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Effects of competitive symmetry on populations of annual plants

Schwinning, Susanne, Ph.D.

The University of Arizona, 1994

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EFFECTS OF COMPETITIVE SYMMETRY ON POPULATIONS OF ANNUAL PLANTS

by

Susanne Schwinning

A Dissertation Submitted to the Faculty of the

DEPARTMENT OF ECOLOGY AND EVOLUTIONARY BIOLOGY

In Partial Fulfillment of the Requirements
For the Degree of

DOCTOR OF PHILOSOPHY

In the Graduate College

THE UNIVERSITY OF ARIZONA

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entitled Effects of competitive symmetry on populations of annual plants

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ABSTRACT

I examine the effects of competitive symmetry on annual plant populations through growth rate analysis, simulation modeling and experiments. I distinguish symmetric from asymmetric competition at several spatial and temporal scales. Local symmetry is defined by the way competitors divide resources in spaces where they overlap. Whole-plant symmetry is defined by the comparison of the total resource interception of competitors. Through plant growth analysis I show that local symmetry of competition is not identical to whole-plant symmetry of competition. Whole plant symmetry of competition also depends on the allometry of space occupancy and, under some circumstances, on the spatial distribution of the limiting resource. If plants capture space more slowly than they accumulate biomass, competition is symmetric at low density and asymmetric at high density. The local symmetry of competition determines the magnitude of the density response.

These results extend to the population-wide, seasonally-integrated level, where the symmetry of competition is expressed in the slope of empirical distribution-modifying functions (DMFs : regression functions of the log-transformed relative biomass increments of individuals between the seedling stage and maturity on the log-transformed seedling biomass). A

neighborhood-based simulation model shows that the slopes of empirical DMFs depend mostly on density and local competitive symmetry. Random variation of height, site quality and plant spacing affect DMFs only slightly, but affect population size structure greatly.

I confirm these simulation results in field experiments with populations of millet (Pennisetum americanum) and cowpea (Vigna unguiculata). Millet plants were grown isolated, at low density (10,000 plants ha^{-1}), and at high density (20,000 plants ha^{-1}). Cowpea plants were grown isolated, or as single cowpea plants within stands of low and high density millet. In both species and in two experimental years the DMF slopes of high density populations were greater than the DMF slopes of isolated plant populations. However, the DMF slopes of high density plants were not always positive. These results suggest that the population-wide, seasonally-integrated symmetry of competition may vary between years, but that the increase of the DMF slope with density may be quite general.

INTRODUCTION

Literature review and explanation of the problem

A central question in ecology is how the emergent properties of populations are explained in terms of the attributes and interactions of their individuals. Most plant interactions are competitive and inseparably tied to the occupancy and utilization of space (Ross and Harper 1972). Plant individuals compete for resources directly only where they overlap in space. Within spaces of overlap, individuals divide available resources in three ways: such that smaller plants receive more resource per unit biomass; such that all individuals receive equal resource per unit biomass; or such that the larger plants receive more resource per unit biomass. The first two forms of resource division have been called symmetric competition, the last form has been called asymmetric competition (Aikman and Watkinson 1980, Turner and Rabinowitz 1983, Firbank and Watkinson 1987, Weiner 1990). The symmetry of competition is believed to have distinct effects on populations. For example, an increase in crowding under symmetric competition is thought to maintain or decrease size variability, while an increase in crowding under asymmetric competition is thought to increase size variability of populations (Koyama and Kira 1956, Kuroiwa 1960, Ford 1975, Harper 1977, Gates 1978, Aikman and Watkinson 1980, Turner and Rabinowitz

1983, Hara 1984a, 1984b, Hara 1986, Weiner 1986, Weiner and Thomas 1986, Firbank and Watkinson 1987, Weiner 1990). Furthermore, competition for light is believed to be predominantly asymmetric and competition for below-ground resources symmetric (e.g. Turner and Rabinowitz 1983, Weiner 1986). These effects of competitive symmetry may have important consequences on population dynamics and species coexistence (Lomnicki 1980, Law 1983, Weiner and Thomas 1986, Biere 1987, Huston and DeAnagelis 1987, Smith and Huston 1989, Pacala and Weiner 1991, Kohyama 1992).

However, these predicted effects of competitive symmetry are based on the assumption that the instantaneous symmetry of resource division on a sub-individual level, i.e. within spaces of biomass overlap, determines resource division and utilization on the whole-plant, seasonally-integrated scale. This assumption hinges on spatial and temporal uniformity, i.e. the condition that resource limitation and utilization is constant throughout the season and the space that individuals occupy.

The present study distinguishes the symmetry of competition and growth on several spatial and temporal scales and examines the link between them. This is done through general analysis, simulation modeling of competition in neighborhoods, and field experiments.

Explanation of the thesis format

The relationships between three spatio-temporal scales of symmetry are defined and examined in the manuscript appearing in Appendix A. This analysis focuses on the short-term and long-term competitive interactions between two individual plants. A fourth scale of competitive symmetry, defined at the seasonally-integrated, population-wide scale, is examined in the manuscript appearing in Appendix B. This study focuses on the effects of various sources of random variation between neighborhoods and between individuals on the symmetry of competition and population size structure. Predictions generated in this study are tested in field experiments. The results of the field study appear in Appendix C.

PRESENT STUDY

A review of the literature, methods, results, and conclusions of this study are presented in the manuscripts appended to this thesis. The following is summary of the most important findings in these manuscripts.

I distinguish the local symmetry of competition from the whole-plant symmetry of competition. Competition is locally asymmetric if, in the space of overlap, the larger plant captures more resource per unit biomass involved in resource uptake. Locally asymmetric competition arises if there exists a mechanism of resource preemption which large plants can take advantage of. Competition is asymmetric at the level of the whole plant, if large plants capture more total resource per unit total biomass involved in resource uptake. An analysis based on the decomposition of the relative growth rates of two competing plants shows that local symmetry is not equivalent to whole-plant symmetry (Appendix A). The symmetry of competition at the level of the whole plant is also influenced by allometry and the spatial distribution of the limiting resource. Allometry determines how much space is occupied by a plant with a certain total biomass. If larger plants occupy less space per unit biomass and competitors are far apart, competition is symmetric, but becomes more asymmetric if competitors are closer. The local symmetry of competition affects the magnitude of the response to

plant distance. If the ability of plants to seek out resource-rich patches in the local environment is positively correlated with total plant biomass, competition at the level of the whole plant is more asymmetric than if all plants have equal access resource rich patches.

In addition, I show the ratio of the relative growth rates of competitors (symmetry of growth) are not fully determined by the symmetry of competition at the whole-plant level. The symmetry of growth also depends on differences in the resource-to-biomass conversion efficiencies and the biomass partitioning ratios of competitors (Appendix A). The resource costs of maintaining existing biomass affects the resource-to-biomass conversion efficiencies of individuals, the ability to acclimate to low resource capture affects the biomass partitioning ratios of individuals. I show that these two factors do not influence the symmetry of growth greatly. On the other hand, I argue that other plant responses, such as certain morphogenetic responses to crowding prior to the onset of significant competition, may allow plants to escape asymmetric competition.

The seasonally integrated, population-averaged symmetry of competition is defined as a statistical property of populations (Appendix B). I define the symmetry of competition at this scale as the slope of empirical distribution-modifying functions (DMFs). Empirical DMFs are regression

functions of the log-transformed relative biomass increase between the seedling stage and maturity on the log-transformed seedling biomass. In a spatial neighborhood-based simulation of competition for light, DMFs have remarkably robust properties: DMFs are nearly linear; they are negatively sloped at low density independent of the symmetry of competition in the spaces of canopy overlap; DMF slopes increase greatly with density only if competition in the spaces of canopy overlap is asymmetric; and random variation of individual canopy height, site quality, and plant spacing have a minimal influence on the DMF slope. On the other hand, all sources of random variation have a large effect on the final size structure of populations. Without any other source of random variation but the variation in the initial seedling sizes, the final size variabilities of populations increase with density if competition in the spaces of overlap is asymmetric, but stay fairly constant, if it is symmetric. This pattern matches closely the pattern observed for DMF slopes. However, with additional sources of random variation, the response of final size variability to density changes. If site quality varies and density is low, size variability decreases with density under both forms of local symmetry. If site quality varies and density is high, size variability increases with density under locally asymmetric competition and decreases with density under locally symmetric competition. If plant spacing

is random, size variability always increases with density, except at very high density where it stays constant. Under random height variation between individuals size variability also increases with density under both forms of variation. Based on these results, I conclude that the density-dependence of the DMF slope is a better indicator for the local symmetry of competition than the density-dependence of the final size variability in populations. The density-dependence of the DMF slopes is explained by the interplay of the allometry of space occupancy and the local symmetry of competition.

Many of the simulation results were confirmed in field experiments on two annual plant species, millet (Pennisetum americanum) and cowpea (Vigna unguiculata). In 1990 and 1991, millet plants grew isolated, at low density (10,000 plants ha^{-1}), and at high density (20,000 plants ha^{-1}). Cowpea plants grew isolated, or as single cowpea plants within stands of low and high density millet in the same years. The experiments had a blocked two-way factorial design with seed size and density as the main factors. DMFs were determined by regressing the log-transformed biomass increment between two and twelve weeks after planting against the log-transformed biomass at two weeks after planting. All empirically derived DMFs lacked significant non-linear trends. Except for cowpea in 1990, the DMFs for isolated plants were negatively sloped. In both species and both

experimental years the DMF slopes of high density populations were greater than the DMF slopes of isolated plant populations, although the DMF slopes of low density populations were not intermediate. In millet populations, final size variation showed a similar density response in both experimental years. In cowpea, the density response was insignificant in 1990, and small, but significant, in 1991. It is concluded that, in millet, the similarity between the density-response of the DMF slope and density-response of final size variability occurs, because millet plants were relatively little affected by sources of random variation other than the variation in initial seedling sizes. On the other hand, there was no such similarity in cowpea populations, because their growth was more highly influenced by random variation. Therefore, as in the simulation models, the density-response of the DMF slopes appeared to be more general than the density-response of final size variability.

In summary, my results illustrate that the symmetry of competition on the scale of the whole plant is not entirely determined by the nature of the limiting resource and its interception. Thus, competition for water and nutrients can also be asymmetric. Environmental variation, for example, in the timing of rainfall events, can vary the seasonally-integrated, population-wide symmetry of competition between years. Therefore, the seasonally-

integrated symmetry of competition cannot be considered a fixed property of annual plant populations. On the other hand, the increase in the asymmetry of whole-plant competition with density appears to be quite general and is explained by asymmetric local resource division and/or the allometry of space occupancy. This means that the fitness differences between individuals with different seedling sizes should often increase with density. However, this increase in asymmetry is not always matched by an increase in the final size variability of annual plants. The response of population size variability to density depends critically on the nature of sources of random variation for the individual growth rates in populations.

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APPENDIX A

AN ANALYSIS OF COMPETITIVE SYMMETRY THROUGH THE DECOMPOSITION OF RELATIVE GROWTH RATES.

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ABSTRACT

The view that the size variability of populations increases with density under competition for light, and that it decreases or stays constant with density under below-ground competition, is based on two assumptions. First, local resource division within spaces of canopy or root system overlap determines the symmetry of competition at the whole-plant scale. Second, the growth rates of competitors are determined by whole-plant resource capture. I show how these assumptions can be violated and examine the consequences on size variation. I begin by distinguishing the symmetries of competition and growth at several spatial and temporal scales. With the help of a simple analysis, based on the decomposition of relative growth rates, and a heuristic model of competition, I illustrate the relationships between the different scales of completion and growth symmetries. I suggest how this may refine our knowledge about the effects of crowding on population size structures, including stating some conditions under which below-ground competition is asymmetric, even though soil resources are not locally preempted.

