

Decomposition Analysis of Competitive Symmetry and Size Structure Dynamics

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An analysis is introduced, based on the decomposition of relative growth rates, to examine the mode of competition (i.e. whether competition is symmetric or asymmetric), the size-dependence of growth, and their interdependence. In particular, the basis for two commonly held views is examined: (1) that the type of resource limitation determines the mode of competition, and (2) that asymmetric competition always leads to size-divergence between unequal competitors. It is shown that in field-grown millet plants, competition for light was symmetric at low density and asymmetric at high density. However, size variation at low density decreased during growth, because small plants had greater relative growth rates than larger plants. Size variation stayed constant at high density, since plants of all sizes had equal average relative growth rates. Based on these results and a general discussion, it is proposed that the type of resource limitation does not determine the mode of competition. Competition for light can be symmetric, and foraging for heterogeneously distributed soil resources can produce asymmetric competition below-ground. Furthermore, the mode of competition alone does not determine size structure dynamics. Size-dependence of resource conversion efficiency and allocation can modify the effects of resource uptake on growth.

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Key words: *Pennisetum americanum* 'Custer', mode of competition, size structure dynamics, plant growth analysis.

INTRODUCTION

An important component of annual plant fitness is determined by how fast a plant accumulates biomass between seedling emergence and the time of reproduction (Harper, 1967; Wall and Begon, 1985; Benjamin and Hardwick, 1986). Crowding reduces the average growth rate of individuals during vegetative growth, but it does not necessarily act on all individuals in the same way. In some instances crowding inhibits the growth of small individuals more strongly than the growth of larger individuals, so that populations develop large size inequalities (e.g., Edmeades and Daynard, 1979; Turner and Rabinowitz, 1983; Waller, 1985; Weiner and Thomas, 1986; Rice, 1990). In other instances, crowding does not appear to add growth rate variation and size inequality. These differences in the crowding response may have important consequences on the outcome of competition at several biological scales. For example, it has been suggested that large size variation caused by crowding maintains genetic diversity in populations (Biere, 1987; Thomas and Bazzaz, 1993), stabilizes populations that would otherwise oscillate (Lomnicki, 1980; Watson, 1980; Pacala and Weiner, 1991), facilitates competitive exclusion (Fowler, 1988; Samson, Philippi and Davidson, 1992; Zobel, 1992) or (to the contrary) enables coexistence (Hara, 1992; Kohyama, 1992), or can do both, depending on other circumstances (Weiner and Conte, 1981; Schwinning and Fox, 1995). These diverse examples underline the importance of identifying general rules about the effects of crowding on population size structure.

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Whether or not crowding increases size variability in populations has been linked to the way in which resources are divided between competitors (Koyama and Kira, 1956; Kuroiwa, 1960; Ford, 1975; Harper, 1977; Gates, 1978; Aikman and Watkinson, 1980; Turner and Rabinowitz, 1983; Weiner, 1986; Weiner and Thomas, 1986; Firbank and Watkinson, 1987). Two main cases or 'modes of competition' (Yokozawa and Hara, 1992; for review see Weiner, 1990) have been distinguished. Resources can be divided in proportion to the biomass of competing individuals (relative symmetric competition), or they can be divided so that large competitors get more than their proportional share (asymmetric competition). Based on this distinction, two generalizations about the relationship between crowding and size structure have been put forward. First, competition for light is generally asymmetric (but see Yokozawa and Hara, 1992) and competition for soil resources is generally symmetric. Second, crowding generates size variability in populations only if individuals compete asymmetrically.

The second generalization is based largely on the assumption that differences in the rates of resource uptake determine differences in the growth rates of plants. To my knowledge, this has no direct experimental support based on the independent measurement of resource uptake and growth. The first generalization originates in our understanding of the mechanisms of light, water and nutrient uptake. Large plants can pre-empt light from smaller neighbours by overtopping and shading (e.g. Ford, 1975; Diggle, 1976; Hara, 1986*a*), but no similar mechanism of resource pre-emption exists for water and nutrients. A small number of experiments indeed showed that size variability does not increase with density if plants compete for below-

ground resources (Newberry and Newman, 1978; Weiner, 1986). However, these experiments were conducted in highly homogeneous artificial soils and different results may be expected in heterogeneous natural soils.

Here, the bases for these two generalizations are critically examined using the technique of growth rate decomposition. This method was used previously to examine the contributions of different physiological and morphological characteristics on plant growth (West, Briggs and Kidd, 1920; Potter and Jones, 1977; Hunt, 1981, 1990). It is used here to determine factors that contribute to the size dependence of resource uptake and growth. First, the analysis is introduced in theory. Then, its application is illustrated using data obtained from a field experiment.

THEORY

There has been some confusion in the literature about the terms ‘mode of competition’ or ‘competitive symmetry’. Some authors (e.g. Weiner, 1990) refer with these terms to the size-dependence of resource uptake, while others (e.g. Hara, 1988) refer to the size-dependence of relative growth rates. To make things worse, many theoretical treatments implicitly set the rate of resource uptake proportional to the growth rate, so that there is no distinction between the two (e.g. Ford and Diggle, 1981; Bonan, 1988; Miller and Weiner, 1989). Below, the size-dependence of resource uptake (which I call ‘mode of competition’) and resource utilization (as growth) are treated separately, then, the relationship between them is delineated.

The decomposition of resource uptake

Decomposition is the mathematical expansion of a term into two or more factors. The mathematical trick is quite simple but useful if it helps to clarify how a complex phenomenon, in this case resource uptake and growth, is composed of several less complex aspects.

