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LIMITED EFFECTS OF SOIL NUTRIENT HETEROGENEITY ON POPULATIONS OF *ABUTILON THEOPHRASTI* (MALVACEAE)[1]

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An experiment was conducted to determine if spatial nutrient heterogeneity affects mean plant size or size hierarchies in experimental populations of the weedy annual *Abutilon theophrasti* Medic. (Malvaceae). Heterogeneity was imposed by alternating 8 × 8 × 10 cm blocks of low and high nutrient soil in a checkerboard design, while a homogeneous soil treatment consisted of a spatially uniform mixture of the two soil types (mixed soil). Populations were planted at three densities. The effect of soil type on the growth of individuals was determined through a bioassay experiment using potted plants. The high nutrient, low nutrient, and mixed soil differed in their ability to support plant growth as indicated by differences in growth rates and final aboveground biomass. Concentrations of N, K, P, and Mg, measured at the end of the growing season in the experimental plots, also differed among all three soil types. Nevertheless, nutrient heterogeneity had little effect at the population level. Mean maximum leaf width measured at midseason was greater for populations on heterogeneous soil, but soil treatment did not affect midseason measurements of plant height, total number of leaves per plant, or canopy width. Population density affected all these parameters except plant height. When aboveground biomass was harvested at the end of the growing season, soil treatment was found to have no main effect on mean plant biomass, total population biomass, the coefficient of variation in plant biomass, or the combined biomass of the five largest plants in the population, but mean plant biomass was greater for populations on heterogeneous soils at the intermediate planting density. Mean plant biomass, total population biomass, and the coefficient of variation in plant biomass all varied with planting density. Mortality was low overall but significantly higher on homogeneous soil across all three densities. Soil heterogeneity had its strongest effect on individuals. In heterogeneous treatments plant size depended on the location of the plant stem with respect to high and low nutrient patches. Thus, soil nutrient heterogeneity influenced whether particular individuals were destined to be dominant or subordinate within the population but had little effect on overall population structure.

Key words: *Abutilon theophrasti*; Malvaceae; population structure; soil nutrient heterogeneity; weedy annual.

Roots occupy a spatially heterogeneous nutrient environment. Considerable variation in nutrients at scales of a metre or smaller has been measured in habitats ranging from a sagebrush steppe to old-growth forest (Beatty, 1984; Robertson et al., 1988; Latham, 1990; Gross, Pregitzer, and Burton, 1992; Jackson and Caldwell, 1993). Some species respond to small-scale soil heterogeneity by foraging preferentially in nutrient-rich patches. Exploitation of nutrient patches can occur through increased density of fine roots (Hackett, 1972; Drew and Saker, 1975; Eissenstat and Caldwell, 1988; Jackson and Caldwell, 1989; Campbell et al., 1991; Gross, Peters, and Pregitzer, 1993) and by increased nutrient uptake kinetics (Jackson, Manwaring, and Caldwell, 1990). Mycorrhizae may also enhance nutrient extraction from heterogeneous soils. Mycorrhizal hyphae are known to proliferate where nutrients are locally abundant, even if these patches are located some distance from the root(s) to which they are connected (St. John, Coleman, and Reid, 1983).

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There are several reasons why heterogeneity over distances of centimetres may have important consequences for the composition of plant communities (Fitter, 1982; Grime, Crick, and Rincon, 1986; Jackson and Caldwell, 1989; Campbell et al., 1991; Gross, Peters, and Pregitzer, 1993). If species differ in their ability to obtain nutrients from a patchy soil environment (Campbell and Grime, 1989; Campbell et al., 1991; Gross, Peters, and Pregitzer, 1993), their relative growth performance and competitive ability may vary with the spatial distribution of nutrients. Heterogeneity could thus influence competitive relationships even if total nutrient quantity is invariant. Nutrient heterogeneity might also affect the intensity or outcome of belowground competition directly (Jackson and Caldwell, 1989). For instance, if roots are concentrated in high nutrient patches, there may be greater overlap of the nutrient depletion zones that surround roots (Caldwell, 1987) and increased exploitative competition. Physical preemption of nutrient patches might also occur through allelopathy (Williamson, 1990; Mahall and Callaway, 1992) or some other mechanism of interference competition.

For similar reasons, nutrient heterogeneity may also have important consequences for the structure of populations. First, if nutrient uptake and plant growth differ with the degree of nutrient patchiness, there should be concomitant changes in productivity that should lead to changes in population size structure. Competitive intensity normally increases with productivity in monospecific

stands (Harper, 1977), and increased competition results in more variable plant sizes (Harper, 1977; Weiner and Thomas, 1986), presumably due to the dominance and suppression characteristic of competition for light (Harper, 1977; Weiner, 1990). Consequently, a greater proportion of the population biomass is concentrated in the few largest plants. Therefore, if heterogeneity affects average plant performance, there should be changes in both mean plant size and variation in plant sizes within populations. Such changes could occur largely independent of planting density.

