

POPULATION-LEVEL RESPONSES TO NUTRIENT HETEROGENEITY AND DENSITY BY *ABUTILON THEOPHRASTI* (MALVACEAE): AN EXPERIMENTAL NEIGHBORHOOD APPROACH¹

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An experimental approach was used to examine the effects of spatial nutrient heterogeneity and planting density on the sizes of plants within populations of *Abutilon theophrasti*. Planting locations were generated using random numbers and replicated among populations growing on two different scales of heterogeneity and homogeneous soils. The same quantity of nutrients (dehydrated cow manure) was added to each population, regardless of the spatial nutrient distribution. The higher density was achieved by adding additional planting locations to those present at the lower density. Plant biomass was compared among ten planting locations present in all populations. Plants in seven locations were smaller at the higher density, but the spatial distribution of nutrients affected plant size in only two locations. At the population level, the higher density reduced mean plant biomass and increased both total biomass and the coefficient of variation in biomass, a measure of size inequality. Only when populations on both scales of heterogeneity were together compared with those on homogeneous soils were population-level measurements found to be significantly affected by soil treatment; heterogeneity resulted in decreased total biomass and an increase in the coefficient of variation, apparently due to an increase in the number of small plants in the population. These results, together with the finding that fine root biomass increased in nutrient-enriched patches, suggest that on heterogeneous soils most plants were able to access nutrient patches.

Key words: *Abutilon theophrasti*; Malvaceae; neighborhood analysis; nutrient heterogeneity; population density; population structure; root distributions.

The effect of small-scale spatial heterogeneity on the performance of plants within populations has been explored through neighborhood models of plant interactions (Pacala, 1987; Biondini and Grygiel, 1994; Yastreb, 1996). These models are used to project population dynamics from information about a plant's immediate environment and local neighborhood structure. The approach is based on the general observation that much of the size variation among individuals can be explained by the size, proximity, and angular dispersion of neighboring plants (Waller, 1981; Weiner, 1982; Silander and Pacala, 1985).

Introducing small-scale habitat heterogeneity into neighborhood models has led to predictions of increased stability of populations and increased likelihood of species co-existence (Pacala, 1987; Yastreb, 1996), but results vary depending on the relationship between the distance over which plants interact and environmental patch size. In the absence of empirical information, modelers make assumptions about the area over which plants forage for belowground resources (and seed dispersal distances), and predictive results generally depend on the relationship between foraging area and the scale of het-

erogeneity assumed (Pacala, 1987; Biondini and Grygiel, 1994; Yastreb, 1996).

Most empirical information about plant response to spatial nutrient heterogeneity comes from studies of isolated individuals, not of populations. Root systems often respond to nutrient-enriched patches with greater proliferation of fine roots or increased nutrient uptake kinetics (Eissenstat and Caldwell, 1988; Jackson and Caldwell, 1989; Jackson, Manwaring, and Caldwell, 1990; Campbell et al., 1991; Gross, Peters, and Pregitzer, 1993). Consequently, a heterogeneous distribution of nutrients may result in overall greater nutrient uptake (Jackson and Caldwell, 1996). Growth responses of potted agricultural species also suggest that a small-scale, patchy distribution of nutrients may be beneficial (Anghinoni and Barber, 1980; Borkert and Barber, 1985). It is not clear, however, that results with single plants are generalizable to situations where plants grow with neighbors (Cahill, 1997). There is little direct evidence for how heterogeneity affects competitive relationships at either the intraspecific or interspecific level.

The purpose of this study was to examine experimentally the effects of nutrient heterogeneity, introduced at two spatial scales, on the productivity and population size structure of the annual *Abutilon theophrasti* Medic. It follows a previous study with the same species (Casper and Cahill, 1996) that examined similar population-level parameters when spatial heterogeneity was presented in a checkerboard pattern and populations were compared with those on spatially homogeneous soils. The current study differs from the previous one in several ways: (1) it introduces two spatial scales of nutrient heterogeneity that differ from the one used in the previous experiment,

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(2) it takes a neighborhood approach in examining responses of individuals within populations, and (3) by examining root distributions in relation to nutrient patches, it measures belowground, as well as aboveground, responses to the heterogeneity.

The experimental neighborhood approach employed here involved replicating a single pattern of randomly generated planting locations among the two heterogeneous soil nutrient treatments and one homogeneous treatment. By maintaining the same spatial arrangement of plants among soil treatments, we could examine whether the spatial distribution of nutrients affected the relative sizes of individuals within a plant neighborhood. Because the experiment was repeated at two population densities and the planting locations present in low-density populations were also present at the higher density, it was also possible to consider simultaneously how the distribution of nutrients and the presence of additional plants (higher density) affect the size of a plant in a particular planting location.