The resource uptake rate of an individual plant depends on three aspects: how much resource is available in the environment, how much space is occupied by the plant, and what fraction of the available resource is taken up from that space. Stated as a decomposition this amounts to:

$$\frac{1}{B_x} \cdot \frac{dU_x}{dt} = \frac{1}{V_x} \cdot \frac{dI_x}{dt} \times \frac{V_x}{B_x} \times \left(\frac{dU_x}{dt} / \frac{dI_x}{dt} \right) \quad (1)$$

where B_x is the biomass involved in the uptake of resource X , V_x is the space occupied by B_x , the time derivative of U_x is the rate of resource uptake and the time derivative of I_x is the rate of resource supply. To simplify the following discussion, I call the first term of this decomposition ‘resource availability factor’, R . The second term may be called the ‘allometry factor’, A ; and the last one the ‘resource capture efficiency factor’, C . The left side of the equation is the ‘relative rate of resource uptake’ and can be abbreviated as S . Thus, eqn (1) can be restated simply as

$$S = R A C \quad (2)$$

Different cases of competitive symmetry are distinguished

by the size-dependence of resource uptake (Weiner, 1990; Hara, 1993), thus by a comparison of the resource uptake rates between individuals of different sizes. Usually, two modes of competition are distinguished (relative symmetry and asymmetry), but in the present analysis it is useful to distinguish three cases, depending on whether larger plants capture more, the same, or less resource per total biomass involved in resource capture than their smaller neighbours. A quick way to check the mode of competition is to calculate a symmetry index $\ln s$:

$$\ln s = \ln S_1 - \ln S_2, \quad (3)$$

where S_1 and S_2 are the relative resource uptake rates of plants 1 and 2 respectively. Assuming

$$B_1 \geq B_2, \quad (4)$$

where B_i is the total biomass of plant i , $\ln s$ indicates the mode of competition: if $\ln s > 0$ the larger plant captures more resource per unit biomass involved in resource uptake than the smaller plant (positively asymmetric competition); if $\ln s = 0$ large and small plants captures the same amount of resource per unit biomass (relative symmetric competition); if $\ln s < 0$ the smaller plant captures more resource per unit biomass than the larger plant (negatively asymmetric competition). Correspondingly, one can define indices characterizing the size dependencies of resource availability, space capture and resource capture efficiency:

$$\begin{aligned} \ln r &= \ln R_1 - \ln R_2 \\ \ln a &= \ln A_1 - \ln A_2 \\ \ln c &= \ln C_1 - \ln C_2 \end{aligned} \quad (5)$$

Thus,

$$\ln s = \ln r + \ln a + \ln c. \quad (6)$$

This formulation reveals that the mode of competition ($\ln s$) is not just determined by the size-dependence of resource capture efficiency ($\ln c$), but also by the size-dependence of resource availability in the occupied space ($\ln r$) and by the allometry of space capture ($\ln a$). These components can work in opposite directions and partly cancel one another. I show below that a resource capture efficiency advantage for larger plants ($\ln c > 0$) can be annulled by an allometric disadvantage ($\ln a < 0$).

The decomposition of growth

Complex physiological processes intervene between resource capture and resource utilization. Some can be expressed as factors in the decomposition of relative growth rates:

$$\text{RGR} = \frac{1}{B} \cdot \frac{dB}{dt} = \frac{1}{B_x} \cdot \frac{dU_x}{dt} \times \frac{B_x}{B} \times \left(\frac{dB}{dt} / \frac{dU_x}{dt} \right) \quad (7)$$

The first term in this decomposition is the relative rate of resource uptake, S [eqn (1)]. The second term may be called the ‘biomass partitioning factor’, P ; and the third term is the ‘resource-to-biomass conversion efficiency’, E . Restated in these simpler terms, eqn (7) is identical to

$$\text{RGR} = S P E \quad (8)$$

The ultimate determinant of the effect of crowding on population size structure, is the way in which plant neighbours affect each other's RGRs. If larger plants have greater relative growth rates than smaller plants, plant size variability (measured for example as the coefficient of variation) increases over time. If smaller plants grow relatively faster, plant sizes converge and size variability declines. In short (for $RGR > 0$) and with the same convention regarding the indices [eqn (4)]: if $\ln RGR_1 - \ln RGR_2 > 0$ the sizes of competitors diverge on a relative scale; if $\ln RGR_1 - \ln RGR_2 = 0$ the size relation of competitors is maintained; if $\ln RGR_1 - \ln RGR_2 < 0$ the sizes of competitors converge on a relative scale. This analysis assumes that all plants have positive growth rates. This restriction is perhaps not too limiting, since the greatest change on the size structure of annual plants often occurs during the early phases of stand development, before self-thinning, when growth is positive for almost all individuals (e.g. Hara, 1984, 1986b; Thomas and Weiner, 1989).

The size-dependence of the two new factors in eqn (8) can also be stated individually:

$$\begin{aligned}\ln p &= \ln P_1 - \ln P_2 \\ \ln e &= \ln E_1 - \ln E_2\end{aligned}\quad (9)$$

Therefore,

$$\ln RGR_1 - \ln RGR_2 = \ln s + \ln e + \ln p. \quad (10)$$

This formulation emphasizes that the mode of competition ($\ln s$) alone does not determine the difference in the relative growth rates of competitors.

MATERIALS AND METHODS

Experimental procedures

All experiments were conducted in the field at the University of Arizona experimental farm in Tucson, Arizona, USA in the months of June to October. The experiment of 1992 was aimed at estimating the light interception of individuals in neighbouring plant pairs. The paired design aimed to distinguish whether differences in the light interception of two plants were based solely on their own size or on the size of their neighbours as well.

Some results of a larger experiment conducted in 1991 are also presented which aimed at measuring the influence of seed size, seedling size, density and neighbour identity on the growth rates of individual plants. This experiment is described in detail elsewhere (Schwinning, 1994).