Secondly, nutrient uptake might differ among individuals growing on spatially heterogeneous soil, even when nutrient patches are very small. This could occur if increased patchiness results in greater belowground competition or if plants simply differ in their proximity and access to nutrient patches. By causing greater variability among individuals in nutrient uptake, heterogeneity might increase size variation within a population while not necessarily affecting mean plant size. Changes in population size structure that are caused by variation among individuals in nutrient uptake should be more pronounced at higher plant densities, where competition is more intense, particularly if competition for nutrient patches proves important.

The goal of this study was to determine whether soil nutrient heterogeneity affects mean plant performance and population size structure in experimental populations of the weedy annual *Abutilon theophrasti* Medic. (Malvaceae) grown at three different densities. Heterogeneity was created by varying the levels of all nutrients in alternating 8 × 8 × 10 cm blocks of high and low nutrient soils, while spatially homogeneous soils consisted of a uniform mixture of the same two soils. Populations growing on heterogeneous and homogeneous soil treatments were examined at midseason for differences in several morphological indicators of plant size and at harvest for differences in mean plant biomass, total aboveground biomass, the coefficient of variation in biomass, and the combined biomass of the five largest plants.

METHODS

Description of species—As an agricultural weed, *Abutilon theophrasti* often occurs in dense, monospecific stands. Native to Asia, it is now widespread between latitudes of 32° and 45° throughout the Northern hemisphere (Spencer, 1984). Its very simple growth form and ease of cultivation make it an attractive research organism. Broad, heart-shaped leaves are borne on long petioles along a strong vertical stem that normally reaches ≈1.5 m in height. In crowded conditions, the stem does not branch. Autogamous flowers, that are also capable of outcrossing (Garbutt and Bazzaz, 1987), are produced singly or in clusters from leaf axils. In our study, >99% of the seedlings survived transplanting. The species tolerates a wide range of nutrient and light conditions (Parrish and Bazzaz, 1982; Garbutt and Bazzaz, 1987) and has been the subject of other studies investigating how population size hierarchies are formed (Hartgerink and Bazzaz, 1984; Pacala, 1986; Pacala and Silander, 1990).

Soil preparation—The experiment was conducted in a garden plot on the University of Pennsylvania campus. Soil was first removed from the garden to a depth of 10 cm. Wooden boards were inserted into the clay subsoil to form square (≈12 cm deep) frames around the perimeter of each 72 × 72 cm experimental plot. The frames were then refilled with soil 10 cm deep to create either spatially heterogeneous or spatially homogeneous soil treatments. This depth includes a large percentage of all roots in a variety of habitats (Richards, 1986). Heterogeneous plots were constructed by alternating 8 × 8 × 10 cm blocks of high and low nutrient soils in a checkerboard design. This was achieved by placing a grid of metal dividers into the frames, filling alternate cells with the two soils, then removing the metal dividers. The homogeneous plots were similarly constructed using the metal grid, but every cell was filled with a 1:1 mixture of the high and low nutrient soils (mixed soil). Thus the spatial distribution of nutrients differed between soil treatments, but total nutrient quantity did not.

Nutrient levels were adjusted by varying the proportion of garden soil that had been enriched in previous years with organic fertilizer. The high nutrient soil was made up of 4.7 parts garden soil, one part sand, and one part "Mr. Garden" (Lost Corner Nursery, Inc., Rockville, MD), a commercial potting soil containing ground peat moss, perlite, and a small quantity of topsoil charged with micronutrients. The low nutrient soil consisted of one part garden soil, 2.5 parts sand, and 1.5 parts "Mr. Garden." Soil constituents were mixed with shovels on an asphalt surface in six batches. Each batch made 0.339 m^3, enough soil to fill three heterogeneous and three homogeneous plots.

Planting design—Plots were planted at densities of 30, 60, or 120 individuals per plot. Six replicates of each planting density × soil type (heterogeneous vs. homogeneous) combination yielded 3 × 2 × 6 = 36 experimental plots, and these were randomly assigned among six rows of plots. Plots were spaced 20-25 cm apart, far enough to allow access to all sides of all plots.

Seedlings of *A. theophrasti* were first grown in "Mr. Garden" in a greenhouse and bare root transplanted into the experimental plots at 14 d of age. The few seedlings that failed to survive transplanting were replaced before 7 d. Planting locations within each plot were marked from a template of randomly generated points. Two different templates were used for each density, and these were applied equally between the two soil treatments. Plots were weeded of all volunteer seedlings and watered about six times weekly using portable lawn sprinklers placed in different locations around the perimeter of the garden.

Midseason measurements—Thirty days after transplanting, ten plants in each plot were selected at random for nondestructive morphological measurements of size: plant height, width of the largest leaf, maximum canopy width (leaf tip to leaf tip at the canopy's widest point), and total leaf number. Because transformation failed to normalize raw data taken from individuals within populations, a mean value per plot was calculated for each parameter, and plot level means were used as dependent variables in ANOVA. The independent variables soil treatment (heterogeneous vs. homogeneous) and density were treated as fixed effects in these and all other analyses.