Key Phrases: symmetric and asymmetric competition, population size structure, cost of maintenance, acclimation, physiological states, plant growth analysis.

INTRODUCTION

Crowding has complex effects on the size structures of plant populations. In some cases, crowding maintains or reduces size variability between individuals (as measured, for example, by the coefficient of variation) by reducing the growth rates of all individuals in equal proportions (Turner and Rabinowitz 1983, Waller 1985, Weiner 1986). In other cases, crowding increases size variability by reducing the relative growth rates of some individuals more than others. (Edmeades and Daynard 1979, Weiner and Thomas 1986, Counce et al. 1989, Rice 1990). These differences in the size structure response to crowding have important implications on population dynamics (Lomnicki 1980, Law 1983, Weiner and Thomas 1986, Pacala and Weiner 1991) and community ecology (Weiner and Thomas 1986, Biere 1987, Huston and DeAnagelis 1987, Smith and Huston 1989, Pacala and Weiner 1991, Kohyama 1992).

The effects of crowding on size structure have been linked to the way in which limited 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, Weiner 1990). These authors hypothesized that if resources are distributed in proportion to the biomass of competitors, plants of all sizes would have, on average, equal relative growth rates. Thus, an increase in crowding should decrease the relative growth rates

of all plants by approximately the same amount and the size variability of a population would remain constant. Furthermore, it was suggested that competition for below-ground resources works in this way, because the roots of large and small plants have equal access to water and nutrients in the soil (e.g. Turner and Rabinowitz 1983, Weiner 1986). This characterization of competition has been called symmetric, or two-sided, competition (Weiner 1990).

On the other hand, if large plants capture more resource per unit biomass than smaller plants, larger plants should have greater relative growth rates than smaller plants. Then, an increase in crowding should increase the differences in the relative growth rates of competitors and increase size variability in a population. Under this form of competition large plants preempt resource from smaller plants. Competition for light is thought to work in this way, as large and tall plants shade smaller and shorter neighbors without being shaded as much by the neighbors. This characterization of competition has been called asymmetric, or one-sided, competition.

However, these inferences from resource capture mechanisms to population-level effects are based on two assumptions that need not hold. The first is that the symmetry of competition is scale-independent, i.e. that the symmetry of resource uptake on a sub-individual scale dictates the symmetry of resource division between whole plants. For example, if larger plants overtop smaller plants, larger plants capture more light per unit leaf biomass than

smaller plants in spaces where the canopies overlap. However, this only implies that larger plants capture more light per unit leaf biomass overall, if smaller plants don't capture more light per unit leaf biomass outside the regions of canopy overlap.

The second assumption is that the rates of resource uptake and the rates of growth are in the same proportion to each other for all plants in a population. For example, the differences in the resource uptake between individuals determines the differences in their relative growth rates only if all plants utilize captured resource identically, i.e. that a unit captured resource serves to synthesize the same amount and type of biomass in all plants. However, resource conversion into biomass and its partitioning towards different plant functions may depend on plant size or the resource status of individuals.

Below, I show that these two assumptions are invalid for biologically quite reasonable and common conditions. First, I explicitly distinguish symmetries of competition and growth on several spatial and temporal scales. Then, I introduce a simple analysis, based on the decomposition of plant growth rates, that characterizes the relationships between the symmetries of competition and growth at certain scales. Unlike other approaches (Kuroiwa 1960, Williams 1963, Ford and Diggle 1981, Hara 1984, Ryel et al. 1990, Burrows 1991), this analysis is not specific to a particular resource and not limited to expressing only the consequences of resource division. The consequences of morphological and physiological responses to competition on

size variation are also examined. Finally, I illustrate the benefits of the decomposition analysis in a heuristic example of competition between two plant individuals and discuss how this may help to refine our understanding of crowding effects on populations.

SCALES OF SYMMETRY

The symmetry of competition is commonly divided into two cases, symmetric and asymmetric competition. Below, I suggest a slightly different characterization of symmetry. What is commonly called 'asymmetric competition', I call 'positively asymmetric competition'. What is commonly called 'symmetric competition', I call 'negatively asymmetric competition' or 'symmetric competition'. In this terminology 'symmetric competition' characterizes a special, non-generic case of resource division.

The symmetry of local competition

I call local competition positively asymmetric if large plants capture more resource per unit biomass responsible for resource uptake than smaller plants in regions where they overlap. For example, local competition for light is positively asymmetric if a larger plant intercepts more light per leaf biomass than a smaller plant within regions of canopy overlap. This would usually occur if larger plants are also taller. Local competition is symmetric, if small plants capture equal amounts of resource, and negatively asymmetric if small plants

capture more resource per unit biomass responsible for resource uptake in regions of overlap with larger plants. In the case of local competition for light, this would occur if large and small plants have the same vertical foliage frequency distribution in the space of overlap (not necessarily the same foliage density distribution).

The symmetry of whole-plant competition

Competition is positively asymmetric at the level of the whole plant, if larger plants capture more total resource per total biomass involved in resource uptake than their smaller neighbors. Thus, competition for light is positively asymmetric at the whole-plant scale, if larger plants intercept more light per unit leaf biomass averaged across the entire canopies. Competition is symmetric at the scale of whole plants if smaller plants capture equal amounts, and negatively asymmetric if smaller plants capture more, resource per total biomass involved in resource uptake than their larger neighbors. I express the symmetry of competition at this scale with an index based on the comparison of the relative resource uptake rates of two adjacent individuals.

$$S^i(t) = \frac{\Delta U^i(t)}{B_X^i(t)} \qquad (1)$$

is the relative resource uptake rate of the ith plant. It is the ratio of the total resource taken up per unit time, $\Delta U^i(t)$, over the total biomass involved in the uptake of resource x, $B^i_x(t)$.

The index for the symmetry of competition at the level of the whole plant is defined as

$$\ln(s(t)) = \ln\left(\frac{S^1(t)}{S^2(t)}\right) . \qquad (2)$$

It is assumed that

$$B^1(t) \geq B^2(t) , \qquad (3)$$

where $B^i(t)$ is the total biomass of the ith plant at time t. Thus, the plant with the index 1 always has the greater total biomass. The sign of $\ln(s(t))$ indicates the symmetry of competition at the whole-plant scale:

if $\ln(s(t)) > 0$	the larger plant captures more resource per unit biomass than the smaller plant (positively asymmetric competition);
if $\ln(s(t)) = 0$	large and small plants captures the same amount of resource per unit biomass (symmetric competition);
if $\ln(s(t)) < 0$	the smaller plant captures more resource per unit biomass than the larger plant (negatively asymmetric competition).

The short-term symmetry of growth

By a parallel definition, the symmetry of growth is based on the comparison of relative growth rates of plants with different size, rather than their relative resource uptake rates. Growth is positively asymmetric in the short-term, if larger plants have greater relative growth rates than their smaller neighbors. Growth is symmetric if large and small plants have equal relative growth rates, and negatively asymmetric if smaller plant have a greater relative growth rates than their larger neighbors. The symmetry of growth can be expressed by the index

$$\ln(i(t)) = \ln\left(\frac{\Delta B^1(t)}{B^1(t)}\right) - \ln\left(\frac{\Delta B^2(t)}{B^2(t)}\right) . \qquad (4)$$

$B^1(t)$ and $B^2(t)$ are the biomass of plants 1 and 2 at time t respectively, and $\Delta B^1(t)$ and $\Delta B^2(t)$ their absolute growth increments during a unit time interval starting at t. Again, it is assumed that the two plants are adjacent and that the plant with the index 1 is larger (equation 3). Additionally, it is assumed that all plants have positive growth rates, thus, this analysis only applies to populations of growing, non-thinning plants. The sign of $\ln(i(t))$ determines the symmetry of growth and whether the biomass ratios of plant pairs increase, stay constant, or decrease:

if $\ln(i(t)) > 0$: the size ratio increases (positively asymmetric growth);

if $\ln(i(t)) = 0$: the size ratio is maintained (symmetric growth);

if $\ln(i(t)) < 0$: the size ratio decreases (negatively asymmetric growth).

The long-term symmetry of growth

The symmetry of growth can also be represented on a seasonally-integrated scale. On this scale, growth is positively asymmetric if larger seedlings have greater relative growth increments until maturity than their smaller neighbors, symmetric if large and small seedlings grow in equal relative increments, and negatively asymmetric if small seedlings gain relatively more biomass during growth than their larger neighbors. The index associated with symmetry on this scale is

$$\ln I = \ln\left(\frac{B^1(T)}{B^1(0)}\right) - \ln\left(\frac{B^2(T)}{B^2(0)}\right) . \qquad (5)$$

where $B^i(0)$ is the biomass of the ith seedling, and $B^i(T)$ is its biomass at the end of the season. As for the short-term index for the symmetry of growth, $\ln I > 0$ indicates positively asymmetric, $\ln I = 0$ indicates symmetric, and $\ln I < 0$ indicates negatively asymmetric seasonally-integrated growth.

DECOMPOSITION ANALYSIS FOR SYMMETRY INDICES

The symmetry of competition at the whole-plant scale and the short-

term symmetry of growth can be decomposed following a common method in plant growth analysis (West et al. 1920, Hunt 1981, Hunt 1990). Below I define five decomposition factors each expressing a different aspect along the pathway of the uptake and utilization of a limited resource.

$$A^i(t) = \frac{V_X^i(t)}{B_X^i(t)}$$ is the allometry factor. It is the ratio of the space occupied by the biomass involved in the uptake of resource X, $V_X^i(t)$, and the same biomass. (6a)

$$R^i(t) = \frac{\Delta X^i(t)}{V_X^i(t)}$$ is the resource availability factor. It is the ratio of resource available to plant i per unit time, ΔX^i, and the space occupied by the ith plant biomass involved in the uptake of X. (6b)

$$C^i(t) = \frac{\Delta U^i(t)}{\Delta X^i(t)}$$ is the resource capture efficiency factor. It is the ratio of the resource intercepted by plant i per unit time, $\Delta U^i(t)$, and the available resource per unit time. (6c)

$$E^i(t) = \frac{\Delta B^i(t)}{\Delta U^i(t)}$$ is resource conversion efficiency factor. It is the ratio of new biomass, $\Delta B^i(t)$, accumulated by plant i in the unit interval and the resource taken up in the same interval. (6d)

$$P^i(t) = \frac{B_X^i(t)}{B^i(t)}$$ is the partitioning factor. It is the ratio of (6e)

the biomass involved with uptake of resource X, $B_X^i(t)$, and total biomass, $B^i(t)$, of the ith plant.

These decomposition factors are general with respect to the nature of the limiting resource. However, it is useful to use different measures of space for different limiting resources. For example, if growth is limited by water, space should be measured as the soil volume occupied by the fine roots of a plant. If growth is limited by light, space could more conveniently be measured as the canopy's area of projection in the direction of the light rays.

Decomposition of the whole-plant symmetry of competition

The previously defined index for the symmetry competition at the whole-plant scale, $\ln(s(t))$ (equation 2), can be expressed in terms of three decomposition factors. Since

$$S^i(t) = A^i(t) * R^i(t) * C^i(t) \qquad (7)$$

(equations 1, 6a,b, and c),

$$\ln(s(t)) = \ln\left(\frac{A^1(t)}{A^2(t)} * \frac{R^1(t)}{R^2(t)} * \frac{C^1(t)}{C^2(t)}\right) . \qquad (8)$$

(equation 2). Substituting

$$a = \frac{A^1(t)}{A^2(t)}, \quad r = \frac{R^1(t)}{R^2(t)}, \quad c = \frac{C^1(t)}{C^2(t)} , \tag{9}$$

into equation 8 yields

$$\ln(s(t)) = \ln(a(t)) + \ln(r(t)) + \ln(c(t)) . \tag{10}$$

This equation shows that the symmetry of competition on the level of the whole plant is determined by the size-dependence of allometry (a), resource availability (r) and resource capture efficiency (c). Allometric relationships determine how much space is occupied per unit biomass involved in resource uptake (equation 6a). Plants that occupy more space per unit biomass involved in resource uptake are competitively favored. The average resource availability in the space occupied by plant individuals also affects the symmetry of competition on the whole-plant scale. Individuals experiencing greater average available resource levels are competitively favored. The resource capture efficiency has a similar effect on the whole-plant symmetry of competition. Plants that capture a greater fraction of the available resource are also competitively favored.