In both experiments, Pearl millet seeds (*Pennisetum americanum*) were planted in rows after the soil had been fertilized with 45 kg ha⁻¹ fertilizer (16:20:0, N:P:K) to ensure non-limiting nitrogen and phosphorus levels. The millet cultivar 'Custer' is a short, drought-tolerant and tillering C4 cereal plant. Mature plants are about 1.2 m tall and have between one and tens of tillers that develop fertile heads. The field was furrow-irrigated with reclaimed water (providing additional nitrogen) when natural rainfall did not suffice to maintain a wet soil. Experimental blocks were separated by high border rows to control the flow of irrigation water into blocks independently. Weeds were

effectively eliminated from the field through manual weeding or, when possible, through mechanical cultivation. As needed, plants were sprayed with biocide to limit predation damage from insect larvae.

In the plant pairs experiment (1992), three low density blocks and three high density blocks were positioned randomly in the field. Low density corresponded to 50000 plants ha⁻¹ or a within-row plant distance of 0.2 m. High density corresponded to 100000 plants ha⁻¹ or a within-row plant distance of 0.1 m. The between row distance was the same (1 m) in all treatments. Two weeks after planting, 36 pairs of millet plants were identified and marked in each block according to a visual classification into six pair categories: large/large (LL), medium/medium (MM), small/small (SS), large/medium (LM), large/small (LS), and medium/small (MS). These pairs had a minimal distance of 1 m, so that harvesting one pair would not affect any other pair. Plant pairs were harvested destructively twice during the season. Each time, at most one representative of each pair was randomly selected in each block. The first harvest was between 17 and 19 Jul., about 3 weeks after planting. Pairs were harvested such that the spatial distribution of their foliage could be determined. For this purpose, a three-dimensional radial grid of thin wire was constructed around each plant. The grid divided a canopy into stacked central cylinders with 10 cm diameter and 10 cm height, and stacked rings with 5 cm width and 10 cm height. The outermost ring had a diameter of 40 cm and the top of the grid was 80 cm above the ground. Once the grid was constructed, leaves were carefully clipped from the top down and the outside in. Leaf area from different segments was measured separately, using a Delta-T Devices Ltd. digital image analyser. Then, the combined above ground biomass was oven-dried and weighed.

The second harvest was 1 and 2 Aug., approximately 5 weeks after planting and shortly before the onset of reproductive growth. This time, only pairs of unequal size (LM, LS, and MS) were harvested from each block. A larger grid was constructed with concentric rings that increased in diameter by 20 cm and that were stacked at 20 cm distance above one another. The outermost ring had a diameter of 120 cm and the top of the grid was 80 cm above the ground.

In the 1991 experiment, the field was divided into four blocks. Each block consisted of a checker-board of 3 × 3 m randomly assigned patches. There were 15 low density millet patches and 15 high density millet patches (low and high defined as above). In addition, there were 15 single plant patches with only one millet plant in the centre of each patch. The size of only one millet plant (the 'focal' plant, located in the centre of each patch) was measured repeatedly using a non-destructive method. For reasons which are not important in the context of this study and which are explained elsewhere (Schwinning, 1994), each patch also contained one cowpea plant (*Vigna unguiculata*). These plants grew at a distance of at least 0.5 m from the focal millet plants and, since they were much smaller, had very little or no influence on the growth of focal millet plants.

Non-destructive size measurements were performed 1, 2, 3 and 4 weeks after planting. The above-ground biomass was estimated based on the product of plant height, width

of the widest leaf, and tiller number. This index was linearly and, with the exception of the first week, highly correlated with the oven-dried weight of millet shoots at each growth stage ($r^2 = 0.61$, $r^2 = 0.94$, $r^2 = 0.96$ and $r^2 = 0.88$ at 1, 2, 3 and 4 weeks after planting, respectively). These regressions were insignificantly different between densities. When all millet plants had fully matured, the focal plants were harvested and their vegetative shoot biomass was oven-dried and weighed.

Estimation of individual light interception in the 1992 experiment

To estimate the light interception of individual plants, a simple light interception model was used in combination with the empirically determined canopy leaf area distributions. The main assumptions of the estimation were: (1) leaf area is uniformly distributed within each measured canopy element; (2) the canopy extinction coefficient is uniform and (3) only the vertical component of light flux is regarded. The assumptions of uniform extinction coefficient and vertical light incidence angle are common to models which estimate light interception in canopies (e.g. Monsi and Saeki, 1953; Charles-Edwards, Doley and Rimmington, 1986; Hara, 1986*b*; Yokozawa and Hara, 1992). However, this model differs from others because it allows for non-uniform leaf area distributions unlike, for example, Hara's models (1986*a, b*) which are based on the assumption of spatially uniform plant size (and foliage) distributions.

The leaf area of plant pairs was mapped into a three-dimensional coordinate system. To both sides of the focal pair, more canopies were mapped into a row with distances 20 cm for low and 10 cm for high density. These neighbours of the focal pair were represented by randomly selected canopies of medium-sized plants which were harvested at the same time at the same density. Neighbourhoods to both sides of the focal pair were constructed symmetrically and identically for all pairs to reduce variation in light interception for any other reason than the differences in the leaf area distribution of the focal pair. Canopies did not overlap across rows.

The total light interception was estimated by determining the light interception in each cell of the three-dimensional grid using the Monsi equation (Monsi and Saeki, 1953) with the extinction coefficient 0.45 (based on the assumption of spherical leaf angle distribution and 10% leaf transmittance). The intercepted light within each cell was then partitioned among plant individuals in proportion to their leaf areas. Finally, the light interception for the two focal plants was determined by summing their light interception across all cells.

RESULTS

All significance tests were based on the Student's *t*-distribution with the criterion $P = 0.01$. *P*-values between 0.05 and 0.01 were called marginally significant.