Harvests—The experiment was harvested after 70 d, when many flowers had initiated fruits but no fruits had released seeds. Each plant was divided into vegetative (stems and leaves) and reproductive biomass (flowers, fruits, and peduncles) and the parts air-dried in a greenhouse before being dried to constant biomass in a 70°C oven. Mass of reproductive and vegetative parts was measured separately, to the nearest 0.01 g. To avoid edge effects, plants in the outermost 8.0 cm of each plot were not harvested. Dead individuals found at harvest were recorded, but because they had dropped all leaves their biomass was not included in the statistical analyses of population size structure described below. Percentage mortality was analyzed as a function of soil treatment and population density using the SAS CATMOD procedure for log linear analysis (SAS, 1985).

From the masses of these harvested individuals, the following measures of productivity and size variation among individuals were calculated for each plot: total biomass, mean individual biomass, the coefficient of variation in biomass, and the total biomass of the five largest

TABLE 1. *F* values from ANOVA for nutrient concentration and pH (Fig. 1). Soil type was defined as a fixed effect, batch as random. Mean squares can be calculated from Error MS and *F* values. Degrees of freedom are in parentheses. Degrees of freedom for Error MS = 18 for all nutrients except N where df for Error MS = 30.

Dependent variable	Soil type (2)	Soil batch (5)	Type × Batch (10)	Error MS
N	42.459***	2.701*	2.875*	11.266
K	28.889***	0.950	1.293	0.002
P	64.749***	3.997*	0.798	819.472
Mg	16.062***	0.135	1.478	0.100
pH	3.592	5.200**	1.471	0.008

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

individuals. The latter measure was used because of the expectation that most of the population biomass would be concentrated in the few largest plants. These parameters were analyzed as a function of soil treatment and density in ANOVA (Statsoft, 1994).

The effect of local soil type on plant biomass was examined in plots with the heterogeneous soil treatment. Plants were separated into three categories according to whether their stem was located within a high nutrient cell, a low nutrient cell, or within 2.0 cm of a high nutrient/low nutrient interface. For each plot, plant biomass was compared among stem locations by ANOVA using mean plant biomass in each soil type as the dependent variable and soil type (random effect), density (fixed effect), and population nested within density (random effect) as the independent variables (SAS, 1985).

Nine experimental plots were omitted from all analyses. These included six plots planted a week later than the others because insufficient seedlings were available at the first planting; mean plant biomass in those plots was substantially lower than in other plots of the same density. Plants in three additional plots located in the southwest corner of the experimental garden were visibly yellowed and stunted in growth, presumably due to inadequate water drainage. After excluding these plots, a minimum of four replicate populations of each density and soil treatment combination remained in the analyses.

Soil analyses—In order to determine whether heterogeneity persisted throughout the growing season, soils were sampled for nutrient analyses when plants were harvested. In heterogeneous plots, two cores (2.5 cm in diameter × 10 cm deep) were taken from each of the two soil types in randomly selected locations. Two cores were similarly taken from each homogeneous soil treatment plot. Soil cores were pooled by soil type (high nutrient, low nutrient, or mixed soil) and the batch in which the soil was originally mixed. Two replicate samples were taken from each of these pooled soils for nutrient analysis. The Pennsylvania State University Agricultural Services Laboratory performed measurements of K, P, Mg, and pH. Total mineralizable N, which correlates well with nitrogen availability (Page, Miller, and Keeney, 1982), was analyzed in our laboratory using the anaerobic incubation methods of Waring and Bremner (1964). Nutrient levels were compared among soil types (fixed effect) by ANOVA with soil mixing batch as a second independent (random) variable.

The high nutrient, low nutrient, and mixed soils were also examined for differential effects on plant growth using potted individuals of *A. theophrasti* as a bioassay. Fourteen day-old seedlings were planted individually in 30.5 cm diameter × 30.5 cm deep pots filled with a single soil type. A large pot size was used in order to minimize spatial constraints on rooting area. The 15 replicate pots of each soil type were randomly interspersed in two rows alongside the experimental garden. Plant height, canopy width, width of the largest leaf, and leaf number were measured at 28 d and again at 35 d after transplanting. These morphological parameters were analyzed as a function of soil type by a repeated-measures one-way ANOVA. The plants were harvested after 70 d and dried to constant biomass. Mean plant biomass was compared between low nutrient and mixed soil and between mixed and high nutrient soil using the Mann-Whitney *U* test.