The local symmetry of competition, i.e. whether large plants have the ability to preempt resource within regions of space affects the resource capture efficiency term, but not necessarily the other terms of equation 10.

In general, local resource preemption would increase the resource capture efficiency advantage of large plants over small plants (i.e. would increase $\ln(c(t))$), but would not necessarily generate positively asymmetric competition on a whole- plant scale (i.e. would make $\ln(s(t))$ positive).

Decomposition of the short-term symmetry of growth

The symmetry of growth index $\ln(i(t))$ can also be decomposed using the relationship:

$$\frac{\Delta B^i(t)}{B^i(t)} = S^i(t) * E^i(t) * P^i(t) \qquad (11)$$

(equations 1, 6d and e). With the substitutions

$$e = \frac{E^1(t)}{E^2(t)}, \quad p = \frac{P^1(t)}{P^2(t)} , \qquad (12)$$

equation 11 becomes

$$\ln(i(t)) = \ln(s(t)) + \ln(e(t))) + \ln(p(t)) . \qquad (13)$$

Thus, the symmetry of growth ($\ln(i(t))$) is not completely defined through the symmetry of competition ($\ln(s(t))$). The relation of the resource-to-biomass conversion efficiencies (e) and the biomass partitioning ratios (p) between

plants of different sizes also influence the symmetry of growth. In general, greater biomass production per unit captured resource and greater allocation of total biomass towards the function of intercepting a limiting resource favors plant growth.

HEURISTIC EXAMPLES

I present heuristic examples of competition between two plants to illustrate how the decomposition analysis can help to explain the symmetries of competition and growth. In the examples, the spaces plants occupy are represented by two-dimensional circular discs. Plant pairs compete for resources only in the region of space in which they overlap. The degree of overlap, thus the strength of competition, is determined by the sizes of the disks and their distance.

Determinants of whole-plant, short-term symmetry of competition

To examine how allometry and resource capture efficiency may interact to determine the symmetry of competition on the whole-plant level, I introduce three assumptions:

First, I assume that the available resource per unit area is constant in space and time. Thus, $\mathbf{R^1(t)} = \mathbf{R^2(t)}$, and $\ln(r(t)) = 0$ (equations 6b and 9). (I examine the implications of relaxing this assumption in **DISCUSSION**).

Second, I assume that the space occupied by plant i is a function of

the biomass involved in resource uptake:

$$V_X^i(t) = \frac{V_X^{max} B_X^i(t)}{B_X^i(t) + K} . \qquad (14)$$

V_X^{max} is the maximal space an individual can occupy with biomass involved in the uptake of resource x and K is the biomass at which half of that space is occupied. This equation was chosen to express that plants accumulate volume more slowly than they accumulate biomass and that, consequently, biomass density increases during growth. This may often be true for annual plants which do not shed a substantial amount of biomass during growth. Substituting equation 14 into equation 6a yields

$$A^i(t) = \frac{V_X^{max}}{B_X^i(t) + K} . \qquad (15)$$

It follows that

$$\ln(a(t)) = \ln\left(\frac{B_X^2(t) + K}{B_X^1(t) + K}\right) \qquad (16)$$

(equation 9). In this example, it is assumed that $B^1(t) > B^2(t)$ (equation 3) implies $B^1{}_X(t) > B^2{}_X(t)$, thus, $\ln(a(t)) < 0$.

Third, I assume that the proportion of the available resource that plant i captures in a unit space and time depends on the density of the biomass involved in resource uptake and the density of biomass belonging to other individuals. I define biomass density as:

$$D_X^i(t) = \frac{B_X^i(t)}{V_X^i(t)} \qquad (17)$$

and assume uniform biomass distribution. The total fraction of available resource that is taken from a unit space in a unit time is

$$\sum f^i(t) = 1 - e^{-k\sum D_x^i(t)} , \qquad (18)$$

where k is a constant. The equation says that the denser the biomass, the greater the proportion of the available resource taken per time interval from a unit space and that resource is available in limited amount. This assumption is generally true for any limiting above- and below-ground resource (Monsi and Saeki 1953, Cowan 1965, deWit 1965, Taylor and Klepper 1978, Caldwell and Richards 1986). Light interception depends on the ratio of leaf area to ground area which is one way of expressing leaf biomass density.

Water and nutrient uptake depend on the total length of fine roots per volume soil, which is a way of expressing root biomass density.

In the regions of space occupied by only one individual (i) the fraction

$$f^i(t) = 1 - e^{-k D_x^i(t)} \qquad (19)$$

of the available resource is taken up per unit space. In regions of space where two plants overlap, the fraction of available resource captured by both plants is divided between individuals. Let $f^{12(t)}$ be the proportion of resource taken up by plant 1 from a unit space in overlap with plant 2 and $f^{21(t)}$ the proportion of the resource taken by plant 2 from a unit space in overlap with plant 1. Then local competition is symmetric if

$$\frac{f^{12}(t)}{D_x^1(t)} = \frac{f^{21}(t)}{D_x^2(t)} , \qquad (20)$$

and positively asymmetric if

$$\frac{f^{12}(t)}{D_x^1(t)} > \frac{f^{21}(t)}{D_x^2(t)} , \qquad (21)$$

assuming, as before, that $B^1{}_X(t) > B^2{}_X(t)$. The following equation satisfies equations 18 and 20, thus describes a case of symmetric local competition:

$$f^{ij}(t) = \frac{D_X^i(t)}{D_X^i(t) + D_X^j(t)} \left(1 - e^{-k(D_X^i(t) + D_X^j(t))}\right) . \qquad (22)$$

To construct a case that satisfies equations 18 and 21, thus, describes a case of positively asymmetric local competition, I assume that a portion $h(t)$ of the larger plant's biomass within the space of overlap does not participate in competition. Furthermore, I assume that the magnitude of that fraction $h(t)$ depends on the size difference between individuals:

$$h(t) = \frac{B^1(t) - B^2(t)}{B^1(t) + B^2(t)} . \qquad (23)$$

With this, I construct a case of positively asymmetric local competition as follows:

$$f^{12}(t) = 1 - e^{-kh(t)D_X^1(t)} + \frac{(1-h(t))D_X^1(t)}{(1-h(t))D_X^1(t) + D_X^2(t)} e^{-kh(t)D_X^1(t)} \left(1 - e^{-k((1-h(t))D_X^1(t) + D_X^2(t))}\right)$$

and $$f^{21}(t) = \frac{D_X^2(t)}{(1-h(t))D_X^1(t) + D_X^2(t)} e^{-kh(t)D_X^1(t)} \left(1 - e^{-k((1-h(t))D_X^1(t) + D_X^2(t))}\right) . \qquad (24)$$

These equations, though seemingly complicated, have three simple defining characteristics: they conform to equations 18 and 21, and if $B^1(t) = B^2(t)$ collapse into equation (20), indicating that resource division is locally symmetric if there are no size differences between individuals.

To find the resource capture efficiency on a whole-plant level, $C^i(t)$ (equation 6c), contributions from the space that is occupied alone, and from the space that overlaps with the competitor are added. If $V_X^{OV}(t)$ is the space in overlap:

$$C^i(t) = [(V_X^i(t) - V_X^{OV}(t))f^i(t) + V_X^{OV}(t)\, f^{ij}(t)] \quad . \tag{25}$$

Thus (equation 9),

$$\ln(c(t)) = \ln\left(\frac{(V_x^1(t) - V_X^{OV})f^1(t) + V_X^{OV}(t)f^{12}(t)}{(V_X^2(t) - V_X^{OV}(t))f^2(t) + V_X^{OV}(t)f^{21}(t)}\right) \quad . \tag{26}$$

Figure 1 shows values of the allometry term, $\ln(a(t))$, the resource capture term, $\ln(c(t))$, and their sum, $\ln(s(t))$, as a function of the log biomass ratio of two competitors if local competition is symmetric (equations 20 and 23). The biomass of plant 1 is fixed. The allometry term is always negative and decreases with the biomass ratio. The resource capture term is always positive and increases with the biomass ratio. This means that larger plants

capture a greater fraction of the available resource, but that they also occupy relatively less space than smaller plants. At the distance d = 1.5 (corresponding approximately to the maximal plant radius) the allometry disadvantage of large plants outweighs their capture efficiency advantage. Thus, competition on a whole-plant scale is negatively asymmetric for all plant pairs as indicated by $\ln(s(t)) < 0$. At d = 0.5 the capture efficiency advantage of larger plants is greater, because larger plants, having a smaller fraction of their entire volume in overlap, lose less resource to competition compared to larger plants The capture efficiency advantage of large plants outweighs their allometry disadvantage only, if the size difference between plant pairs is large enough. Under those conditions, competition on a whole-plant scale is positively asymmetric as indicated by $\ln(s(t)) > 0$. Thus, the important result of this example is that even though local competition is symmetric, competition at the whole-plant scale can be positively asymmetric, favoring the relative resource uptake of larger plants.

Figure 2 shows values of $\ln(a(t))$, $\ln(c(t))$ and their sum $\ln(s(t))$ if competition in the space of overlap is positively asymmetric (equations 21 and 24). In this case $\ln(c(t))$ is greater for all biomass ratios than in the previous case, reflecting the additional resource capture advantage given to large plants in the space of overlap. However, at d = 1.5, $\ln(c(t))$ is only minimally greater, so that $\ln(s(t))$ remains negative. Since the space of overlap is small at this distance, positively asymmetric local competition

gives too little advantage to large plants to overcome their allometric disadvantage. At d=0.5, larger plants enjoy a much greater resource capture advantage, because the overlap is much larger. Thus, $\ln(s(t))$ is positive and quite high, indicating highly positively asymmetric competition on a whole-plant scale. The important result is that, in spite of positively asymmetric resource division in the space of overlap, competition on the whole-plant scale can be negatively asymmetric if competitors are above a certain distance.

Under symmetric and positively asymmetric local competition, whole-plant competition becomes more positive as the distance between individuals decreases. This increase is much greater if local competition is positively asymmetric.

This example illustrates three general results. First, the local symmetry of competition, i.e. the way plants divide resources in the space of overlap, does not fully determine the symmetry of competition on the whole-plant level. Second, the closer competitors, the more positively asymmetric is competition at the scale of whole plants. Local competition influences the rate of change for whole-plant symmetry with distance. Third, the symmetry of competition also depends on the biomass ratios of competitors.

Determinants of the short-term and long-term symmetries of growth

I expand the previous example to examine the relationships between the symmetries of competition and growth. These relationships depend on the size-dependence of resource-to-biomass conversion efficiencies (equation 6d) and resource partitioning (equation 6e). I consider three alternative conditions:

The null model:

Total biomass increases in a constant proportion to resource uptake:

$$\Delta B^i(t) = \epsilon \Delta U^i(t) \quad . \tag{27}$$

Thus, $E^1(t) = E^2(t) = \varepsilon$, and $\ln(e(t)) = 0$ (equations 6d and 12).

The biomass of plant i involved in resource uptake, $B^i_X(t)$ is in a constant proportion to its total biomass, $B^i(t)$:

$$B^i_X(t) = gB^i(t) \quad , \tag{28}$$

where g is the partitioning coefficient. Since $P^1(t) = P^2(t) = g$, $\ln(p(t)) = 0$ (equations 6e and 12).