Below, the states of plants in two consecutive experimental years are compared. This requires some justification, since the growth dynamics of plants in different years are never

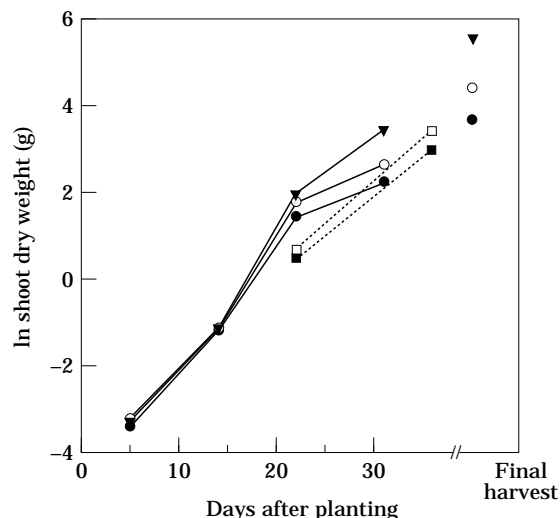


Fig. 1. The average ln-transformed shoot dry weight of selected individuals in both experimental years plotted against time. ▼: single plants, ○: low density plants, ●: high density plants in 1991; □: low density, ■: high density in 1992.

identical. In Fig. 1 the development of the average log-transformed dry weight of the selected individuals for both years is compared. Note that 3-week-old plants in 1992 were smaller than 3-week-old plants in 1991. However, the plant size data for both years fall very nearly onto a straight line, indicating that growth in the first 36 d was very nearly exponential with similar relative growth rates for plants in low and high density in both years. After 36 d plants accumulated little more biomass on a logarithmic scale.

The mode of competition for light

Three weeks after planting in the 1992 experiment, there was no significant difference in the average biomass of the selected plants in low and high density. Their average shoot dry weight was 2.4 g and average leaf area was about 600 cm². Leaf area, leaf area index (LAI, the ratio of leaf area over ground area) and leaf area weighted height (LWH, the sum of the proportions of the total leaf area in a layer times the height of a layer) were linearly related to biomass with regression coefficients that were insignificantly different between densities (Fig. 2). Five weeks after planting (Fig. 3), the average dry weight of the selected plants was 38 g for low density plants and 25 g for high density plants with 5300 and 4000 cm² average leaf area, respectively. At this stage, the allometries of leaf area and LAI were still linearly related to biomass with insignificantly different regression coefficients between high and low density; but the regression of LWH on plant biomass had marginally different slopes for low and high density, indicating that the height differences between plants of different sizes were generally greater at high density than at low density.

These morphological differences affected the division of light between individual plants. The mode of competition for light was analysed using eqns (1) and (6) with the allometry factor *A* expressed as the ratio of ground area

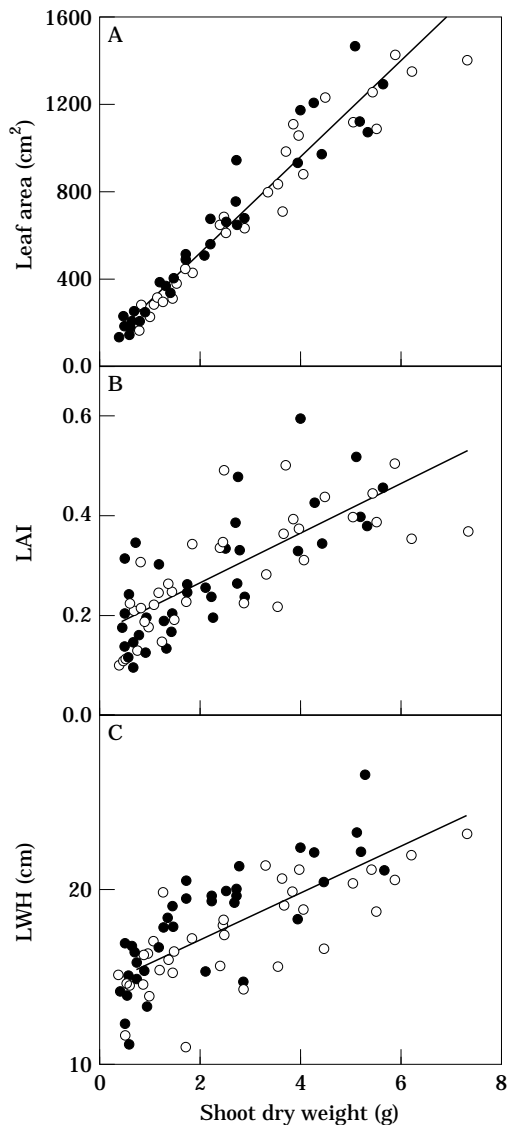


FIG. 2. Total leaf area (A), LAI (B) and LWH (C) of individuals plotted against shoot dry weight for 3 week old millet plants in 1992. ○: low density plants, ●: high density plants. Regressions were performed on the pooled data from both densities, as individual regressions were not significantly different.

cover to shoot weight (ground area cover is the measure of occupied space V_x) and the resource capture efficiency factor C expressed as the fraction of the incident light that is intercepted. The resource availability factor R is ignored, because all plants encountered the same amount of incident light per unit ground cover and therefore $\ln r = 0$. In Fig. 4, $\ln a$, $\ln c$ and their sum, the symmetry index $\ln s$ is plotted against the log of the biomass ratios of the neighbour pairs 3 weeks after planting.