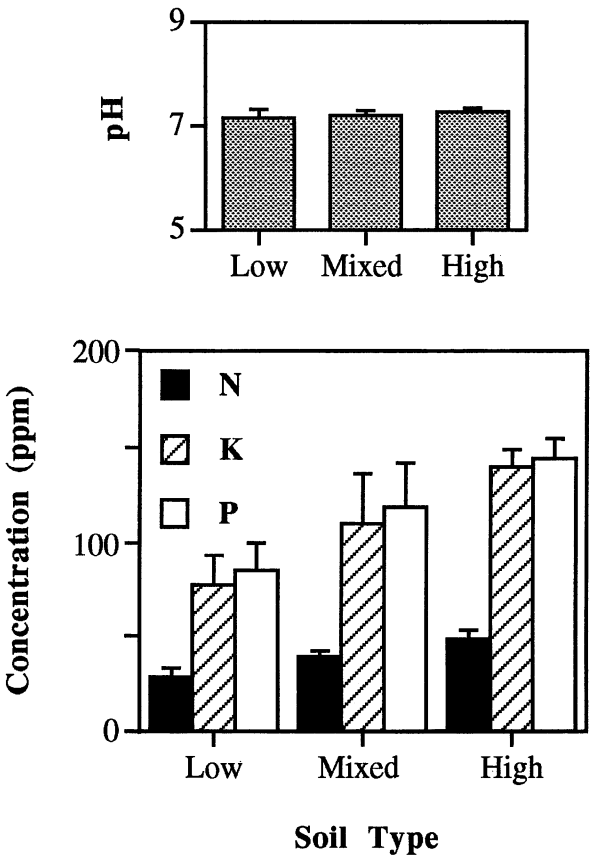

Fig. 1. Nutrient levels and pH compared for the low and high nutrient soils of the heterogeneous soil treatment and the mixed soil of the homogeneous soil treatment. Levels of Mg are given in the text. Error bars represent 1 SD.

RESULTS

Soil analyses—Nutrient levels at the end of the growing season differed greatly among the soil types used in our experiments, but pH did not (Table 1). Actual levels of measured soil parameters are shown in Fig. 1 except for Mg, which was present in much greater concentrations than the other nutrients: $\bar{X}$ (SD) = 210.00 (30.96), 273.96 (63.72), and 316.08 (12.84) ppm for the low, mixed, and high nutrient soils, respectively. Planned comparisons (Statsoft, 1994) verified that the high nutrient soil differed from the mixed soil which differed from the low nutrient soil, for all nutrients measured ($P < 0.02$ for all pairwise comparisons). In general, high nutrient soils contained about 70% higher nutrient levels than low nutrient soils. Phosphorus, N and pH differed among the batches in which the soil was mixed (Table 1). For all three variables, only one soil batch was statistically distinguishable from any of the other five batches according to the Student-Newman-Keuls test ($P < 0.05$). The most extreme value occurred in a different batch for each of the three variables, indicating that no one soil batch differed greatly from the others. The magnitude of differences among batches was also small. For example, mean

TABLE 2. Repeated-measures ANOVA for morphological measurements made twice on potted plants grown exclusively in one of the three soil types used in the population-level experiment. Error mean squares can be calculated from the mean squares and F values given. Degrees of freedom are in parentheses. Soil type, date of measurement, and the soil type × date interaction were significant ($P < 0.001$) for all dependent variables.

Dependent variable	Soil treatment (2)		Date of measurement (2)		Soil × Date (2)	
	MS	F value	MS	F value	MS	F value
Plant height	723.758	361.878	478.403	614.776	162.289	81.440
No. leaves	35.438	54.051	24.544	83.584	3.811	12.978
Canopy width	1370.289	104.728	801.025	180.166	131.558	29.590
Maximum leaf width	186.369	111.848	97.136	202.467	13.919	29.013

pH values ranged between 7.18 and 7.27 for five soil batches, while the value of the sixth was slightly lower at 7.05.

Results of the bioassay experiment corroborated differences in fertility levels among soil types. Nondestructive size measurements made after 28 and 35 d revealed significant variation among soil types for all plant size parameters (Table 2). Posthoc comparisons (Student-Newman-Keuls test; $P < 0.001$) revealed consistent differences between plants in low nutrient vs. mixed soil and between plants in mixed vs. high nutrient soil. Only canopy width is presented here (Fig. 2) because graphs of other measured parameters were nearly identical. Significant soil type × measurement date interactions for all parameters reflect higher plant growth rates with higher levels of nutrients (Table 2). Three plants in the mixed soil and four in the high nutrient soil died after the midseason measurements. Mortality was apparently caused by a toxic insecticide applied to a nearby nest of hornets. At harvest, the dry biomass of the remaining plants was $\bar{X}$ (SD) = 1.01 (1.0), 5.44 (5.20), and 6.57 (3.98) for individuals grown in low, mixed, and high nutrient soils, respectively. Dry biomass differed between plants grown in low nutrient vs. mixed soil (Mann-Whitney U test; $U = 23$, $P < 0.001$), but not between those in mixed vs. high nutrient soil ($U = 46$; NS). Given the strong difference in plant growth among all three soil types early in the experiment, we question the result that final biomass did not differ between plants in mixed vs. high nutrient soil. Mortality reduced sample sizes, and we cannot be sure that the surviving plants, which were interspersed with the dead ones, were not also affected by the insecticide. Plants in the adjacent experimental plots appeared to be unaffected.