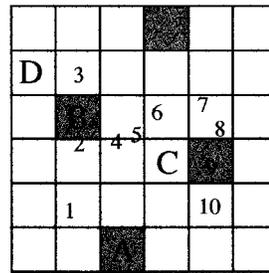
MATERIALS AND METHODS

Description of species—Commonly called velvet-leaf, *Abutilon theophrasti* is a widespread agricultural weed throughout much of the Northern hemisphere (Spencer, 1984). Its sturdy vertical stems support softly pubescent, heart-shaped leaves. Under favorable growing conditions plants may reach over 1 m in height and produce leaves that are more than 20 cm wide. Plants produce branches, which arise from leaf axils, only at low population densities. Yellow flowers (1.5–2.5 cm in diameter), which are normally autogamous but capable of outcrossing (Garbutt and Bazzaz, 1987), are also borne in leaf axils. A taproot develops, and in most individuals, lateral roots originate in four vertical columns within 10 cm from the top of the taproot (Casper and Cahill, personal observations). The species tolerates a wide range of nutrient and light conditions (Parrish and Bazzaz, 1982; Garbutt and Bazzaz, 1987) and has been used in many studies investigating how population size hierarchies are formed (Hartgerink and Bazzaz, 1984; Pacala and Silander, 1990; Shumway and Koide, 1995; Casper and Cahill, 1996).

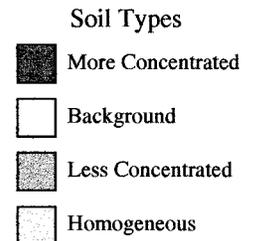
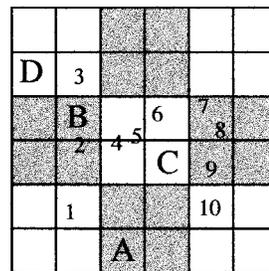
Experimental design—The experiment was laid out in a randomized block design in an outdoor garden on the University of Pennsylvania campus. Each 48 × 48 cm plot (population) contained one of three soil treatments—a smaller or a larger scale of heterogeneity or a homogeneous treatment—and planted with either 28 (122 individuals/m²) or 56 (243 individuals/m²) individuals per plot. The size of nutrient-enriched patches and the nutrient concentration within patches differed between the two scales of heterogeneity, but the same quantity of supplemental nutrients (1024 cm³ of commercial dehydrated cow manure) was added to each population in all three soil treatments. The terms “larger scale” and “smaller scale” are used to distinguish the two patterns of heterogeneity in this experiment and are not intended to imply absolute measures of spatial variance. Plots were organized in six blocks, with three rows of four plots per block. Each soil treatment × density combination was replicated twice per block, resulting in 12 replicates total.

In constructing soil treatments, the garden soil was removed to a depth of 10 cm, and wooden boards were inserted into the clay subsoil to form frames around each row of plots. Within rows, plots were separated by a piece of plastic garden edging. Soil treatments were created in each plot using as a template a three-dimensional metal grid that divided the space into six rows of six 8 × 8 × 10 cm cells. In heterogeneous soil treatment plots, some cells were filled with a background soil relatively low in nutrients, while others were filled with same soil supplemented with the dehydrated cow manure (2-1-1, NPK). In homogeneous plots, all cells were filled with the same soil type, which

Smaller Scale Heterogeneity



Larger Scale Heterogeneity



Homogeneous

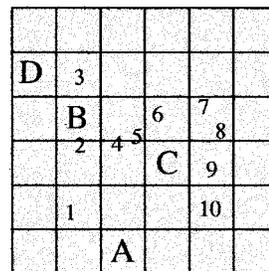


Fig. 1. The three soil treatments used in the experimental plots: smaller scale and larger scale heterogeneity treatments and the homogeneous treatment. Nutrient-enriched patches in the two heterogeneity treatments, indicated by shading, differed in size and nutrient concentration. The locations of plants included in the neighborhood analyses, which examined the effect of soil treatment and density on the relative sizes of individuals, are indicated by numbers. The locations of four soil cores used to examine the spatial distribution of fine roots are indicated by A–D.

had nutrient levels intermediate between the background soil and the nutrient-enriched patches. The grid was removed before planting.

In the smaller scale heterogeneity treatment, 32 of the 36 cells were filled with the background soil, which consisted of four parts sand, three parts topsoil that had been enriched with organic fertilizers in previous years, one part “Mr. Garden” potting soil, and one part Profile, a commercial clay (Applied Industrial Materials, Deerfield, Illinois). Mr. Garden (Lost Corner Nursery, Inc., Rockville, Maryland) consists of ground peat moss, perlite, and a small quantity of topsoil charged with micronutrients. The four remaining cells, always located in the same positions within each plot (see Fig. 1), were filled with nutrient-enriched soil made up of the low-nutrient background soil supplemented with 40% per volume manure. Hereafter, we will refer to the nutrient-enriched patches of the smaller scale heterogeneity treatment as the more concentrated soil type.

In the larger scale heterogeneity treatment, nutrient-enriched patches were both larger and less concentrated. The four patches each consisted

of four contiguous cells (see Fig. 1 for locations) in which the low nutrient background soil had been supplemented with 10% per volume manure. The remaining cells contained the same low-nutrient background soil used in the smaller scale heterogeneity treatment. We refer to the nutrient-enriched patches in the larger scale heterogeneity treatment as the less concentrated soil type.