There were no significant differences between any regressions for high and low density. $\ln a$ was negative for most pairs and decreased significantly with an increase in the biomass ratio. $\ln c$ was positive for most plant pairs and increased with the size difference between individuals. The net result of these opposing advantages was an about equal

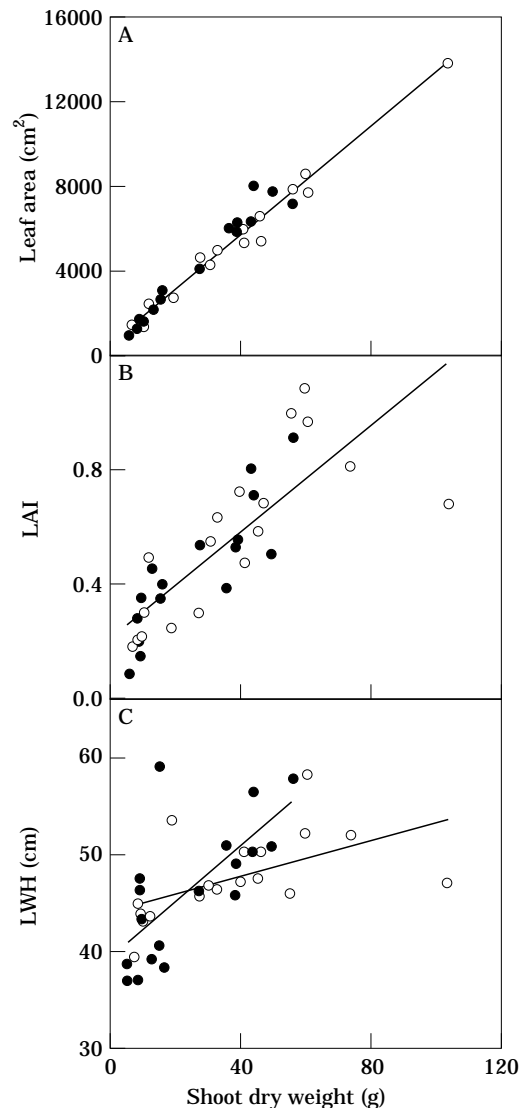


FIG. 3. Total leaf area (A), LAI (B) and LWH (C) of individuals plotted against shoot dry weight for 5 week old millet plants in 1992. ○: low density plants, ●: high density plants. Except for LWH, regressions were performed on the pooled data from both densities, as individual regressions were not significantly different. The regressions for weighted height were marginally different ($0.05 > P > 0.01$).

advantage for unequal plants in a pair: $\ln s$ had no significant trend with respect to size differences at both densities, and the average $\ln s$ was not significantly different from zero. This analysis illustrates that although larger plants captured a greater fraction of the available light (since they had greater LAI and were taller, see Fig. 2), they captured as much light per unit shoot biomass as smaller plants, because larger plants covered relatively less ground area than smaller plants.

The average light interception per unit leaf area was significantly lower at high density than at low density (Fig. 5). Thus, there was symmetric competition for light at high density. The two regression slopes were significantly (low density) or marginally significantly (high density) negative, but not significantly different from each other. Smaller

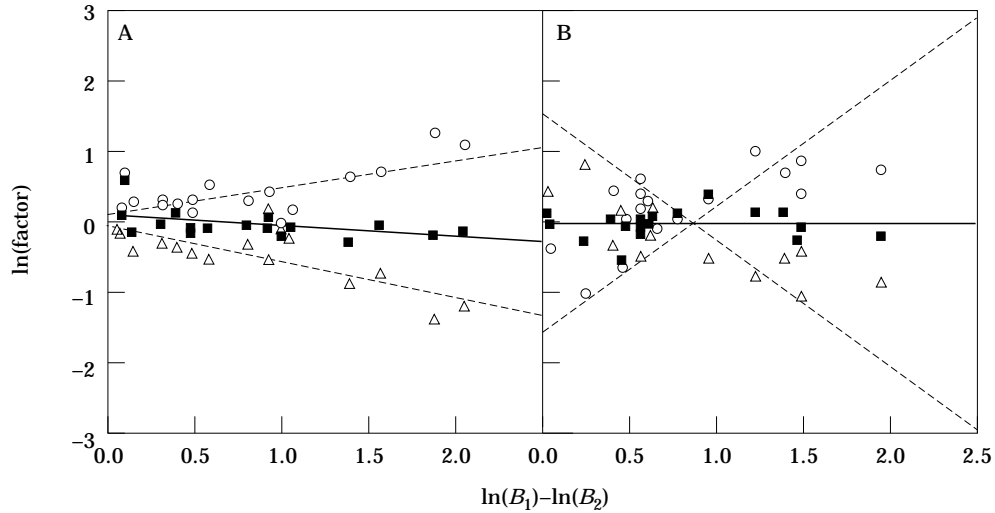


FIG. 4. $\ln c$ (\circ), $\ln a$ (\triangle) and their sum $\ln s$ (\blacksquare) plotted against the difference in the \ln -transformed shoot dry weight of plant pairs ($B_1 > B_2$) 3 weeks after planting. A, Low density; B, high density. (---) Regressions for $\ln c$ and $\ln a$, (—) regressions for $\ln s$.

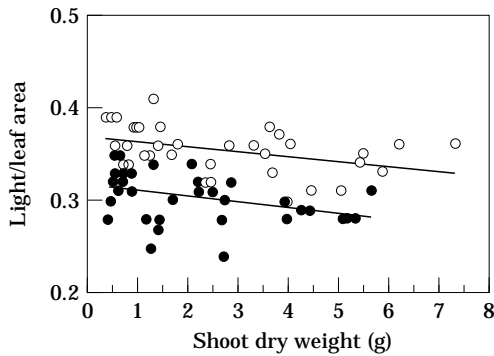


FIG. 5. The estimated light interception per unit of leaf area plotted against shoot dry weight 3 weeks after planting. \circ : low density plants, \bullet : high density plants.

plants intercepted slightly more light per unit leaf area than larger plants in both densities, because they self-shaded less. This size-dependence of light interception was produced by the absolute sizes of individuals and not by the size differences between competitors.