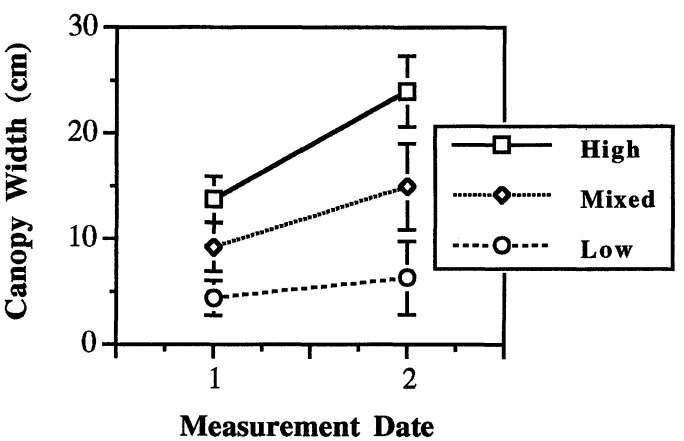

Fig. 2. Mean canopy maximum width for individuals growing exclusively in low nutrient, mixed, or high nutrient soil measured at 28 and 35 d after transplanting seedlings. Error bars represent 1 SD.

Midseason measurements—Soil treatment (heterogeneous vs. homogeneous soil) had no effect on the mean value per plot for plant height, the number of leaves per plant, or canopy width (Fig. 3; Table 3), but the mean plot level value of maximum leaf width was greater for populations growing on heterogeneous soils ($P < 0.05$). The size of all parameters except plant height decreased with planting density. The soil treatment × density interaction was not significant for any dependent variable.

Population measurements at harvest—Because vegetative and reproductive biomasses were highly correlated (Spearman rank correlation $r_s = 0.94$, $P < 0.001$), they were combined in population-level measurements of productivity and population size structure. The main effect of soil treatment was not significant for either mean plant biomass or total biomass per plot (Fig. 4; Table 4). Likewise, the size structure of the population was unaffected by soil treatment; neither the coefficient of variation in biomass nor the combined biomass of the five largest individuals in the population differed between homogeneous and heterogeneous soils (Figs. 4, 5; Table 4). The soil treatment × density interaction was significant ($P < 0.05$) for mean plant biomass and nearly significant ($P < 0.06$) for total biomass. This interaction reflects higher average biomass in the heterogeneous plots at intermediate (60) density only (Student-Newman-Keuls test; $P < 0.02$). All measured parameters except the combined biomass of the five largest individuals varied with planting density.

In heterogeneous soil treatment plots, plant biomass depended on stem location with respect to high and low nutrient patches ($P < 0.02$; Table 5). Plants whose stems were located within low nutrient cells were, on average, the smallest (Fig. 5). As indicated in the previous analysis, density significantly affected plant size, but the density × soil type interaction was not significant.

Overall mortality was <10%, but twice as many plants died in the homogeneous soil treatment plots at all three densities (Fig. 6; $\chi^2 = 6.77$, df = 1, $P < 0.01$). Mortality did not vary with density ($\chi^2 = 1.04$; df = 2), and the interaction between soil type and density was not significant ($\chi^2 = 0.23$; df = 2).

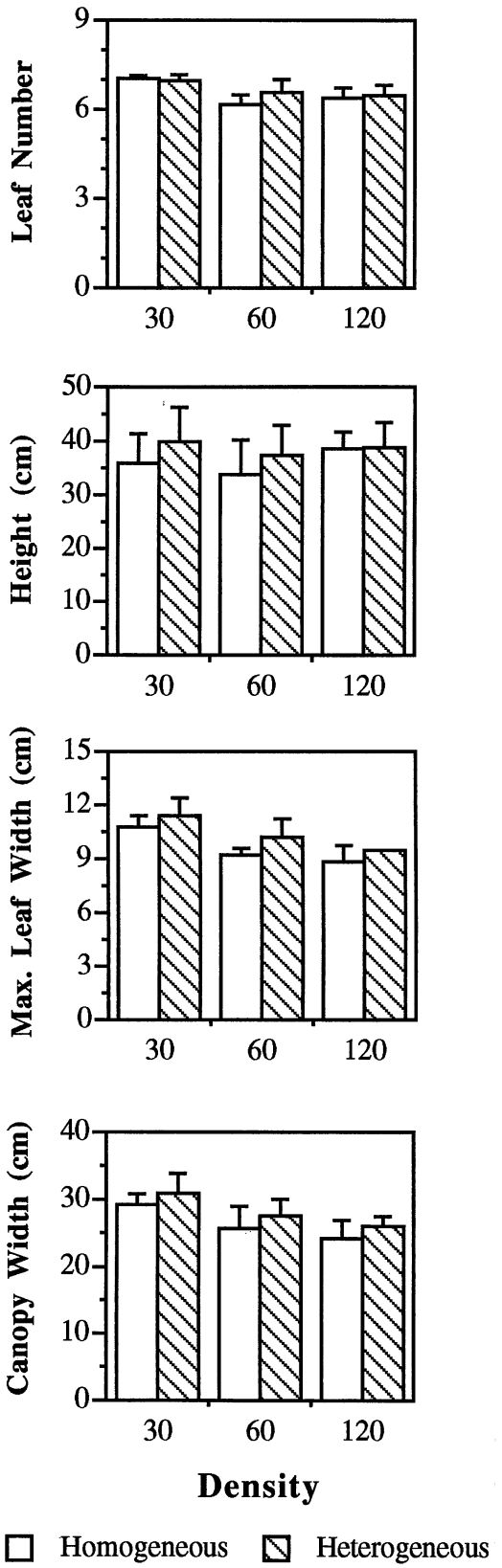

Fig. 3. Morphological measurements made at midseason on ten randomly selected plants per population. Values represent $\bar{X}$ (SD) of population level means.