The homogeneous soil treatment was achieved by mixing an identical quantity of manure uniformly into the background soil. Soils in homogeneous plots were still constructed using the metal grid, even though all cells contained the same soil type, to maintain the same soil compaction. The soil type used in the homogeneous soil treatment is also referred to as homogeneous.

Plantings—Seedlings were started in the greenhouse in commercial vermiculite without added nutrients and bare-root transplanted into the plots 7–9 d after seedling emergence. Care was taken to select seedlings of uniform size. The planting locations were determined using a template constructed from randomly generated coordinates. The same planting template was used for all plots of the same density, so neighborhood structure (the spatial arrangement of plants) remained constant among soil treatments. The planting template for the high-density plots was constructed by adding additional planting locations to the low-density template so that all planting locations used in the low-density plots were also present in the high-density plots. The few plants (<0.5%) that did not survive transplanting were replaced within the 1st wk. After planting, the plots were watered daily and weeded when necessary.

Effects on populations—Populations were harvested after 6 wk, immediately following a heavy rainstorm that caused extensive lodging of plants in some populations. Many individuals had begun to flower, but no fruits had ripened. Plants were cut at ground level, marked by planting location, air dried in the greenhouse, and then dried to constant biomass in a 70°C oven and weighed. Vegetative and reproductive biomasses were not separated because previous work with this species showed vegetative and reproductive biomasses to be highly correlated (Casper and Cahill, 1996). Aboveground biomass measurements of individual plants were used to find the following population-level measures: mean plant biomass, total biomass (productivity), and the coefficient of variation (cv) in plant biomass. Both mean biomass and total biomass were calculated because mortality, although very low, was uneven among plots. The cv is used as a measure of inequality in plant sizes (Weiner and Thomas, 1986). The nature of differences in plant size variation was further examined by calculating the combined biomass of the four largest plants and the combined biomass of the four smallest plants in each population. To reduce edge effects, plants in perimeter cells were not included in the calculation of population-level variables, which were thus based on a maximum of 14 individuals in low-density and 28 individuals in high-density populations.

Population-level measures were compared using ANOVA, which included soil treatment (fixed), density (fixed), and block (random) as independent variables. Planned comparisons were used to compare the two heterogeneous soil treatments with the homogeneous treatment for differences in the population-level variables. Data were ln transformed when necessary to satisfy assumptions of ANOVA.

Neighborhood analyses—Plants in ten planting locations present in both densities were specifically examined for their growth response to soil heterogeneity and density. This was possible because all of the planting locations used in the low-density plots were also present in high-density plots. The ten planting locations were selected from among those farther than 10 cm from the perimeter of the plot with the criterion that some of them fall on nutrient-enriched patches in the two heterogeneous soil treatments (Fig. 1). We wanted to determine whether the sizes of these plants were affected by either the spatial distribution of nutrients and/or local neighborhood structure (density). We expected plants growing on nutrient-enriched patches in heterogeneous soils to be

larger than plants in the same planting locations on homogeneous soil types. A separate ANOVA was conducted for each of the ten planting locations to examine the effect of soil treatment and density on above-ground biomass. The ANOVA model was identical to that used for the population-level variables described above.

Root biomass distribution—In order to determine whether the spatial distribution of roots differed among soil treatments, dry root biomass was measured from soil cores (1.5 cm in diameter and 10 cm deep) removed from the same four locations in every population. These locations were chosen because in both heterogeneous treatments, two (cores A and B) fell on nutrient-enriched patches while two (cores C and D) fell on the background soil (Fig. 1). No seedlings had been planted in the four cells from which soil cores were removed, and the closest plant stem was at least 3.5 cm away. Therefore, the cores contained lateral (fine) roots but no taproots. Roots were removed from the cores by washing over a 2.0-mm mesh sieve and then dried to constant biomass and weighed. Root biomasses in each of the four cores served as dependent variables in a MANOVA in which the independent variables were population, block, soil treatment, and density. Population was nested in the interaction of block \times soil treatment \times density. Because soil treatment proved significant in the overall MANOVA model, univariate tests were conducted to compare root biomass among soil treatments for each of the four soil core locations.

Nutrient levels—At the time of harvest, soil samples were taken from the four soil types within the experimental populations for nutrient and pH analyses to determine differences in nutrient concentration and the extent that soil heterogeneity persisted until the end of the experiment. Four 1.5-cm diameter, 10-cm deep soil cores were removed from each plot (Fig. 1). In heterogeneous soil treatments, two cores were sampled from nutrient-enriched patches and two from the background soil. Cores were pooled by soil type (regardless of planting density) in each block, mixed thoroughly, and passed through a 2.0-mm mesh sieve to remove roots. One subsample was taken from each pooled soil sample for nutrient analyses. Mineralizable nitrogen was measured in our laboratory using the methods of Waring and Bremner (1964). This involves incubating samples under anaerobic conditions, allowing bacterial activity to convert available nitrogen to ammonium, which is then extracted with KCl. All other analyses were conducted by the Pennsylvania State University Agricultural Services Laboratory. The background soils from the larger and smaller scale heterogeneity treatments within a block were pooled separately, but only one background soil sample was analyzed per block. For three blocks, these samples were taken from the pooled background soil from smaller scale heterogeneous plots, and for the other three blocks, the samples were taken from the pooled background soil from larger scale heterogeneous plots. The values for background soil reported in Table 1 are the means for these six samples.