Five weeks after planting, the size-dependence of light interception had become significantly different between densities (Fig. 6). The regression of $\ln s$ had a marginally significant negative slope at low density and a positive slope at high density. The average value of $\ln s$ was not significantly different from zero at low density, but was positive at high density. This means that competition for light was relative symmetric for all but the most unequally-sized plant pairs in low density (then it was negatively asymmetric), but that competition for light was positively asymmetric at high

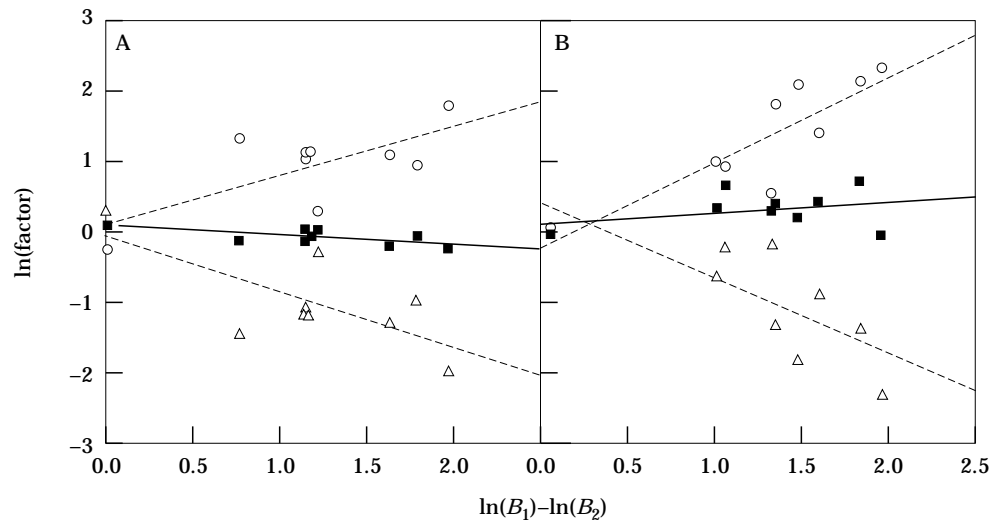


FIG. 6. $\ln c$ (\circ), $\ln a$ (\triangle) and their sum $\ln s$ (\blacksquare) plotted against the difference in the \ln -transformed shoot dry weight of plant pairs ($B_1 > B_2$) 5 weeks after planting. A, Low density; B, high density. (---) Regressions for $\ln c$ and $\ln a$, (—) regressions for $\ln s$.

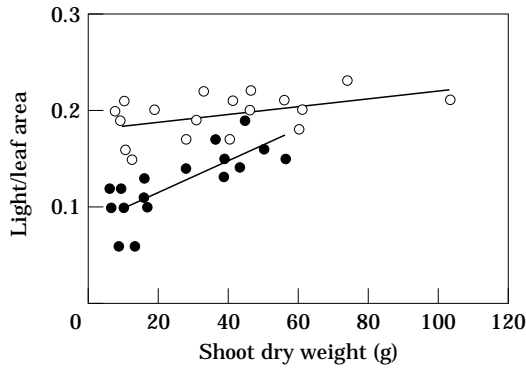


FIG. 7. The estimated light interception per unit of leaf area plotted against shoot dry weight 5 weeks after planting. \circ : low density plants, \bullet : high density plants.

density. Lack of statistical power made it impossible to distinguish which component(s) of $\ln s$ caused this density effect.

Figure 7 confirms that competition for light may have been positively asymmetric at high density. The regression slope of the light interception per unit leaf area on biomass was not significantly different from zero at low density and was positive at high density. Notice that relative light interception was most different between small plants in high and low density, while the largest plants at high density captured about as much light as similarly sized plants at low density.

Size-relative growth

Average RGRs were not different between densities during the second week of growth in 1991, but they were significantly different during the third week of growth (single plants: 0.391 d^{-1} , low density: 0.368 d^{-1} , high density: 0.329 d^{-1}). This supports that plants had started to compete sometime between 2 and 3 weeks after planting. During the third and fourth week of growth, the regressions of RGR on shoot biomass at low and high density had significantly or marginally significantly negative slopes (Fig. 8A, B), indicating that small plants had greater relative growth rates than large plants. However, during the remainder of the growing season the size-dependence of growth diverged dramatically between high and low density (Fig. 8C). At high density, the regression slopes for high density plants was not significantly different from zero, but at low density and for single plants, the slope was negative. The difference between the regression slopes for high and low density was highly significant.

Consistent with these differences in the size-dependence of growth, the coefficient of variation decreased between the seedling stage and maturity in single and low density plants (from 56 to 33% and from 48 to 33%, respectively), but stayed constant in high density plants (from 59 to 62%). Thus, even though competition for light was positively asymmetric at high density 5 weeks after planting, as seen in the pairwise (Fig. 6) and in the individual comparison (Fig. 7), large plants had no growth rate advantage and no size variation was generated; and although competition for