TABLE 3. *F* values from ANOVA for morphological measurements made at midseason (Fig. 3). Mean squares can be calculated from Error MS and *F* values. Degrees of freedom are in parentheses.

Dependent variable	Soil treatment (1)	Density (2)	Soil treatment × Density (2)	Error MS (21)
Plant height	1.582	0.869	0.344	28.806
No. leaves	0.297	10.147***	1.346	0.101
Canopy width	3.313	8.130**	0.005	6.556
Maximum leaf width	5.343*	11.515***	0.103	0.722

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

DISCUSSION

Soil nutrient heterogeneity, comparable to levels of variation measured in nature (Jackson and Caldwell, 1993), was nearly inconsequential for populations of *A. theophrasti.* The spatial distribution of nutrients had little effect on mean plant performance or population size hierarchy. Planting density affected population parameters far more strongly than did the spatial distribution of nutrients. The low response to nutrient heterogeneity occurred even though the different soils used in this experiment differed in their ability to support plant growth. The results suggest that at the population level, nutrient availability was no greater in homogeneous than in heterogeneous soils.

In fact, populations growing on heterogeneous soils performed slightly better. This is based on plants in heterogeneous soils exhibiting a greater maximum leaf size at midseason across all three densities, and populations of intermediate density on heterogeneous soils yielding a greater mean plant biomass at harvest. Using data from the bioassay experiment, maximum leaf size at 35 d after transplanting was highly correlated with dry biomass when plants were harvested after 70 d (Spearman rank correlation $r_s = 0.839$), indicating that at midseason plants on heterogeneous soils were slightly larger. These results suggest that plants may benefit when nutrients are patchily distributed. Agricultural experiments with potted plants provide evidence that plants can exploit small nutrient patches. Experiments with several species demonstrate that both nutrient uptake and plant growth can increase as the same nutrient quantity is added to smaller fractions of the soil volume (Anghinoni and Barber, 1980; Borkert and Barber, 1985).

The interaction between planting density and soil treatment for mean plant biomass is difficult to interpret. The effect of heterogeneity on final biomass does not appear to be very strong since it occurred at only one density. Based on results of the agricultural experiments, which used isolated plants in pots, we would have expected an effect of heterogeneity at the lowest planting density, where competition should be least important. Not enough is known about how a plant's neighbors alter its response to nutrient heterogeneity for us to offer an explanation for our result.

The higher mortality on homogeneous soils serves as another indicator that populations on heterogeneous soils performed, as a whole, slightly better. The twofold difference in mortality between the two soil types may not be of great ecological significance since mortality was

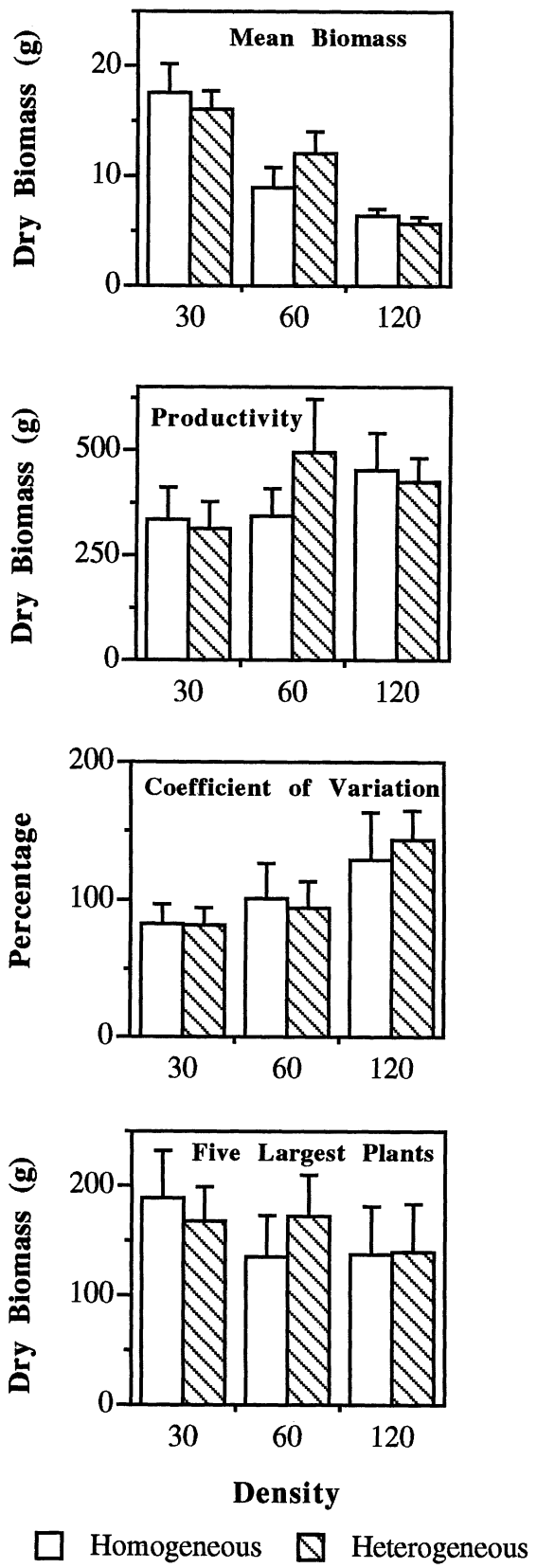

Fig. 4. Measures of final aboveground biomass from harvested plants. Mean biomass is the mean for individual plants. Productivity is the total biomass of all plants. Values represent $\bar{X}$ (SD) of population level means.