Thus, in the null model, the symmetry of growth is entirely determined by the symmetry of competition (equation 12):

$$\ln(i(t)) = \ln(s(t)) \quad . \tag{29}$$

The cost of maintenance model:

I modify the foregoing example in only one way. Instead of letting biomass increase in a constant proportion ε with the captured resource, I now assume that a portion of the captured resource goes towards maintaining the existing biomass. Energy and nutrient costs for keeping existing biomass alive and functional are ubiquitous in plants, although there may be large differences in the magnitude of the cost for maintaining different tissues (Bloom et al. 1985, Chiariello et al. 1986). I express this cost in γ, the resource necessary to maintain a unit biomass. Thus,

$$\Delta B^i(t) = \epsilon(\Delta U^i(t) - \gamma B^i(t)) \quad . \tag{30}$$

Since

$$E^i(t) = \epsilon(1 - \gamma \frac{B^i(t)}{\Delta U(t)}) \tag{31}$$

(equation 6d),

$$\ln(e(t)) = \frac{1 - \gamma \dfrac{B^1(t)}{\Delta U^1(t)}}{1 - \gamma \dfrac{B^2(t)}{\Delta U^2(t)}} \quad . \tag{32}$$

(equation 12). Equation 30 can generate zero or negative values for biomass increments. In those cases, $\ln(e(t))$ is infinite or undefined. In the following computations, negative growth rates are reset to zero, assuming that physiological activity is reduced or stops, once resource capture becomes insufficient to maintain biomass. However, if both growth rates are positive:

$$\ln(i(t)) = \ln(e(t)) + \ln(s(t)) \quad . \tag{33}$$

(equation 12). Thus, the symmetry of growth is not identical to the symmetry of competition, because plants may have differences in their resource use efficiency.

The maintenance of growth and acclimation model:

In this final example, I add the assumption that plants can acclimate to low resource capture in the cost of maintenance model. Acclimation responses are also quite common in plants, although species may differ in plasticity (Bradford and Hsiao 1982, Bloom et al. 1985, Turner 1986, Crick and Grime 1987). In this example, plants acclimate by allocating a greater proportion of the newly acquired biomass to the task of resource capture. I express the dependence of partitioning on the average resource capture per unit biomass, $S^i(t)$ (equation 1):

$$\Delta B_X^i(t) = \left(g_{\max} - \Delta g * \left(\frac{S^i(t)}{S^i(t)+W}\right)\right)\Delta B^i(t) \quad , \qquad (34)$$

where g_{max} is the maximal partitioning coefficient, g_{max}-Δg is the minimal partitioning coefficient, and W is the value of $S^i(t)$ for which the partitioning coefficient is half-way between its maximum and minimum. Variation in the partitioning of biomass between competitors is reflected in non-zero values for $\ln(p(t))$. The exact value depends, however, on the history of competitive interaction and cannot be expressed as a function of the current size difference alone. The symmetry of growth is now fully described by three terms:

$$\ln(i(t)) = \ln(p(t)) + \ln(e(t)) + \ln(s(t)) \quad . \qquad (35)$$

(equation 13).

The changes in the log of the biomass ratio with time is summarized in Figure 3 for all three models and symmetric competition in the space of overlap. Negative slopes indicate negative $\ln(i(t))$, thus episodes of negatively asymmetric growth, while positive slopes indicate positive $\ln(i(t))$ and episodes of positively asymmetric growth. For the null model, negative slopes also indicate negative $\ln(s(t))$ as well, thus episodes of negatively asymmetric competition, while positive slopes indicate positive $\ln(s(t))$ and episodes of

positively asymmetric competition at the scale of whole plants (equation 27). At d=1.5, the biomass ratios decrease throughout the period of 30 iterations for all models, indicating that whole-plant competition and growth are always negatively asymmetric (Figure 3A). At d=0.5, whole-plant competition and growth are positively asymmetric between the 5th and the 12th iteration (Figure 3B). The resulting temporary increase in the biomass ratio is responsible for a difference in the final biomass ratios at d=0.5 and d=1.5, for which there was no such temporary increase. Neither the cost of maintenance, nor the acclimation response have a large influence on the biomass ratios of competitors. At d=1.5, the effect of the cost of maintenance is negligible. The acclimation response, on the other hand, tends to favor the growth of the large plant, at least temporarily. This signifies that large plants capture less biomass per unit biomass involved in resource uptake and, in response, allocate more to this function. This opposes the trend to decrease the biomass ratios between competitors for a short while.

At d=0.5, the cost of maintenance has a slightly greater effect on the growth of competitors. It accelerates the rate of increase in the biomass ratio, thus facilitating the effect of whole-plant positively asymmetric competition on the symmetry of growth. On the other hand, acclimation opposes this effect and decelerates the rate of increase in the biomass ratios. However, acclimation appears to have no lasting effect on the

biomass ratios. After about 30 iterations, the biomass ratios of plant pairs with and without acclimation are nearly indistinguishable.

Under positively asymmetric local competition (Figure 4), the response of biomass ratio to plant distance is far greater. At $d=1.5$, whole-plant competition has nearly the same symmetry as in the case of symmetric local competition in the first third of growth (Figures 3A and 4A). The cost of maintenance and the acclimation response also have similar effects. In the last two thirds of growth, biomass ratios increase very gradually. At $d=0.5$, the biomass ratio increases sharply throughout the period of 30 iterations (Figure 4B). This indicates that the relative resource capture benefit given to the large plant increases with the increasing overlap between two expanding plants. The cost of maintenance slightly favors the larger plants initially, but then favors the growth of smaller plants. However, its effect is virtually zero. Growth is less positively asymmetric if there is acclimation. However, acclimation merely slows, but does not prevent, the increase in the biomass ratios of competitors.

The important result taken from these examples is that the symmetry of growth is estimated quite well by neglecting that physiological costs of maintenance and acclimation responses to resource capture.

Figures 3 and 4 illustrate that symmetries of competition and growth continuously change throughout the growth of competitors. In some instances, the effects of early positively asymmetric competition are later

canceled through negatively asymmetric competition on the scale of whole plants, so that the initial and the final biomass ratios are very similar (Figure 3B). This suggests that it is also necessary to evaluate competitive symmetry on a whole-plant, seasonally integrated scale (equation 5).

The seasonally integrated index of competitive symmetry, $\ln I$, is shown for a period of 30 iterations as a function of plant distance in Figure 5. In all three models, $\ln I$ increases with decreasing distance. In general, competition on a seasonal basis is negatively asymmetric at large distances and positively asymmetric at short distances. At some critical distance, which varies with the way resources are divided in the regions of overlap, $\ln I$ passes through zero, thus growth and competition switch from negatively to positively asymmetric. The response to plant distance is larger if competition in the space of overlap is positively asymmetric. The cost of maintenance and acclimation to low resource capture do not greatly interfere with the seasonally-integrated symmetry of growth. If plant distances are small, the cost of maintenance increases $\ln I$ slightly, but has little effect if plant distances are large. Acclimation has a large negative effect on $\ln I$ only if local competition is positively asymmetric and plant distances are small. Its effect declines with increasing plant distance and can even turn into a positive effect on $\ln I$ if local competition is symmetric and plant distance is large.

DISCUSSION

Above I showed that the symmetry of competition is scale-dependent. However, I also showed that the symmetries of competition at different scales have certain predictable relationships. Furthermore, I demonstrated that the symmetry of growth, i.e. the size ratio dynamics of neighboring plants, is not greatly affected by variable costs of maintenance and acclimation to low resource capture.

I defined and illustrated the symmetries of competition and growth on several temporal and spatial scales. The local symmetry of competition describes how resources are divided in the short term between competitors in regions of space where their biomass mixes. Symmetry at this scale is closely linked to the physics of resource uptake and supply and easily lends itself to direct measurement. Decomposition analysis (equations 10 and 13) and the examples illustrate that the local symmetry of competition has effects on competition on all other scales, but that it is not equivalent with it.

The symmetry of competition on the scale of whole plants compares the entire resource capture of plants with different sizes. The size-dependence of total resource capture depends on the allometry of space occupancy, the distribution of available resource within the occupied space, and the resource capture efficiencies. The latter is highly influenced by the distances between plants (which determines their degree of overlap) and the

local symmetry of competition (Figures 1 and 2). Local symmetry appears to determine how the symmetry of competition on the whole-plant scale responds to variation in plant distances, thus density. Measuring the symmetry of competition at this scale should often be quite difficult, since it requires the measurement of resource capture across the entire space that individuals occupy.

The seasonally-integrated symmetry of growth characterizes the long-term consequence of initial seedling size. This symmetry appears to be determined by the cumulative effects of short-term growth symmetry and whole plant competition (Figures 3 and 4). If competitors go through episodes of negatively and positively asymmetric growth, their effects on the seasonally-integrated symmetry of growth partly cancel. Therefore, the seasonally-integrated symmetry of growth would be difficult to predict for natural populations, since the short-term symmetry of growth is likely to change continuously due to variation in resource limitations. However, it is relatively easy to measure by a comparison between the seedling sizes and the final sizes of competitors. Nevertheless, there appear to be predictable effects of local symmetry conditions. As for the short-term symmetries of competition and growth, the seasonally-integrated symmetry of growth should become more positively asymmetric with increasing density, and responds more strongly to density, the more positively asymmetric local competition is (Figure 5).

The analysis was restricted to the comparison of plant pairs. However, simulation and field experiments showed that these results extend to the population level (Schwinning 1994). In simulated populations, larger than average seedlings had a relative growth disadvantage over smaller than average seedlings if density was low, whether local competition was symmetric or positively asymmetric. If local competition was positively asymmetric, an increase in density made it increasingly more advantageous to be a large seedling until eventually the disadvantage of large seedlings turned into an advantage over small seedlings. If local competition was symmetric, an increase in density affected the disadvantage of large seedlings very little. In experimental populations, the advantage of large seedlings also generally increased with density, but the seasonally-integrated symmetry of growth at any particular density varied considerably between years.

Schwinning (1994) did not examine effects of the initial seedling size variation. The present study suggests, however, that the symmetry of whole-plant competition may depend on biomass differences between competitors. Particularly at high density and under positively asymmetric local competition, competition becomes more positively asymmetric at the scale of whole plants the larger the biomass ratios of competitors (Figure 2B). This also means that if seedling size variation in annual plant populations varies between years, as is quite likely, this alone could generate

variation in the seasonally-integrated symmetry of growth.

This new perspective on the symmetries of competition and growth may help to explain previously unexplained crowding effects on populations. For example, several simulation models showed that size variability in a population increases with density if plant spacing is random, even if local resource division is symmetric (Miller and Weiner 1989, Bonan 1991, Schwinning 1994). This is viewed as an apparent contradiction to the idea that size variability increases with density only under positively asymmetric competition. I suggest that random spacing does indeed generate positively asymmetric competition at the whole-plant scale. Variable plant spacing, in models and also quite likely in reality, magnifies the variability of the spaces that individuals occupy (Ross and Harper 1972). For example, individual canopy volumes may be more variable under random spacing than under uniform spacing after some time of initial growth in which open space is filled with biomass. The present analysis shows that differences in volume alone can generate differences in the relative resource capture of plants. Plants that occupy a greater volume have a smaller fraction of the occupied volume in overlap with neighbors. In addition, if plants that occupy a greater volume also have lower biomass density within, they may capture more resource per unit biomass. Either way, plants that occupy more space would capture relatively more resource and would have greater relative growth rates. Therefore, differences in the available space would soon generate size

differences and, by definition, positively asymmetric competition at the whole-plant scale. However, Schwinning showed that random spacing does not affect the seasonally-integrated symmetry of growth, since plants of all sizes have equal chances of securing a lot of space for themselves.