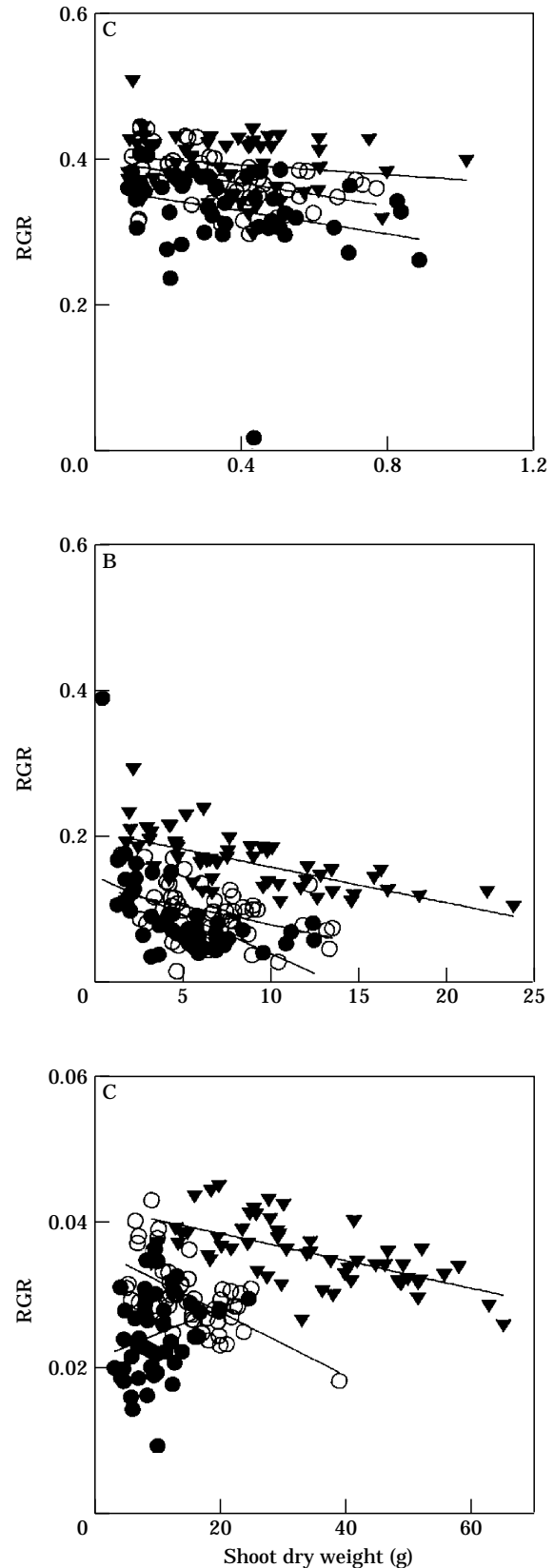


FIG. 8. The relative growth rates (RGR in d^{-1}) of individuals plotted against shoot dry weight during the third (A), the fourth (B), and the last 8 weeks (C) after planting. \blacktriangledown : single plants, \circ : low density plants, \bullet : high density plants.

light was symmetric at low density, smaller plants had a growth rate advantage and plant sizes converged during growth.

DISCUSSION

Does the mode of competition depend on the type of limiting resource?

The data presented in this study suggest that competition for light can be symmetric (or negatively asymmetric) early in growth or throughout growth at low density. Estimation of the light interception of neighbouring individuals indicated that, 3 weeks after planting, light interception had become significantly reduced at high density. Although large plants intercepted a greater fraction of the available light per unit ground area ($\ln c > 0$), they occupied less ground relative to their size ($\ln a < 0$), so that overall, large plants had no competitive advantage over smaller plants ($\ln s = \ln a + \ln c = 0$). Five weeks after planting, there were greater height differences between high density plants than between low density plants (Fig. 3C) and this suggests that the resource capture efficiency advantage of large plants had come to outweigh their allometry disadvantage at high density ($\ln s = \ln a + \ln c > 0$), producing asymmetric competition, but not at low density.

Two sources of potential error in the light interception estimation may be important. First, the light extinction coefficient may have been estimated inaccurately. However, the results did not fundamentally differ for extinction coefficients between 0.25 and 0.85. Consistent with the results of Hara (1986*b*), an increase in the extinction coefficient resulted in an increase of the average symmetry index $\ln s$ at high density (5 weeks after planting), but at low density, variation in the extinction coefficient had very little effect on $\ln s$. Second, error in the light interception estimation may have resulted from considering only the vertical component of light flux. The experimental site was located at a latitude of 32° N where this assumption is quite adequate. However, since the populations in this study were planted in rows, a small fraction of light also entered individual canopies from the sides. In general, height differences between individuals are less important for the interception of light from lateral incidence angles. Thus, if all incidence angles of light had been considered, competition

for light would have been estimated less asymmetric at high density and equally symmetric at low density. Both sources of potential error would therefore affect the estimated degree of positively asymmetric competition at high density. But the main result, that high and low density millet populations differed in the mode of competition, would remain.

The experiment suggests that population density has to exceed some threshold, before competition for light becomes asymmetric. A recent study on the size-relative growth in pine trees (*Pinus sylvestris*) confirms this hypothesis. Stoll, Weiner and Schmid (1994) found that pines in a 45 year old stand appeared to compete almost symmetrically and that size variation decreased during stand development. This unusual finding for a tree population (see, in contrast, Ford and Diggle, 1981; West and Borough, 1983; Kohyama, Hara and Tadaki, 1990) was attributed to low density: even though competition was clearly detectable, it was considered too weak to generate positively asymmetric competition.

The reason for the density threshold is a shift from predominant self-shading (at low density) to predominant neighbour shading (at high density). To see this, consider two populations (Fig. 9). Assume that the average stand LAI is the same for the two populations (according to the constant yield law), but there are fewer plants with dense, non-overlapping canopies in population 1 and more plants with less dense, but overlapping canopies in population 2. Competition for light is negatively asymmetric in the first population, if large plants suffer more self-shading than smaller plants, but positively asymmetric in the second population, because larger plants can outshade smaller neighbours, and self-shading is weaker. Notice that the argument does not depend on differences in the LAI, but only on the degree of canopy mixing which is assumed to be greater at higher density. Models that do not take different degrees of canopy mixing into account (e.g. Hara, 1986*a, b*) can predict a density threshold for asymmetric competition only if populations at different densities have *qualitatively* different vertical foliage distribution (generating, for example in Hara's (1984) terminology, a linear $G(t, x)$ function at low density and a convex function at high density).