Bioassay in pots—A separate bioassay experiment was conducted to determine whether plant growth differed among the soil types used in the different soil treatments. We expected plant size to increase with increasing nutrient concentration, and we especially wanted to verify that plant growth differed between the nutrient-enriched soils and the background soil of the heterogeneous plots. Individual seedlings were planted singly in 4100-cm³ pots filled with one of the four soil types: the background soil used in both heterogeneous soil treatments, the more concentrated soil type from the smaller scale heterogeneous soil treatment, the less concentrated soil type from the larger scale heterogeneous soil treatment, and the homogeneous soil. The ten replicate pots of each soil type were randomly interspersed, placed near the experimental plots, and watered daily. The plants were measured after 13 and 34 d for several morphological indicators of plant size: plant height, width of the largest leaf, width of the canopy at its widest point, and leaf number. Repeated-measures ANOVA was used to examine the effect of soil type on these morphological parameters. The plants were

TABLE 1. Means (SD) of nutrient levels and pH in the four soil types ($N = 6$) at the end of the main experiment and mean (SD) above-ground plant biomass ($N = 10$) produced by these same soil types in the bioassay experiment. Values for nutrients are in ppm. Univariate ANOVAs were used to examine differences among the four different soil types in nutrient levels, soil pH, and plant biomass. For each variable, values sharing the same superscript are not statistically different (LSD test; $P > 0.05$).

Variable	Soil type			
	Background soil	Homogeneous	Less concentrated patches	More concentrated patches
N	11.60 ^a (5.15)	16.15 ^b (5.27)	16.15 ^b (3.21)	28.12 ^c (2.82)
P	62.33 ^a (19.26)	109.58 ^b (8.86)	185.00 ^c (23.07)	360.83 ^d (66.58)
K	77.35 ^a (11.68)	104.65 ^b (12.68)	115.05 ^b (10.96)	114.40 ^b (11.74)
pH	7.25 ^a (0.26)	7.28 ^a (0.29)	7.18 ^a (0.46)	7.50 ^a (0.17)
Biomass (g)	5.12 ^a (2.87)	7.92 ^b (3.38)	8.92 ^b (2.24)	11.64 ^c (2.36)

harvested after 6 wk. Aboveground parts were clipped at the soil surface, dried to constant biomass, and weighed to the nearest 0.01 g.

RESULTS

Nutrient levels—At the time the experiment was harvested, the background soil used in the heterogeneous soil treatments had lower levels of N, P, and K than did the other soil types (Table 1). P differed among all four soil types, while K was statistically indistinguishable among the homogeneous, less concentrated, and more concentrated soils. N was highest in the more concentrated soil but did not differ between the homogeneous and less concentrated soil types. Soil pH did not differ among soil types.

Bioassay in pots—Morphological measurements made 13 d after the beginning of the bioassay experiment indicated that plants in the more concentrated soil were smaller than those in any of the other soil types (Fig. 2). However, by the time measurements were repeated at 34 d, plants in the more concentrated soil had grown larger than any of the others. These changes in plant size rankings among soil types occur for canopy width presented in Fig. 2, and other morphological measurements showed

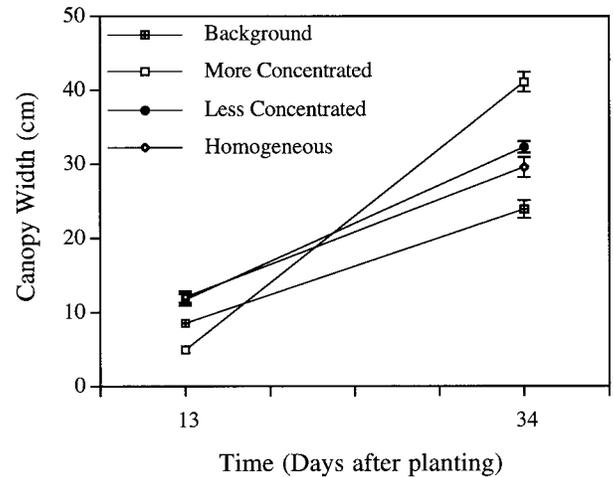


Fig. 2. The width of the canopy at its widest point (\pm SE) measured after 13 and 34 d for plants in the bioassay experiment. Plants were grown singly in each of the four soil types used in the experimental plots: the background soil used in heterogeneous plots, the more concentrated soil type from the smaller scale heterogeneity treatment, the less concentrated soil type from the larger scale heterogeneity treatment, and the homogeneous soil from the homogeneous soil treatment plots.

similar patterns. The change in relative plant performance among soil types is reflected in a highly significant measurement date \times soil type interaction in the repeated-measures ANOVA (for canopy width: $F = 41.21$; $df = 3, 33$; $P < 0.001$). Soil type and measurement date were also highly significant ($P < 0.001$).