The analysis also suggests plausible conditions for positively asymmetric (whole-plant) competition below the ground. Competition for water and nutrients could be positively asymmetric at the whole-plant scale, if the root system volumes of individual plants increase with total root biomass, and if root systems partly overlap. This seems reasonable, although little direct evidence is available. Comparisons between the root systems of heterospecific individuals (Taylor and Klepper 1978, Crick and Grime 1987, Jackson and Caldwell 1989) suggest that root systems can overlap extensively and use water and nutrients from the same soil locations. Clearly, without knowledge of the allometry of root system expansion, evidence for the nature of competition below the ground is incomplete. What evidence there is for the symmetry of below-ground competition comes largely from greenhouse experiments, in which plants are raised in pots (Newberry and Newman 1978, Weiner 1986). In pots plant roots are constrained to occupy the same rooting space. Therefore, below-ground competition could not be positively asymmetric at the scale of whole plants via this mechanism. General conclusions about the symmetry of below-ground competition should thus not be drawn from such experiments.

The effects of variation in resource availability (equation 6b) were not illustrated by example, but the decomposition analysis suggests possible effects. If larger plants have less available resource per unit occupied space than smaller plants, competition is more negatively asymmetric (or less positively asymmetric) than it would be under equal resource availability (equations 9 and 10). If smaller plants have less resource available, the converse is true. What biological circumstances could give rise to heterogeneous resource availability? If the root systems of large plants are more supply limited than the root systems of smaller plants, larger plants would have lower average water or nutrient availability. Based on models of water extraction by root systems (Cowan 1965, Taylor and Klepper 1978, Hainsworth and Aylmore 1986) the rate of water or nutrient uptake from a unit soil volume is a function of the root length density. If larger plants have denser root systems than smaller plants, or if for any other reason larger plants take up more resource per unit soil volume, local water or nutrient depletion should correlate with plant size. Particularly solutes with low diffusion coefficients in the soil, such as phosphate, and water in relatively dry soil can be locally depleted (Nye 1966, Bhat and Nye 1973, Fitter and Hay 1981). This mechanism of negatively asymmetric competition at the scale of whole plants does not exist for light competition, however, because light is not supplied by diffusion.

Random spatial variation in resource availability, on the other hand,

can give rise to more positively asymmetric (or less negatively) competition. This can occur if larger plants have better access to resource-rich patches. This is another plausible mechanism for positively asymmetric below-ground competition, because water and nutrients are typically heterogeneously distributed in the soil. It is also well known that roots 'forage' for resources (Grime 1979, Crick and Grime 1987, Jackson and Caldwell 1989, Gersani and Sachs 1992). This means that root growth is prolific in spaces of high water or nutrient content and inhibited in water or nutrient depleted regions. However, root growth in resource-poor soil patches does not stop altogether, rather, roots increase their elongation rates. Plants are thought to increase their chances of finding better patches in this way (Jackson and Caldwell 1989). If the ability of root systems to 'find' resource-rich patches depends on their total plant biomass, perhaps because they 'sample' a greater soil volume, large plants would enjoy greater average resource availability per volume occupied space. At least in some plant populations, this seems reasonable, for example in plants with deep tap roots (Richards and Caldwell 1987, Caldwell and Richards 1989, Dawson 1993), provided that the ability of plants to extend deeper into the soil depends on root biomass.

This mechanism for positively asymmetric competition at the scale of whole plants does extend to above-ground competition for environments with patchy light distribution, since many plants also have the ability to seek high light environments (Givnish 1982, Smith and Morgan 1983, Cosgrove

1986, Smith 1986). The effect of plant foraging on competitive symmetry on a whole-plant scale undoubtedly depends on the scale of the environmental patchiness in relation to the sizes of the spaces plant individuals occupy.

The examples indicated that certain physiological differences between individuals can influence the symmetry of growth in the short and long term, but the influence should be small. Can this result be generalized? I introduced physiological differences in two ways: through imposing a cost of maintenance and an acclimation response to low research capture. The cost of maintenance is by no means the only mechanism that affects resource utilization efficiency. In high light environments, for example, plants that capture more light typically receive a greater average light intensity, have greater leaf temperatures, and lower humidity at the leaf surface. Some photosynthesis models suggest that the carbon gain is maximal from the upper midsection of canopies, rather than the top (Barnes et al. 1990). In such canopies, the photosynthetic efficiency of light utilization may be lower for the largest plants than for medium-sized plants. High light intensities may even intermittently stop photosynthesis during intervals of high transpiration demand by inducing stomatal closure (Schulze 1986). Many, perhaps most, natural populations go through cycles of alternating light and water limitation, diurnally, or between rainfall events. During periods of water limitation, plants are more susceptible to photoinhibition, which may

additionally depress the growth rates of large, tall plants. Therefore, the times in which large plants can turn greater light capture into a growth advantage may be limited. At other times, short plants may have the benefit through reduced exposure to high light intensity and lower transpiration demand. Since the seasonally-integrated symmetry of growth reflects the cumulative growth symmetries throughout the season, it is probably often overestimated by the assumption that growth is continuously governed by competition for light.

Acclimate to low resource capture opposed the effects of positively asymmetric competition on the symmetry of growth without preventing it (Figure 4B). However, there may be other mechanisms of acclimation that do not depend on resource capture directly, but on cues of future competition. For example, seedlings are known to respond to crowding, before there is any resource competition (Ballare et al. 1990). Such responses to the light environment are mediated by the photoreceptor phytochrome, which detects the proximity of neighboring plants through the modification of light quality. If such 'anticipatory' mechanism of acclimation prevail, small seedlings may, in fact, largely escape competitive suppression (Grace 1977, Morgan and Smith 1993, Smith 1983). Phytochrome-induced responses may also be responsible for differences in the 'static' and 'dynamic' allometry of plants, i.e. the observation that plants of the same size at different planting densities can have quite different structure (Weiner

and Fishman 1994).

In summary, I have argued that the symmetries of competition and growth are not simply a function of the type of limiting resource, but that they are determined by spatial relationships between competitors, their resources, and the interactions between them. Nevertheless, some generalizations seem possible. Whole plant competition and growth will generally be more positively asymmetric the greater population density. The magnitude of the density response of the symmetries of whole-plant competition and growth depend on the local symmetry of competition. The seasonally-integrated symmetry of growth is determined by the cumulative growth symmetries between the seedling stage and maturity. Thus, the seasonally integrated symmetry of growth for annual plant populations may be quite variable between years, but within years, the symmetries of whole plant competition and growth should become more positive with density. Thus, at least within neighborhoods or in environments without site differences, size variability should increase with density.

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LEGENDS

Figure 1. The symmetry of growth index, $\ln(s)$ (solid lines), and two components, $\ln(c)$ and $\ln(a)$ (broken lines), as functions of log ratios of the biomass involved in resource uptake, $\ln(B_X^1/B_X^2)$. Competition for resource in the region of overlap is symmetric. A: at the distance $d=1.5$. B: at the distance $d=0.5$. Other parameter settings are: $B^1=100$, $\alpha=0.7$, $V_{max}=7$, $K=20$, and $k=0.4$.

Figure 2. The symmetry of growth index, $\ln(s)$ (solid lines), and two components, $\ln(c)$ and $\ln(a)$ (Broken lines), as functions of the log rations of the biomass involved in resource uptake, $\ln(B_X^1/B_X^2)$. Competition for resource in the region of overlap is positively asymmetric. A: at the distance $d=1.5$. B: at the distance $d=0.5$. Other parameter settings are: $B^1=100$, $\alpha=0.7$, $V_{max}=7$, $K=20$, and $k=0.4$.

Figure 3. The change in the log of the biomass ratio $\ln(B^1/B^2)$ with time for symmetric competition in the space of overlap under the null model (solid lines), the cost of maintenance model (long-dashed lines), and the cost of maintenance and acclimation model (short-dashed lines). A: at the distance $d=1.5$. B: at the distance $d=0.5$. Other parameter settings are: $B^1(0)=1.0$, $B^2(0)=0.5$, $V_{max}=7$, $K=20$, $k=0.4$, and $\varepsilon=4$. For the two

models without acclimation: $\alpha = 0.7$, for the model with acclimation: $c_{max} = 0.9$ and $\Delta c = 0.4$.

Figure 4. The change in the log of the biomass ratio $\ln(B^1/B^2)$ with time for positively asymmetric competition in the space of overlap under the null model (solid lines), the cost of maintenance model (long-dashed lines), and the cost of maintenance and acclimation model (short-dashed lines). A: at the distance $d = 1.5$. B: at the distance $d = 0.5$. Other parameter settings are: $B^1(0) = 1.0$, $B^2(0) = 0.5$, $V_{max} = 7$, $K = 20$, $k = 0.4$, and $\varepsilon = 4$. For the two models without acclimation: $\alpha = 0.7$, for the model with acclimation: $c_{max} = 0.9$ and $\Delta c = 0.4$.

Figure 5. The seasonally-integrated symmetry of growth index, $\ln I$, for a 30 iteration interval as a function of the distance between competitive pairs. Results are shown for positively asymmetric (+ asymmetric) and symmetric local competition. Solid lines: the null model, long-dashed lines: the cost of maintenance model, short-dashed lines: the cost of maintenance and acclimation model. Parameter settings are: $B^1(t = 0) = 1.0$, $B^2(t = 0) = 0.5$, $V_{max} = 7$, $K = 20$, $k = 0.4$, $\varepsilon = 4$, and $\gamma = 0.005$.

For the models without acclimation: $\alpha = 0.7$, for the model with acclimation: $c_{max} = 0.9$, $\Delta c = 0.4$, and $W = 0.10$.

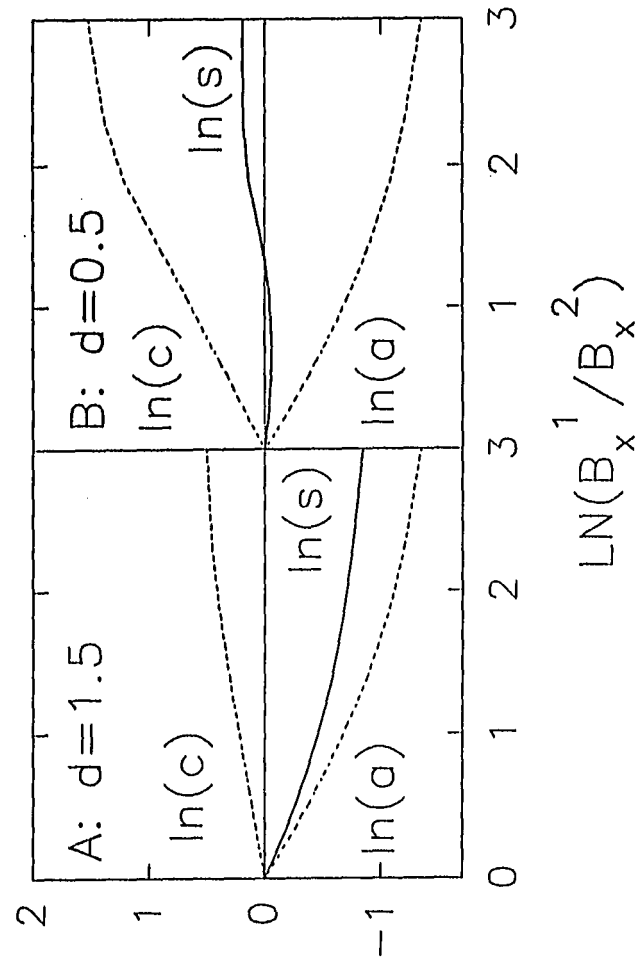


Figure 1.