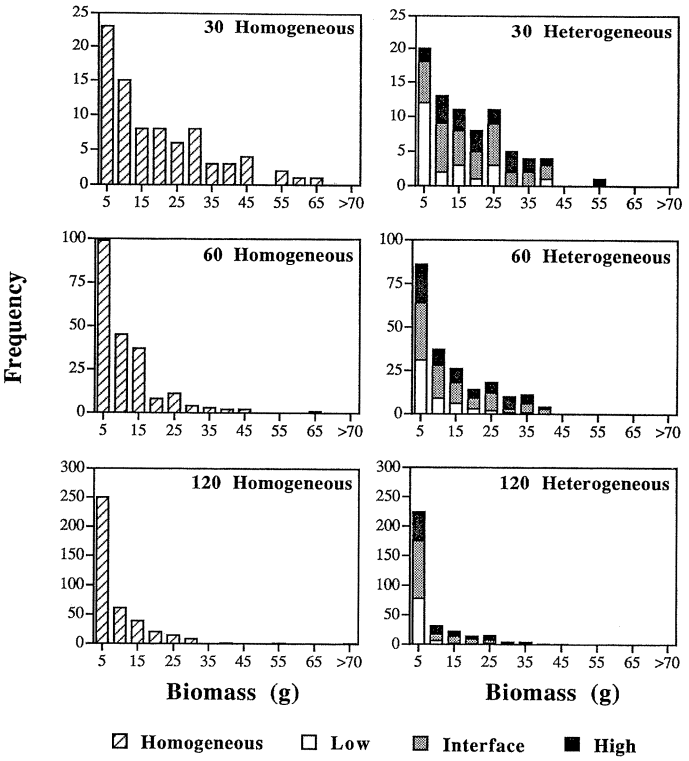

Fig. 5. Histograms of total aboveground biomass for populations (plots) pooled by soil treatment and density. For heterogeneous soil treatment plots, individuals are grouped by the soil type in which their stem was located. The three possible stem locations were high nutrient cells, low nutrient cells, or within 2.0 cm of a high nutrient/low nutrient interface.

still very low, but the pattern is consistent across planting densities. Our ability to detect mortality apparently did not differ between soil treatments because we accounted for the same total numbers of individuals in both heterogeneous and homogeneous soils. Because mortality did not increase with density and because there was no change in population size skewness associated with differential mortality, death must not have resulted directly from interactions with other individuals. Some density-independent factor might account for this pattern. The probability of death might have been related to differences between soil treatments in plant nutrient status. For example, if the smallest individuals in the heterogeneous soil treatment plots had access to at least one high nutrient block, they may have actually experienced greater nutrient supply rates than the smallest individuals on homogeneous soil. The nutrient content of plant tissues is known to affect susceptibility to pathogens (Matson and Waring, 1984), one possible cause of density-independent mortality.

An important result from this experiment is the finding that local soil nutrient levels in heterogeneous plots influenced plant size rankings within populations even though overall population size hierarchies did not differ between heterogeneous and homogeneous soils. Thus, soil nutrient heterogeneity influenced whether a particular individual became dominant or subordinate within the population even though the overall population size structure was unaffected. Local soil nutrient levels immedi-

TABLE 4. *F* values for population-level parameters calculated from harvested plants (Fig. 4). Mean squares can be calculated from Error MS and *F* values. Degrees of freedom are in parentheses.

Dependent variable	Soil treatment (1)	Density (2)	Treatment × Density (2)	Error MS (21)
Mean biomass	0.176	80.410***	4.716*	3.069
Total biomass	1.037	4.344*	3.379	7193.833
Coefficient of variation	0.066	12.625***	0.525	526.778
Biomass of five largest plants	0.136	1.873	1.060	1819.043

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

ately surrounding the root system must have affected seedling growth rates with size differences established early in growth becoming more pronounced through dominance and suppression as individuals competed over time. Dominance and suppression are characteristic of asymmetric competition for light (Harper, 1977; Weiner, 1990), but belowground competition may not be asymmetric (Wilson, 1988; Weiner, 1990; Gerry and Wilson, 1995). Any sort of environmental heterogeneity that influences seedling growth rates or emergence times (Ross and Harper, 1972; Hartgerink and Bazzaz, 1984) should similarly affect final plant size in a population of competing individuals.