Analysis of mean aboveground biomass of harvested plants verified that individuals in the more concentrated soil eventually grew larger than those in any other soil type (Table 1); plants grown in the background soil were significantly smaller. Mean plant biomass was statistically indistinguishable for plants in the homogeneous and less concentrated soil types. Three individuals growing in more concentrated soil died early in the experiment and were replaced. Only one of the replacement transplants survived, leaving a sample size of eight (instead of ten) in the more concentrated soil type.

Response of populations—ANOVA revealed a strong effect of density and block on three population-level variables: mean plant size, total plant biomass, and the coefficient of variation in biomass (Table 2). Soil treatment was not significant in any of these analyses, but associ-

TABLE 2. ANOVA results for population-level measurements: mean aboveground biomass/plant; total aboveground biomass; and coefficient of variation in aboveground biomass.

Variable	df	Mean biomass			Total biomass			Coefficient of variation		
		MS _{effect}	MS _{error}	P	MS _{effect}	MS _{error}	P	MS _{effect}	MS _{error}	P
Soil treatment (S)	2,10	1.391	0.547	0.13	507.614	176.172	0.10	725.73	339.91	0.17
Density (D)	1,5	19.394	0.061	0.001	7050.583	93.110	0.001	4918.96	225.50	0.01
Block (B)	5,36	2.524	0.497	0.001	1053.502	131.188	0.001	1872.38	349.70	0.001
S \times D	2,10	0.341	0.640	0.60	29.119	214.837	0.14	154.56	640.01	0.79
S \times B	10,36	0.547	0.497	0.39	176.172	131.188	0.25	339.91	349.70	0.48
D \times B	5,36	0.061	0.497	0.99	93.110	131.188	0.62	225.50	349.70	0.67
S \times D \times B	10,36	0.640	0.497	0.27	214.838	131.188	0.14	640.01	349.70	0.09

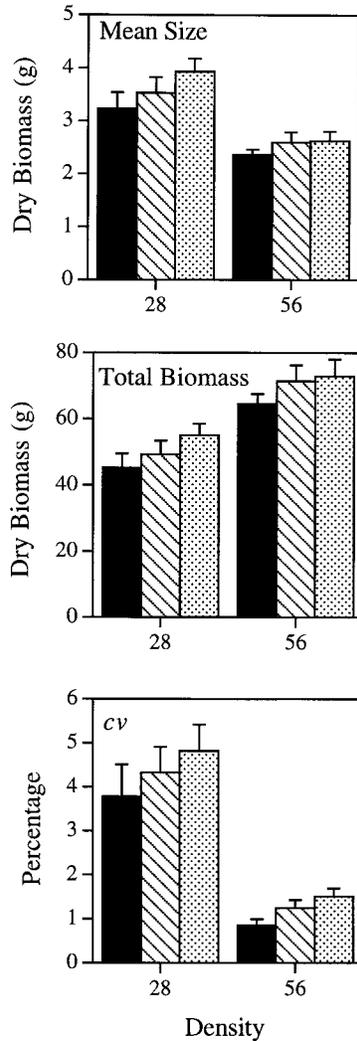


Fig. 3. Population-level parameters: mean aboveground size (biomass), total aboveground biomass, and the coefficient of variation in aboveground biomass (\pm SE), compared among soil treatments and population densities. Black bars represent the smaller scale heterogeneity, cross-hatched bars the larger scale, and stippled bars the homogeneous soil treatment.

ated P values were relatively small ($0.10 < P < 0.17$). No interaction terms were significant, although the three-way interaction was nearly significant for the cv in plant biomass ($P = 0.09$). Planned comparisons used to contrast both heterogeneity treatments with the homogeneous treatment revealed that total biomass was significantly greater (Fig. 3) on homogeneous soils ($F = 4.98$; $df = 1, 36$; $P = 0.03$) while the cv was greater on heterogeneous soils ($F = 4.12$; $df = 1, 36$; $P = 0.05$). The difference in mean biomass was marginally significant ($F = 3.88$; $df = 1, 36$; $P = 0.06$). Density, soil treatment, and block were all significant for the combined biomass of the four smallest plants (Table 3), indicating differences in minimum plant size, but only block was significant for the combined biomass of the four largest plants. Minimum plant size decreased with heterogeneity ($F = 6.51$; $df = 1, 36$; $P = 0.02$) and at the higher density (Fig. 4).

TABLE 3. Results from separate ANOVAs for measures of minimum and maximum plant size. Dependent variables were the combined biomass of the four smallest plants and the combined biomass of the four largest plants. (df are the same as in Table 2).