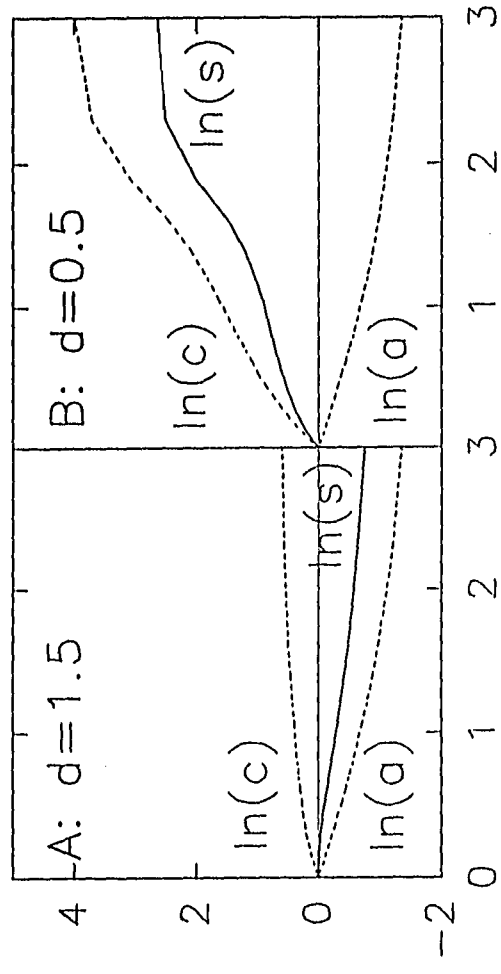
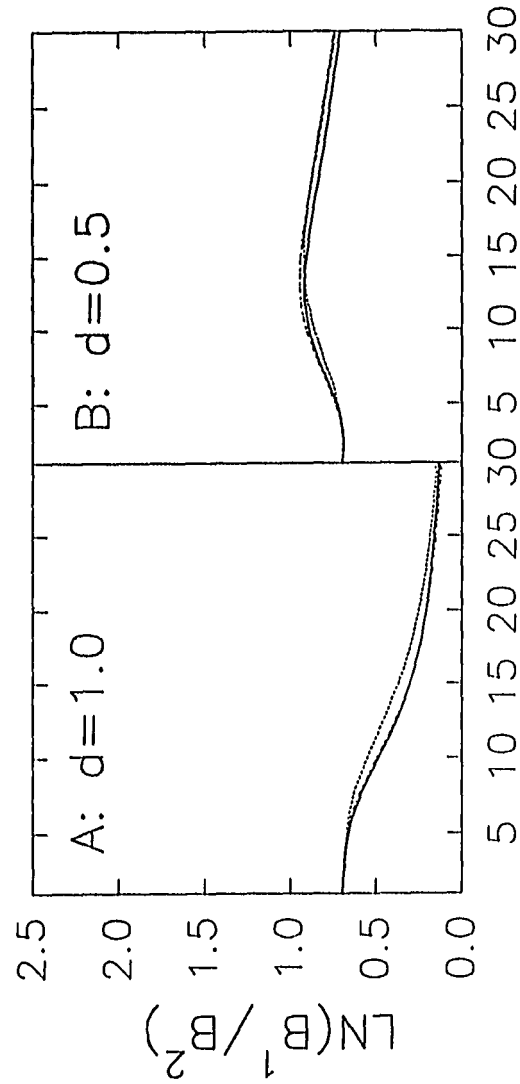


Figure 2


A: d=1.0
B: d=0.5
LN(B¹/B²)
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TIME

Figure 3

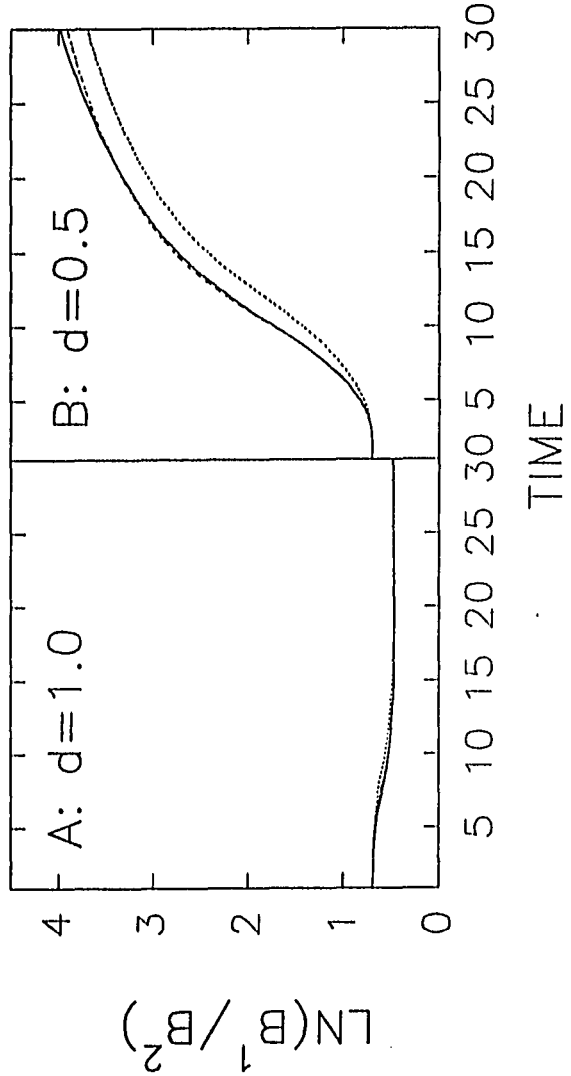
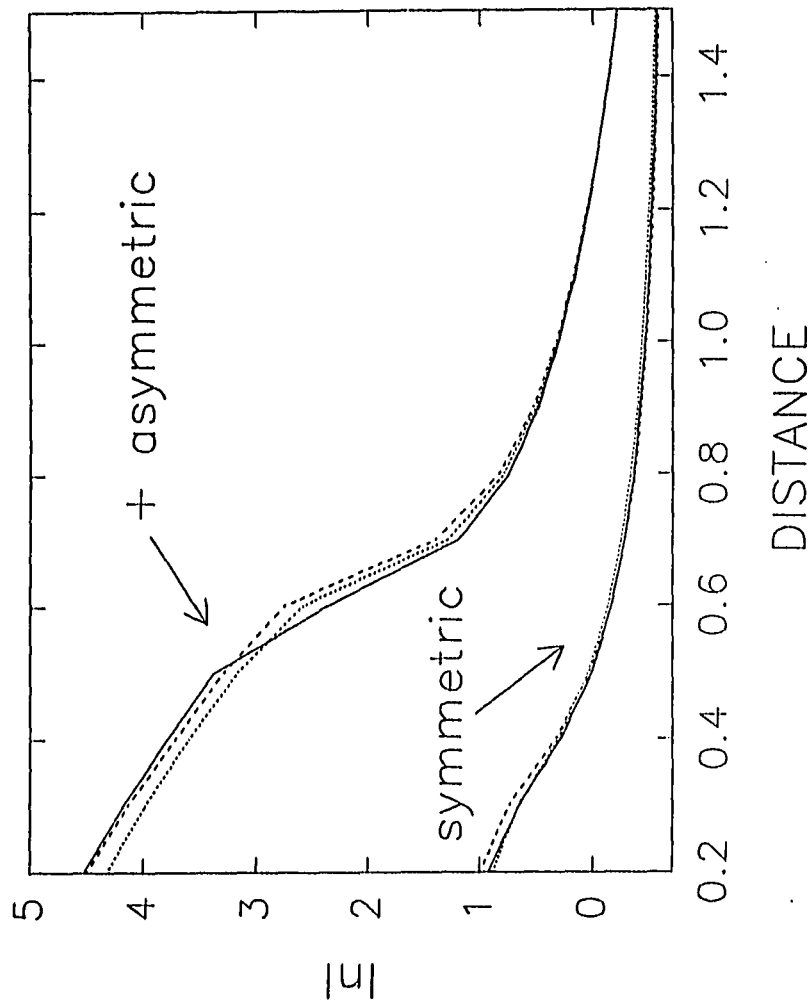


Figure 4

Figure 5



APPENDIX B

EFFECTS OF COMPETITIVE SYMMETRY ON SIZE STRUCTURE AND DISTRIBUTION-MODIFYING FUNCTIONS OF ANNUAL PLANT POPULATIONS.

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ABSTRACT

I reconsider the effects of competitive symmetry on even-aged non-thinning populations of annual plants. I do this by using a suite of simulation models that differ in competition type, spatial complexity, and sources of random variation. I show that the effects of competitive symmetry on size structure and their interactions with density depend critically on the nature of random variation. On the other hand, random variation has very little influence on empirical distribution-modifying functions, which may be interpreted as indicators of the seasonally-integrated, population-wide symmetry of competition. However, empirical distribution-modifying functions are often poorly correlated with changes in the size distribution of populations.

Key Phrases: symmetric and asymmetric competition, population size structure, distribution-modifying functions, random environmental variation, random height variation.

INTRODUCTION

One of the important questions in ecology is how the emergent properties of populations are explained in terms of the attributes and interactions of its individuals. In plants, individual performance is recorded in plant size. The size structure of a population reflects the many processes that influence the growth of individuals. In turn, size structure governs important aspects of population ecology and genetics, for example, population dynamics (e.g. Lomnicki 1980, Law 1983, Pacala and Weiner 1991), competition and community ecology (e.g. Biere 1987, Huston and Smith 1987, Smith and Huston 1989, Kohyama 1992), and population genetics (e.g. Altfinger et al. 1985, Wall and Begon 1985, Schmitt et al. 1987, Ackerly and Jasienscki 1990, Rice 1990).

However, understanding the generation of size structure in plant populations -- even if composed of even-aged individuals -- is very difficult (Huston and DeAngelis 1987). In addition to intrinsic factors that regulate plant growth and vary between individuals (e.g. morphological and physiological states), plant growth is strongly influenced by the immediate local environment, such as site quality, and the distances and the sizes of competing neighbors. The present study examines how crowding, in combination with other intrinsic and extrinsic sources of variation, affects the growth rates of individuals and population size structure.

The effects of crowding on population size structure have been

investigated for nearly 40 years (starting with Koyama and Kira 1956). One of the main results is a general consensus that there are two forms of competition with contrasting effects on populations (Weiner and Solbrig 1984, Firbank and Watkinson 1985, Weiner 1990). One form is called scramble, two-sided, or symmetric competition . It often has no effect or reduces relative size variation in populations (as measured, for example, by the coefficient of variation). The other form of competition is called pre-emptive, one-sided, or asymmetric competition. It often increases the relative size variation in populations. It has been suggested (e.g. Weiner and Thomas 1986) that the size structure of crowded populations is determined to a great extent by the symmetry of competition.

The two competition types are often, but not always, distinguished by the way that individual plants divide a resource to which they have simultaneous access (e.g. Ford 1975, Firbank and Watkinson 1985, Miller and Weiner 1989). Plants compete directly only in spaces in which they overlap with other plants. If individuals 'scramble' for resources within the region of overlap, i.e. if each individual captures resources in proportion to the biomass involved in resource uptake, competition is considered symmetric. If larger plants pre-empt resources from smaller ones within the region of overlap, competition is considered asymmetric.

Recently, Weiner (1990) introduced a slightly different definition for the symmetry of competition. He calls a competitive interaction absolute

symmetric, if competitors receive the same amount of resources, independent of size. Competition is relative symmetric if competitors capture resources in proportion to their sizes. Competition is asymmetric, if large plants capture a disproportionally large share of the resources, while smaller plants receive less than the proportional share. The absolute asymmetric case is a form of competition in which the resource capture of larger plants is completely unaffected by smaller competitors. Thus, Weiner's definition is based on the comparison of the resource uptake of whole plants, rather than on the comparison of the resources uptake between only those fractions of the total plant biomass which are in direct interaction. These two definitions are not equivalent and can lead to contrasting assessments of competitive symmetry (Schwinning 1994). In the present study, I adhere to the first definition of symmetric and asymmetric competition, distinguished by the attributes of resource division within spaces where competitors overlap.