Although seedlings may have perceived the soil heterogeneity used in this experiment as coarse grained, adult plants apparently did not. Based on the lengths of roots we excavated from within the experimental plots, we estimated that the entire root system of a large adult plant traversed at least 16 of the 8 × 8 cm blocks used in our experiment. Blocks of high nutrient soil contained more fine roots (J. Cahill, personal observation) than did low nutrient blocks, as reported for several other species (Hackett, 1972; Drew and Saker, 1975; Eissenstat and Caldwell, 1988; Jackson and Caldwell, 1989; Campbell et al., 1991; Gross, Pregitzer, and Burton, 1993). Rooting densities were far greater in the 10 cm deep experimental soil than in the hard-packed clay subsoil, and the taproots of some individuals even turned horizontally where they encountered the clay layer. Mycorrhizae were abundant in the plots (J. Cahill, personal observation) and may have also played a role in enabling plants to forage successfully in the heterogeneous soils (St. John, Coleman, and Reid, 1983).

The scale of heterogeneity could be critical to whether spatial variation in nutrient levels affects either intraspecific or interspecific interactions (Pacala, 1987; Biondini and Grygiel, 1994). We deliberately chose to work with a scale of heterogeneity smaller than the root system of an adult plant so that nutrient availability would not likely differ among individuals. The distinction between this scale of heterogeneity and larger scales that necessarily result in plant-to-plant differences in nutrient availability, as is assumed in Tilman's models (Tilman, 1982, 1988; Tilman and Pacala, 1993), is an important one.

Some workers predict that small-scale heterogeneity will influence interspecific competitive relationships because species differ in their root responses to nutrient patches (Fitter, 1982; Grime, Crick, and Rincon, 1986; Jackson and Caldwell, 1989; Campbell et al., 1991; Gross, Peters, and Pregitzer, 1993) and because experimental evidence shows that plants can compete for localized nutrient pools (Caldwell et al., 1985; Caldwell, Manwaring, and Jackson, 1991). Campbell et al. (1991) suggest that a trade-off exists between the ability of a species to harvest nutrients from small-scale patches and the scale over which its root system forages. By this reasoning, annuals like *A. theophrasti* should be more capable of harvesting nutrients from localized patches than larger perennials. On the other hand, Gross, Pregitzer, and Burton (1992) and Gross, Peters, and Pregitzer (1993) speculate that species arriving later in the succession of old fields should be better able to handle the nutrient heterogeneity that becomes more pronounced in that habitat over time. Our finding that heterogeneity is inconsequential to the growth of *A. theophrasti* is inconsistent with such a pattern; *A. theophrasti* is common in newly abandoned fields that are relatively homogeneous environments.

TABLE 5. ANOVA examining effects of density and local soil type (high nutrient, low nutrient, or interface) on mean plant biomass per soil type per plot for the heterogeneous soil treatment only. Plots are nested within density.

Source of variation	df	MS	*F* value	Significance level
Density	2	345.437	13.78	0.001
Plots (density)	10	13.279	0.53	NS
Soil type	2	150.886	6.02	0.02
Density × soil type	3	13.287	0.53	NS
Soil type × plots (density)	16	25.06		

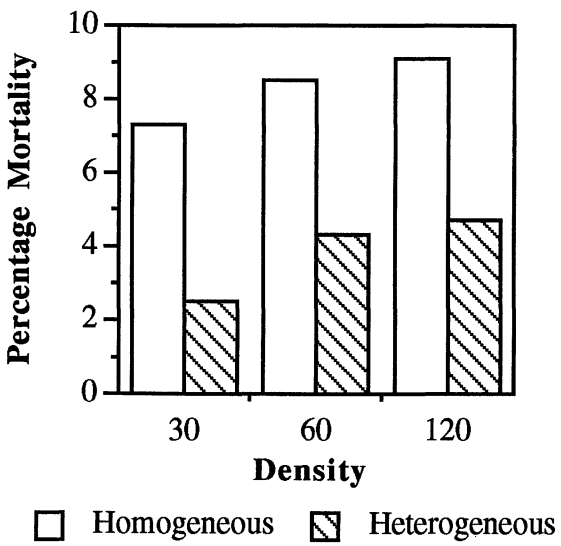

Fig. 6. Mortality expressed as the percentage of all individuals in each planting density and soil treatment combination.

Evaluating how small-scale heterogeneity affects overall plant performance is crucial to understanding its importance in affecting either interspecific or intraspecific competition. Many assumptions about the energy costs of nutrient uptake (Kovar and Barber, 1988; Gross, Peters, and Pregitzer, 1993), whether plants physiologically integrate their soil environment (Campbell et al., 1991; Biondini and Grygiel, 1994), and how small-scale heterogeneity affects competition and the composition of plant communities (Jackson and Caldwell, 1989; Campbell et al., 1991) seem to be based exclusively on how roots respond to nutrient patches. For heterogeneity to have important effects at the community level it must, for at least some of the competing species, affect vegetative performance or some other component of fitness. Our study evaluating plant growth and mortality suggests that soil heterogeneity at small scales could prove less important in affecting competition than is often thought. Future studies should extend our experimental approach to a wide variety of species and species mixtures and examine how vegetative and reproductive performance, population structure, and interspecific competition are affected by heterogeneity at other spatial scales.

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