Variable	Biomass of the four smallest plants			Biomass of the four largest plants		
	MS _{effect}	MS _{error}	P	MS _{effect}	MS _{error}	P
Soil treatment (S)	1.608	0.206	0.01	0.062	0.071	0.44
Density (D)	29.267	0.084	0.001	0.002	0.045	0.86
Block (B)	1.206	0.270	0.003	0.552	0.058	0.001
S \times D	0.133	0.224	0.56	0.043	0.038	0.36
S \times B	0.206	0.270	0.66	0.071	0.058	0.31
B \times D	0.084	0.270	0.90	0.045	0.058	0.57
S \times D \times B	0.224	0.270	0.60	0.038	0.058	0.76

Neighborhood analyses—Among the plants in the ten locations examined for biomass response to planting density and soil treatments, seven were smaller at the higher planting density ($P \leq 0.05$), but only two (locations 8 and 9) showed a significant response to soil treatment (Table 4). Both locations fell on nutrient patches of the larger scale heterogeneity treatment, but location 9 was the only location to occur on a concentrated nutrient patch in the smaller scale heterogeneity treatment. The

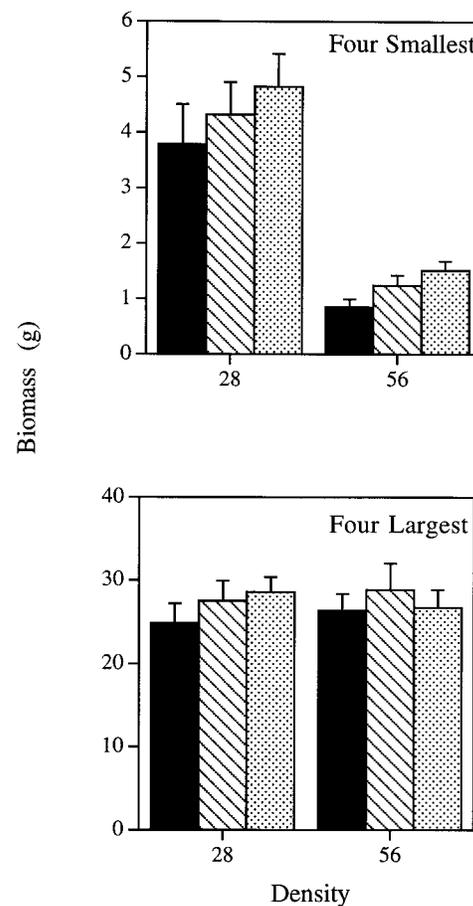


Fig. 4. The combined biomass of the four smallest plants in the population and the combined biomass of the four largest plants in the population (\pm SE), compared among soil treatments and population densities. Shading of the bars is the same as in Fig. 3.

TABLE 4. Mean (SD) dry biomass (g) for plants in each of the ten planting locations shown in Fig. 1, presented by soil treatment and density ($N = 12$). Means were compared for each location using an ANOVA model identical to that in Tables 2 and 4. Main effects and interactions significant at $P \leq 0.05$ are indicated by letters; S = soil treatment, D = density. Block was not significant for any location.

Location	Density of 28 plants			Density of 26 plants			Significant effects
	Smaller het.	Larger het.	Homogeneous	Smaller het.	Larger het.	Homogeneous	
1	3.79 (4.41)	2.53 (2.50)	4.84 (3.04)	3.38 (3.81)	2.90 (2.56)	2.79 (2.01)	—
2	3.78 (2.38)	3.44 (2.80)	3.76 (2.33)	2.31 (2.17)	1.73 (1.62)	2.70 (3.24)	D
3	2.97 (2.36)	5.41 (5.38)	4.08 (2.61)	2.24 (2.36)	3.27 (3.28)	2.72 (1.74)	D
4	2.89 (1.59)	3.65 (2.74)	2.69 (1.95)	1.76 (1.94)	1.79 (1.38)	2.61 (2.26)	D
5	3.51 (3.28)	3.60 (2.02)	6.08 (4.41)	2.55 (1.78)	2.23 (1.89)	3.00 (2.65)	D
6	3.55 (2.40)	4.22 (2.76)	3.63 (2.95)	2.50 (1.32)	2.16 (2.35)	1.98 (1.71)	D
7	4.68 (2.26)	3.29 (2.22)	4.18 (2.33)	3.80 (1.73)	2.84 (2.50)	2.24 (1.91)	D
8	4.37 (3.22)	1.89 (1.15)	4.59 (2.67)	2.17 (1.93)	2.93 (3.55)	3.10 (2.06)	S
9	0.82 (0.96)	3.31 (2.55)	3.96 (2.57)	0.50 (0.75)	2.41 (1.83)	1.40 (1.15)	S, D, S × D
10	5.28 (2.23)	3.88 (2.33)	4.03 (2.27)	2.60 (0.79)	4.01 (3.56)	2.95 (2.68)	—

soil treatment × density interaction was also significant for location 9; plants on the concentrated patches were smaller than those on homogeneous soils only at the lower density (Student-Newman-Keuls test, $P < 0.05$). For location 8, plants in the larger scale heterogeneity treatment were significantly smaller than plants in the homogeneous soil treatment (Student-Newman-Keuls test, $P < 0.05$). Although two other planting locations, 2 and 7, fell on the less concentrated soil in the larger scale heterogeneity treatment, soil treatment did not affect plant size in these locations.