Direct evidence for the distinct effects of symmetric and asymmetric competition on population size structures has come largely from simulation models. In simulations, symmetric competition tends to maintain the shape of the initial size distribution throughout growth. Increasing density has either no effect on relative size variation or decreases it. Asymmetric competition generates highly positively skewed size distributions reflecting a 'hierarchy of exploitation' (Harper 1967), or bimodal distributions. Bimodal distributions usually occur only at intermediate levels of asymmetric competition. In

asymmetric models, increasing density increases relative size variation (e.g. Ford 1975, Diggle, 1976, Gates 1978, Aikman and Watkinson 1980, Ford and Diggle 1981, Firbank and Watkinson 1985, Weiner and Thomas 1986).

There is some evidence for the distinct effects of symmetric and asymmetric competition in real plant populations. This is based on the assumption is that competition for light is asymmetric and competition for water and nutrients is symmetric (Harper 1977, Weiner and Thomas 1986, Weiner, 1990). For example, greenhouse populations of annual plants that are subjected to light limitation develop greater relative size variation than populations that are subjected to competition for soil resources (Newberry and Newman 1978, Weiner 1986, Wilson 1988). The common observation that crowded monocultures of annual plants increase relative size variation and skewness until the beginning of self-thinning is interpreted as a consequence of asymmetric competition for light (e.g. Ford 1975, Weiner and Thomas 1986; Schmitt et al. 1987).

These generalizations about the distinct effects of competition type do not, however, always hold. For example, if there is variation in the intrinsic growth rates of plants, relative size variation and skewness increase in time independent of the form of competition, or whether there is competition at all (Koyama and Kira, 1956; Koch, 1966). In some cases, relative size variation increases with time but not with density even though competition is asymmetric (Waller 1985). Bimodal distributions tend disappear if the intrinsic growth rate

variation is high (Ford and Diggle 1981). On the other hand, if plant spacing is random, size variation increases with time and density under both forms of competition (Bonan 1988 and 1991, Miller and Weiner 1989). Size distributions can even become bimodal under symmetric competition (Huston 1986).

These counter-examples suggest that the effects of competition on size structure depend critically on the types of heterogeneities contained in the models. Here, I test this hypothesis systematically, by comparing the effects of competitive symmetry between models that differ in spatial complexity and the nature of random variation.

The models are spatially explicit like the models of Gates (1975), Aikman and Watkinson (1980), and Ford and Diggle (1981), but also realistic with respect to resource uptake, like the model of Hara (1986). In all models competition is for light, so that the symmetry of competition is determined by the nature of the allometric relationship between biomass and height. In model 1, competition is symmetric, since biomass does not give a height advantage. In model 2, competition is asymmetric, because height is positively correlated with biomass. In both models, all individuals in the population are of the same type, although individuals vary in biomass or height. In model 3, I examine the consequences of asymmetric competition on a rare genotype or species with a height disadvantage relative to the resident genotype or species.
Random variation is imposed on 1) the height of individuals, 2) site quality, and 3) plant spacing in all three models. I interpret the simulation results with the

help of empirically derived distribution-modifying functions (DMFs). The concept that DMFs characterize aspects of plant competition and predict changes in population size structure was introduced by Westoby in 1982 and elaborated by Hara in the following years. I review the basic concept below and then show, how I modify it to use it as an analytical tool in the present study.

Distribution-modifying functions.

Westoby (1982) defined distribution-modifying functions (DMFs) as functions that relate the growth rates of individuals to their initial biomass. They are at least in part influenced by competitive interactions among individuals, thus, by competitive symmetry, but the exact relationship between competitive symmetry and the shape of these functions is unclear. Weiner (1990) speculated that the shape of DMFs should signify the symmetry of competition, by indicating how the average growth rates of small and large individuals compare.

DMFs can be represented on an absolute or log scale. Either way, there are simple relationships between the shape of a DMF and the changes imposed on plant size distributions. They permit, in principle, the prediction of final size distributions, if the initial size distributions are known. These relationships are briefly reviewed in Figure 1. A linear DMF increases the standard deviation of a distribution if its slope is positive (Figure 1A), and

decreases the standard deviation if its slope is negative (Figure 1B). Higher moments are not affected. If the DMF is a second order polynomial the skew of a distribution is affected, but not higher moments. A concave DMF introduces positive skew (Figure 1C), and a convex DMF negative skew (Figure 1D). Finally, if the DMF is a third order polynomial, standard deviation, skew, and kurtosis are affected. For example, a sigmoidal DMF generates bimodality (Figure 1E).

These predictions are true only if the DMFs are exact. However, there may be variation in the growth increment of individuals of a certain size, which would also affect the final size structure. Hara (1984a,b) included the effect of such variation in the prediction of size structure using the Kolmogoroff forward equation. Hara's G-function describes the average growth increment of individuals as a function of size. Except for describing the average rather than the exact value, it is equivalent with Westoby's DMF. Hara's D-function describes the variance of individual growth increments as a function of size. This variation would be caused, for example, by genetic variation or local variation of crowding. Hara showed that positive skewness is generated not only by a concave DMF, but can also be generated by the combination of a linear DMF, and a positively sloped D-function.

Empirical distribution-modifying functions

Westoby's (1982) discussion of DMFs and Hara's (1984a,b) discursion of

G- and D-functions are based on the assumption that these functions are known from morphological and physiological characteristics of the species. However, in this study, I use empirically derived DMFs as indicators for the symmetry of competition on a seasonally-integrated, population-wide scale and examine their potential to predict changes in the population size structure.

When DMFs are derived empirically, they are regression functions surrounded with some amount of scatter. The regression function can be regarded as a lower bound for changes in size variation. To illustrate the accuracy of this approximation, I assume DMFs are linear on a log scale. (Later, I will show that this assumption is generally adequate). If the DMF is exact, the final size $B_i(T)$ of plant i is completely determined by its initial size $B_i(0)$:

$$\ln[B_i(T)] = (1+s)\ln[B_i(0)]+a \quad , \qquad (1)$$

where a is a constant (the y-intercept of the DMF) and s is the DMF slope. The resulting size structure dynamics can be expressed as the ratio of the standard deviation of $B(T)$ and the standard deviation of $B(0)$:

$$\frac{\sigma\ [\ln(B(T))]}{\sigma\ [\ln(B(0))]} = 1+s \quad . \qquad (2)$$

If the ratio is above 1, relative variation increases, and if it is below 1, relative

variation decreases during growth. The ratio is a linear function of the DMF slope (*s*) with slope 1 through (1,0). Note that the sign of the DMF slope determines if variation increases or decreases during growth.

If the DMF is not exact, but a regression line with deviations e_i, $B_i(T)$ can be expressed as

$$\ln[B_i(T)] = (1+s)\ln[B_i(0)] + a + e_i \quad . \tag{3}$$

Then, the change in variation is

$$\frac{\sigma\,[\ln(B(T))]}{\sigma\,[\ln(B(0))]} = \sqrt{(1+s)^2 + \left(\frac{\sigma\,[e]}{\sigma\,[\ln(B(0))]}\right)^2} \quad . \tag{4}$$

This relationship is shown in Figure 2 with different values for $\sigma[e]$.

As expected, random variation in the growth rates add to the increase in the size variation above what is explained by the DMF slope (equation 2). The effect of random variation is greater if the DMF slope is small. The greater its standard deviation, the less is size structure dynamics correlated with the DMF slope.

This simple example suggests that competitive factors (which are presumably reflected in the DMF slope) and random effects on growth rates can contribute to size structure non-additively. This may represent a serious problem for using empirical DMFs to explain changes in size structure.

METHODS

Simulations

Resource division and growth

Here, I explain only the central ideas behind the model. It is fully explained in Appendices 1 and 2. Plants of a population are grouped in neighborhoods containing one or more individuals. The growth of individuals is modeled in discrete time, driven by the conversion of daily intercepted light into biomass. Light is intercepted by plant canopies which, depending on canopy sizes and distances, may overlap. Competition for light occurs only where canopies overlap. Within these regions of overlap, taller canopies intercept more light per unit leaf biomass than shorter ones. Thus, the symmetry of competition in the present models is determined entirely by the relationships between plant biomass and canopy height.

The daily intercepted radiation determines the daily rate of photosynthesis. The daily photosynthetic flux above a unit ground area is maximal, if all daily incident light is intercepted. However, if only a fraction of the daily incident light is intercepted, the daily photosynthetic flux is also only a fraction of its maximum. The daily photosynthesis of an entire canopy is determined by the daily maximal photosynthetic flux P_{max}, the ground area covered by canopy, A_i, and the proportion of the incident daily light flux that is intercepted by the canopy Q_i:

$$P_i(t) = Q_i(t) P_{max} A_i \quad . \qquad (10)$$

The proportion of the incident light that is intercepted depends on the leaf area index, $l_i(t)$, of canopies. The leaf area index is defined as the ratio of leaf area to ground area. For single plants and assuming that leaf area is distributed evenly above the ground, Q_i is a negatively exponential function of $l_i(t)$:

$$Q_i(t) = (1 - e^{-\varepsilon l_i(t)}) \quad , \qquad (11)$$

where ε is the canopy extinction coefficient (Monsi and Saeki 1953). Where plants overlap, the proportion of intercepted daily light flux is a function of the combined leaf area indices of all plants present in the overlap. The distribution of the intercepted light among individuals, thus, the symmetry of competition, depends on the vertical leaf area distribution of individuals. I examine three symmetry models.

Model 1: The seedlings in a population are either equally tall, or have only random height variation with respect to biomass. If seedlings are equally tall, they remain so throughout growth. In that case, individual plants differ only in the ground area they cover and in the biomass density within. This pattern of growth is equivalent to an extreme form of a growth pattern that Hara (1993) called the 'width-growth type', and may be exemplified by species with stunted

shoot axes such as grasses or certain rosette plants. If seedlings have random height variation, individuals maintain their relative height differences throughout growth. However, since taller plants intercept more light and grow faster, a correlation between biomass and height may develop in time.

Model 1 is a case of symmetric competition, because light is divided, either exactly or on average, in proportion to the leaf area within the regions where plant canopies overlap.

Model 2: Height is a saturating function of biomass $B_i(t)$:

$$H_i(t) = H_{\max} \frac{B_i(t)}{B_i(t) + \alpha} \qquad (12)$$

α is the biomass at which plants have half-maximal height. This relationship between height and biomass signifies that there are limits to how tall annual plants can become and, therefore, that height differences between plants decrease during the growth of a stand. H_{max} is a constant or a random variable.

Model 2 is a case of asymmetric competition between equal competitors, because plants with greater biomass are taller than plants with less biomass, either always, or on average. The plants in the population are equal in the sense that all seedlings with the same biomass have the same height exactly, or the same mean height.

Model 3: Height is a saturating function of biomass, but one plant in

each neighborhood (called focal plant with index i=1) is a short genotype or species:

$$H_i(t) = H_{\max} \frac{B_i(t)}{B_i(t) + \alpha} \quad , \quad i \neq 1$$
$$H_1(t) = \beta H_{\max} \frac{B_1(t)}{B_1(t) + \alpha} \quad , \quad 0 < \beta < 1. \qquad (13)$$

where β is a constant defining the height disadvantage of focal plants. As before, H_{max} is a constant or a random variable. Model 3 is a case of asymmetric competition between unequal competitors. Focal plants are always, or in most instances, overtopped by neighbors with equal biomass. Thus, model 3 signifies the growth of a rare, competitively suppressed genotype or species.

These three models set up three cases of competition through the division of light between individuals. I now describe how the daily photosynthesis determines plant biomass accumulation. I assume that the proportion between daily biomass accumulation and daily photosynthesis is maximal at the onset of growth and then gradually declines in time with $\tau(t)$:

$$B_i(t+1) = B_i(t) + \tau(t) P_i(t) \quad , \text{ where} \qquad (14)$$

$$\tau(t) = 1 - \left(\frac{t}{50}\right)^2 . \qquad (15)$$

Since $\tau(t)$ slows the growth of all plants in the population simultaneously and in equal proportions, this function has no other effect on size structure, than to weigh the effect of resource division on growth with time. The result of this assumption is to produce sigmoidal growth curves for individuals and entire populations.

