem, and numerous individuals will exploit a single large nutrient patch (Casper *et al*. 2003). This extensive root overlap may reduce the variation in nutrients available to each plant, and may even out population-level measures (Casper & Cahill 1998). This study has shown that lone *Abutilon* plants benefit from nutrients concentrated in patches, but although most plants in the populations studied by Casper & Cahill (1996, 1998) accessed patches, these benefits of heterogeneity are not found at the population level. Similarly, individuals of the old-field forbs *Ambrosia artemisiifolia* and *Phytolacca americana* benefit from heterogeneous soils, but not when grown with neighbours (Cahill & Casper 1999). These studies indicate that there are costs associated with foraging in a shared patch that counteract the benefits of the greater amounts of nutrients available in the patch. For example, Gersani *et al*. (2001) found that plants competing for a shared nutrient patch shifted allocation to roots, reducing the biomass of shoots and reproductive structures, and others have shown that aggressive root proliferation into shared patches is important for nitrogen capture (Hodge *et al*. 1999; Robinson *et al*. 1999). An understanding of how *Abutilon* roots from separate plants interact within a shared patch may identify why these patterns found at the individual plant level do not appear in populations. A subsequent study on *Abutilon* is planned to examine the root proliferation responses and outcome of competition when two plants are forced to compete for small patches similar to those used in this study.

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