Root biomass distributions—In the MANOVA using root biomass in each of the four soil core locations as dependent variables, soil treatment had a significant effect (Wilk’s lambda = 0.044; df = 6, 8; $P = 0.02$). No other main effect or interaction was significant. Univariate tests were used to examine each of the core locations separately (cores A–D) for differences in root biomass among soil treatments. Root biomass differed significantly among soil treatments for cores A and B; these two cores were both located on nutrient-enriched patches in each of the two heterogeneity treatments (Table 5, Fig. 5). In both core locations, root biomass was highest when the core fell on the more concentrated soil type of the smaller scale heterogeneity treatment. Root biomass in core C, located on the low-nutrient background soil in both heterogeneity treatments, also differed among soil treatments but less strongly ($P = 0.05$). For core C, root biomass was highest in the larger scale heterogeneity treatment, where the location fell within 4 cm of two nutrient-enriched patches.

TABLE 5. MS values and significance levels for the main effect soil treatment in separate univariate ANOVAs in which root biomass measures in each of the four soil cores were used as dependent variables. Analyses were conducted after soil treatment was found to be significant in a MANOVA in which the four core locations were used as dependent variables in a single analysis.

Core location	MS _{effect}	MS _{error}	P
A	1.653	0.240	0.03
B	2.426	0.111	0.01
C	1.514	0.303	0.05
D	0.541	0.174	NS

DISCUSSION

This study revealed subtle effects of spatial nutrient heterogeneity on the aboveground size structure and productivity of plant populations. Only when the two heterogeneity treatments were together compared with the homogeneous soil treatment were differences detected in total biomass and the coefficient of variation in biomass, a measure of size inequality among plants within a population. We expected that population size structure would change with a patchy distribution of nutrients through increased maximum plant size, because plants located on or near nutrient patches would have access to more nutrients than any individuals in the homogeneous soil treatments. Likewise, minimum plant size might decrease because individuals on the low nutrient background soil would experience lower nutrients. Differential plant performance among soil types in the bioassay experiment supports these expectations. Results point to heterogeneity affecting the smallest plants within populations but not for the reasons just explained.

The combined biomass of the four smallest plants was lower for populations on heterogeneous soil treatments, apparently because soil used in nutrient patches proved detrimental, at least initially. This conclusion is based on two pieces of evidence. First, some individuals located on nutrient patches were smaller than individuals in the same planting locations on homogeneous soils. Second, the bioassay experiment indicated detrimental effects of the more concentrated soil type for a short period after seedlings were transplanted. Within the bioassay, plants in the more concentrated soil eventually outgrew those in other soils, but within populations some plants on nutrient patches remained small until harvest, probably due to aboveground competition from neighboring plants. Asymmetric competition for light causes even small differences in initial plant sizes to become exaggerated as plants grow (Wilson, 1988).

The nearly inconsequential effects of spatial nutrient heterogeneity on the productivity of populations found in this experiment and a previous one (Casper and Cahill, 1996) differ somewhat from results of other studies conducted with single plants. Experiments with agricultural species show that plant growth is often enhanced by a patchy distribution of nutrients (Anghinoni and Barber, 1980; Borkert and Barber, 1985). Jackson and Caldwell

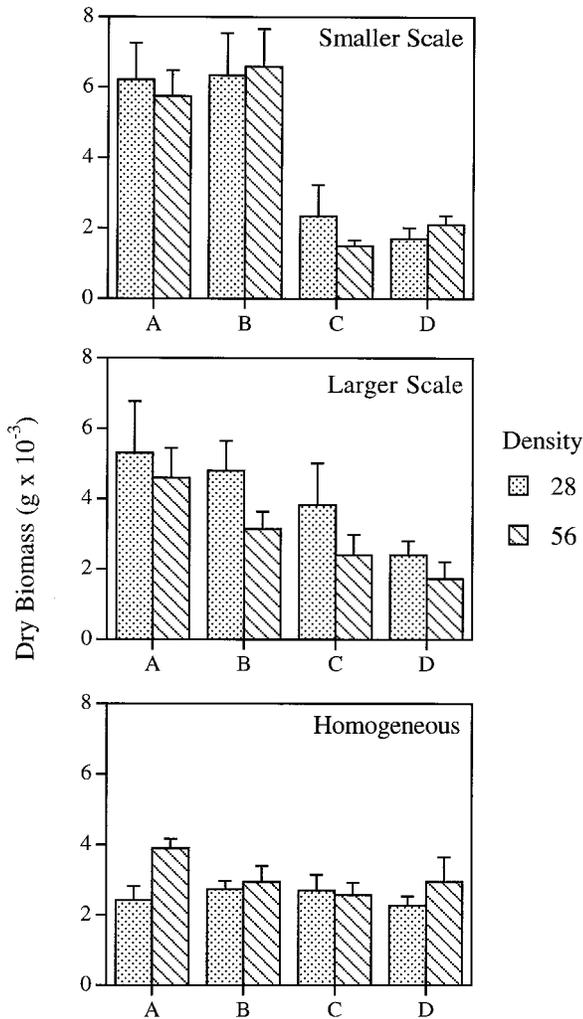


Fig. 5. Root biomass (\pm SE) in cores taken from the same locations in all three soil treatments. In both heterogeneity treatments, cores A and B were located on nutrient-enriched patches, while cores C and D were located on the background soil. See Fig. 1 for exact locations.