There is no process of resource pre-emption, similar to shading, in the soil. However, eqn (6) suggests another

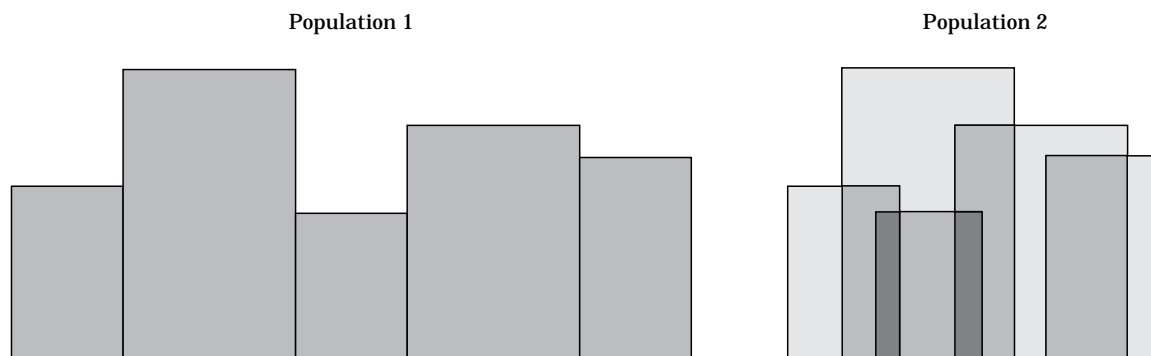


FIG. 9. A comparison of two populations with the same average LAI, the same average vertical foliage distribution, but different planting densities: plants in population 1 have high individual LAI and do not overlap; plants in population 2 have half the individual LAI, but twice as many plants per unit ground. Competition for light is negatively asymmetric for population 1 and positively asymmetric for population 2.

mechanism for positively asymmetric competition that is mediated by a size-dependence of resource availability ($\ln r$).

Soil resources are almost always heterogeneously distributed in the field, and roots are well known to respond to this heterogeneity by concentrating in areas of high water or nutrient availability (Grime, 1979; Crick and Grime, 1987; Jackson and Caldwell, 1989; Gersani and Sachs, 1992; Grime, 1994). If the ability of root systems to 'find' resource-rich patches depends on total plant biomass, perhaps because they 'sample' a greater soil volume or they have more energy reserves to support a 'search', then large plants would enjoy greater average resource availability. Indeed, if plants optimize growth by the physiological integration of parts experiencing different local environments as some models claim (e.g. Caraco and Kelly, 1991), larger plants should have an advantage because they can optimize resource capture across a larger range of micro-habitats, whereas smaller plants with limited access to micro-habitat variation, have limited ability to optimize. This mechanism of asymmetric competition may equally apply to a patchy light environment, since many plants also have the ability to seek high light environments (Smith and Morgan, 1983; Cosgrove, 1986; Smith, 1986; Novoplansky, Cohen and Sachs, 1989; Schmitt and Wulff, 1993; Ballare, 1994). Though this new mechanism for asymmetric competition is still speculative, it does not invoke unknown plant capabilities and its existence could quite easily be tested experimentally.

The size-dependence of growth does not depend on the mode of competition alone

In the present experiment, competition for light was positively asymmetric at high density, yet there was no indication that the RGRs of large plants were at any time greater than the RGRs of smaller plants. Competition for light was symmetric at low density, yet small plants had greater average RGRs than larger plants. These discrepancies between the size-dependencies of light interception and of growth may just indicate that growth did not at all depend on light interception. This is unlikely, however, since the plants in this study had C4 photosynthesis (which saturates at very high light levels) and were growing in usually well-watered and fertilized soil. Moreover, it is uncanny that the regression slopes of light interception (Fig. 7) and of RGR (Fig. 8C) on biomass *differed* similarly between high and low density and that this difference appeared at about the same time approximately 4 weeks after planting.

These observations are consistent with the idea that the mode of competition for light did affect the size-dependence of growth, but that other *intrinsic* factors systematically boosted the growth of smaller plants. In terms of eqn (10), $\ln e$ or $\ln p$ may have been negative. The present study did not resolve the reason behind the dissociation of light capture and growth. However, it can be resolved in principle by appropriate experimentation.

Many physiological processes can dissociate the size-dependencies of resource uptake and growth. Universally, plants must use a portion of all acquired resources to

maintain old biomass (Penning de Vries, 1975; Amthor, 1984). This resource cost of maintenance reduces the resource conversion efficiency of larger plants more than that of smaller plants ($\ln e < 0$), simply because they have more biomass to maintain. These and other mechanisms should give smaller plants a relative growth advantage. Individual differences in biomass allocation patterns can also affect the size-dependence of growth. Allocation to roots, stems, leaves and reproductive structures commonly vary with plant size and the environmental resource status. Some of these responses are interpreted as adaptive mechanisms to alleviate competitive suppression (e.g. Boardman, 1977; Hunt and Nicholls, 1986; Gutschick and Wiegand, 1988; Gleason and Tilman, 1992; Grime, 1994). If this is true, phenotypic plasticity of allocation should oppose the effect of positively asymmetric competition on growth ($\ln p < 0$).

But not all morphological density effects are passive responses to reduced resource availability. It has been shown that seedlings can respond to density, even before resources become depleted (Ballare, Scopel and Sanchez, 1990; Ballare, 1994; Küppers, 1994). Usually, plants become taller at higher density and reduce diameter. A trade-off between 'height growth' and 'diameter growth' appears to be quite common in plants (Geber, 1989; Hara, Kimura and Kikuzawa, 1991; Bonser and Aarssen, 1994; Weiner and Fishman, 1994). When plants become taller at the cost of covering less ground area, they increase self-shading and decrease the shading of neighbours. Such a morphologic density response should increase the density threshold for asymmetric competition for light and may indeed preclude the establishment of positively asymmetric competition altogether (Ballare, 1994).

Can a generalization be made?

Above, I questioned two commonly held views about the circumstances that generate asymmetric competition and size inequality in monospecific populations. I did not mean to suggest, however, that there are no correlations between a type of resource environment and its consequences on populations. For example, competition for light may very well be asymmetric more often than symmetric. I just wished to point out that there is no fundamental conceptual basis for these generalizations. To a large extent, the mode of competition and size structure dynamics in monocultures are governed by the plants' own plastic responses to density and heterogeneously distributed resources. In this regard, the mode of competition and size structure dynamics are properties of the populations themselves and therefore, subject to evolution. Perhaps more fundamental generalizations will be found by asking what circumstances favour the evolution of symmetric and asymmetric competition.

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