(1996) modeled uptake of nitrate and phosphorus from patches by the tussock grass *Agropyron desertorum* and showed that plants may obtain more nutrients from spatially heterogeneous soils than from a uniform distribution of nutrients. Their model is based on heterogeneity measured in the field and known plastic responses of this species in both fine root growth and increased nutrient uptake kinetics. While both sorts of studies demonstrate that a patchy distribution of nutrients can be advantageous for plant growth, the effect of neighbors on any such advantage has not been directly explored. Our studies suggest that the presence or absence of competing individuals may be an important variable.

Differences among species in response to heterogeneity are also expected (Gross, Peters, and Pregitzer, 1993). Earlier work by Campbell et al. (1991) suggests a trade-off in the ability of a species to forage over a broad spatial area, apparently characteristic of community dominants, and the ability to forage precisely in nutrient patches, more typical of subordinate species. The root response of *A. theophrasti* to nutrient patches and its an-

nual growth habitat are consistent with this classification scheme.

Populations of *A. theophrasti* clearly do respond belowground to nutrient heterogeneity. Fine roots were aggregated in nutrient-enriched patches in both scales of heterogeneity. The increase in root biomass observed in one core (core C) located on low-nutrient background soil in the larger scale heterogeneous soil treatment, compared to the same location on homogeneous soil, probably occurred because the core location fell very near two high-nutrient patches. Root growth may have increased in that core location as a response to mobile nutrients from neighboring patches or because roots traversed the space in accessing patches. Resource mobility is another potentially important factor affecting competitive outcomes in plant communities (Huston and DeAngelis, 1994).

The spatial aggregation of roots in nutrient-enriched patches coupled with the small effect of heterogeneity on productivity suggests that most plants in the population have access to the patches. Nutrient availability appeared to differ little among soil treatments when the supplemental nutrients were concentrated in only one-ninth of the area occupied by the population. If it is true that many plants in the population shared the nutrient-enriched patches, then root systems may extend over greater distances than leaf canopies and an individual may interact with more neighbors belowground than aboveground (Casper and Jackson, 1997).

Our neighborhood analysis also indicates that an increase in local plant density, and thus a change in the structure of a plant's neighborhood, is more likely to affect plant size than is a heterogeneous distribution of nutrients, at least at the scales of heterogeneity and density examined here. Plant size in most locations was reduced by doubling plant numbers, while far fewer were affected by heterogeneity. The higher density increased both the number of suppressed individuals and the degree to which they were suppressed, without altering the size of the dominant plants in the population.

Belowground competition is generally regarded as size symmetric, in contrast to asymmetric competition for light (Wilson, 1988; Weiner, 1990; Weiner, Wright, and Castro, 1997). However, Schwinning and Weiner (1998) have predicted that a spatially heterogeneous distribution of nutrients is one circumstance in which belowground competition could become asymmetric, the idea being that individuals with larger root systems would be more likely to encounter and exploit a nutrient patch. We found no evidence for this effect in our experiment since maximum plant size did not increase on heterogeneous soils.

While it is clear that the roots of *A. theophrasti* responded to the spatial distribution of nutrients, mycorrhizal hyphae potentially contribute to functional rooting area and exploitation of nutrient patches in this and other mycorrhizal species (St. John, Coleman, and Reid, 1983; Allen and Allen, 1990). We know that mycorrhizae were present in our study populations, but we have no information regarding their role in helping plants integrate the heterogeneous nutrient environment. Mycorrhizal relationships should be taken into account in future empirical and theoretical studies examining the impact of environ-

mental variation on plant population and community structure (Simard et al., 1997).

A better understanding of how plants respond physiologically and morphologically to nutrient patches in the presence of neighbors would facilitate construction of realistic neighborhood models of population and community dynamics for spatially heterogeneous habitats. More information is also needed about lateral rooting areas, the spatial overlap of neighboring root systems, and how these change with the scales of heterogeneity used in the models (Casper and Jackson, 1997). Although some root excavation studies reveal minimal overlap of adjacent root systems (Brisson and Reynolds, 1994; Mou et al., 1995), other evidence suggests that roots may grow preferentially into nutrient patches, even over considerable distances from the plant stem (Mou et al., 1995; Mordelet, Barot, and Abbadie, 1996). At least one study provides evidence that occupation of nutrient patches may be influenced by a neighboring plant of another species (Caldwell, Manwaring, and Durham, 1996). Additional studies of belowground neighborhood structure, using a variety of species and experimental approaches, are clearly warranted.

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