A decline in the effectiveness of light capture to support growth is quite common in populations for a variety of reasons. For example, the cost of maintaining biomass increases, more biomass is used to build stems or reproductive structures rather than to build leaves, or plants become increasingly more limited by soil resources than by light. Whatever the reasons, the growth rates of annual plants eventually become zero, as in the present model. However, in the present model the efficiency of light utilization declines synchronously for all plants in the population, while in real populations, individuals may commonly vary in the efficiency of light utilization.

I have discussed the effects of size-dependent variation in the resource utilization efficiencies and other factors that influence the responses of plant growth rates to competition elsewhere (Schwinning 1994). There, I demonstrated that such variation can only modify, but not fundamentally change

the effects of competitive symmetry on the dynamics of relative size variation. Therefore, I chose to eliminate the size-dependence of resource utilization for the sake of simplifying the model and its interpretation, without loss of generality.

The principles of growth and resource division described above are applied in two types of models differing in spatial complexity. I call the first type non-spatial, because plants do not expand and competing plants overlap completely. I call the second type spatial, because competitors have explicit distances to one another. In both model types, I maintain the distinction between models 1, 2, and 3, since it is based only on height allometry.

The structure of non-spatial models

In the non-spatial models, the effects of resource division are disconnected from the effects of spatial expansion. Plants of one neighborhood can be visualized as occupying the ground area from the beginning to the end of growth (Figure A1). Thus, all plants in the neighborhood interact directly and all the time. Plant density in non-spatial neighborhoods is defined as the number of plants per neighborhood. Single plants, i.e. plants that grow in the absence of competitors, have density 1.

The structure of spatial models

Plants in spatial neighborhoods are aligned in rows, so that all plants

have only two direct neighbors (Figure A2). To avoid edge effects, the two row ends are linked to form a circle. The row circle is the neighborhood. It always contains 40 plants. Plant density in spatial neighborhoods is defined as the number of plants per unit area.

As plants gain biomass, they expand along both row directions with constant leaf area index until their expansion growth stops. There are two limits to horizontal expansion: 1) if plants reach a constant maximal width; or 2) if plants run into the centers of their next neighbors. After expansion growth stops, the ground area cover remains constant and the leaf area index increases. Thus, plants overlap at most with the two immediate neighbors to the "left" and "right" and nowhere do more than two plants overlap.

Unless plant density is very low, plants start to overlap before they reach their maximal width. The closer the neighbors, the sooner start plants to overlap. Within these areas of overlap, light is divided according to the height of competitors and their leaf area indices within, as in the non-spatial models. Outside the areas of overlap plants utilize the intercepted light entirely.

The assumption that plants are aligned in rows reduces the model to two spatial dimensions (plant height and diameter) rather than three. This simplifies the model and reduces the computational effort. Nevertheless, some crucial properties of a fully spatial model are captured by this model: 1) there are few direct interactions between plants; 2) the intensity of the interaction (measured by canopy overlap) changes in time; and 3) density alters the length of time for

which neighbors interact.

Sources of random variation

There are four sources of random variation:

1. Initial seedling size. Variation in the seedling sizes ($B_i(0)$) is normal with mean 0.4 and standard deviation 0.1 in all simulations. Thus the sizes of focal plants and their neighbors vary, but are drawn from the same distribution.

2. Plant height. In model 1, a 15% normal height variation is imposed on individual seedlings independent of biomass, and maintained throughout growth. In models 2 and 3 a 15% normal variation is imposed on the maximal height of individuals (H_{max}, equations 12 and 13) independent of seedling biomass, and maintained throughout growth.

3. Site. Site variation is introduced as a normal variation in the maximal daily photosynthesis (P_{max}, equation 10), as may be brought about by a variation in soil resources (It is assumed that competition for soil resources reduces the photosynthetic flux of all plants equally). Where applied it has a mean of 2 and a standard variation of 0.3 (15%).

4. Local crowding. In the spatial models, local crowding is either uniform, or entirely random. Uniform crowding it is expressed through constant, and random crowding through exponentially-distributed distances between neighbors. The exponential distribution is defined by single parameters equivalent to the average neighborhood density.

Statistics

Only one plant per neighborhood (the focal plant) enters statistical analyses to satisfy the requirement for independent observations where it applies. For model 3, this is necessary anyway, because focal plants are different from their neighbors. In models 1 and 2, excluding neighbor plants is not always necessary. On the other hand, analyzing only neighbor plants does not introduce bias. Therefore, in the interest being consistent, I chose to apply the same procedure for all analyses.

To characterize final size distributions, I calculate four univariate statistics. They are the statistics most commonly used in the description of the size structure of plant populations (e.g. Benjamin and Hardwick 1986).

The coefficient of variation (*CV*) is calculated as the percent ratio of the standard deviation of the biomass *B*, and its mean:

$$CV = \frac{100\sqrt{\frac{\sum(\bar{B}-B_i)^2}{n-1}}}{\bar{B}}, \qquad (16)$$

where n is the number of focal plants. *CV* is a relative measure of variation, i.e. it is independent of the mean. Another relative measure of variation is the standard deviation of ln(*B*), $\sigma[\ln(B)]$:

$$\sigma\ [\ln[B]] = \sqrt{\frac{\sum(\ ln\bar{n}[B] - \ln[B_i]\ )^2}{n-1}} \quad . \qquad (17)$$

A third measure of relative variation is the Gini Coefficient (*GINI*). It has recently been suggested, that *GINI* is the most appropriate index of size hierarchy (Weiner and Solbrig 1984):

$$GINI = \frac{\sum_{i=1}^{n}\sum_{j=1}^{n}|(B_i - B_j)|}{2\ n^2\ \bar{B}} \quad . \qquad (18)$$

A relative measure of skewness is the dimensionless third moment around the mean (g_3) (Sokal and Rohlf 1981):

$$g_3 = \frac{(\ \bar{B} - B_i\ )^3}{n * \sigma^3[B]} \quad , \qquad (19)$$

where $\sigma[B]$ is the standard deviation of *B*.

I define empirical DMFs as regression functions of the relative growth increment of individuals during their entire life spans (50 iterations) on the log of their initial size. The relative growth increment of the ith plant is defined:

$$RGI_i = \ln(B_i(50)) - \ln(B_i(0)) \quad . \qquad (20)$$

RESULTS

I discuss the simulation results in two parts. First, I present characteristics of the size structures generated by the three models. Second, I examine empirical DMFs and their capability to reflect changes in size structure.

1. Competitive symmetry and size structure

The shapes of size distributions

In the absence of individual and site variation, and if local crowding is uniform, models 1, 2, and 3 produce three distinct size structures. Qualitatively, they are most distinctive in the non-spatial models (Figure 3), but are essentially the same in the spatial models (Figure 4A). In the spatial models, relative size variation is, however, much lower, because competitors interact for a smaller amount of time and at first in only a fraction of their total volume (see discussion of this point in **METHODS**).

Under model 1 (in Figures 3 and 4A), an initially normally distributed seedling population stays normal or becomes negatively skewed. This happens, because plants are always equally tall, so that all plants in a neighborhood receive nearly equal amounts of light per leaf area. They can become negatively skewed, particularly in the spatial model, because large plants self-shade more than small plants and consequently, have lower relative growth rates.

Under model 2, size distributions tend to become bimodal. Populations

divide into two sub-populations: one containing small, short plants that are heavily shaded by neighbors, and one containing large, tall plants that are predominantly self-shaded.

Under model 3, size distributions stay unimodal and become positively skewed. Since focal plants are half as tall as their neighbors for the same biomass (**METHODS**, equation 7), they are almost always intensely neighbor-suppressed and do not form a distinct sub-population of predominantly self-shaded plants.

The effects of different sources of random variation on size structures are shown only for the spatial models. In Figure 4B, plants have random variation in height. In model 1, this gives the distribution a little more right-skew. In models 2 and 3, random height variation has a surprisingly small effect on the shape and range of the size distributions.

In Figure 4C, sites differ in the maximal photosynthetic flux a plant can have (P_{max}, see **METHODS**, equation 10). In Figure 4D, plants are randomly spaced. In both cases, the distributions of all models become more variable and right-skewed. The bimodal distributions of model 2 in Figures 4A and B are replaced by unimodal distributions. Thus, if site quality or the distances between plants vary, the distributions of the three models become less distinctive.

Density effects on size variation in spatial models

If there is no site or individual variation and plant spacing is uniform, relative size variation, as expressed in *CV*, $\sigma(\ln(B))$, and *GINI* (see **METHODS**) increases with density only if competition is asymmetric (Figure 5, models 2 and 3). Skewness (g_3) increases slightly under model 1, and most dramatically under model 3.

Nevertheless, in some cases asymmetric competition allows relative variation and skewness to decrease between the beginning and the end of the growing season. In Figure 5, the dotted lines indicate the values of the statistics for the initial size distributions of populations. At low density, all statistics have lesser value, indicating that the plants of a population gain similarity in relative sizes during growth.

Relative variation (*CV*, $\sigma(\ln(B))$, and *GINI*) is usually higher in model 2 than in model 3. In contrast, skewness (g_3) increases much faster with density in model 3. Of the three measures of relative variation *GINI* appears least robust to random variation between samples, and $\sigma(\ln(B))$ shows the greatest difference between models 2 and 3.

If plant heights vary randomly but site quality and plant spacing remain uniform, the density responses of size variation are very similar to the previous ones (Figure 6). Random height variation makes the greatest difference in model 1, where it permits relative variation and skewness to increase slightly with density. If sites vary randomly, relative variation first drops at low density, then increases in models 2 and 3, but continues to drop with density in model

1. Skewness tends to decrease with density in models 1 and 2, but increases in model 3.

Again, there are several cases in which relative variation decreases during growth, for example, at low density under any model if heights vary randomly, and at high density under model 1, if sites vary randomly.

The density responses of size variation in randomly-spaced populations is shown in Figure 7. With or without site or height variation, the response of all models is similar: relative variation and skewness increase with density. In models 1 and 3 relative variation may drop slightly at high density. Models 1, 2, and 3 are distinguished only by the magnitudes of the responses.

Relative variation and skewness almost never decline during growth, if spacing is random. Even at very low density, some plants have to compete with neighbors, grow with reduced rate, and consequently increase the population size variation.

In short, there is no general relationship between the symmetry of competition and size structure. Different sources of variation interact with the symmetry of competition and density in different ways. Under symmetric competition, density does not influence relative size variation if height, site and plant spacing are non-random, it increases relative size variation if height or plant spacing is random, and it decreases relative size variation if site quality is variable. Under asymmetric competition, density usually increases relative size variation, except at low density if site quality varies. At low density, the

influence of asymmetric competition on the growth of whole plants is generally low, because plant canopies overlap only for a short time and late during growth, when height differences and the effects of resource capture on growth are smaller. Thus, populations miss a phase of most effective asymmetric competition and act more as though competition is symmetric.

2. Competitive symmetry and empirical DMFs

The shapes of the DMFs

Figure 8 shows DMFs for the non-spatial models at three densities. Single plants (density=1) in all models have DMFs with negative, nearly constant slope. They illustrate that small plants have a greater relative biomass gain than large plants. This surprising result is explained by the fact that initially smaller plants start to self-shade later than initially larger plants and consequently, stay longer in a phase of nearly exponential growth.

In model 1 (Figure 8A), increasing density does not affect the curvature of the DMF very much. It lowers the y-intercept and increases the DMF slope slightly, but never above zero. In effect, symmetric competition tends to diffuse the advantage of being initially small, but stops short of giving an advantage to initially large individuals.

In model 2 (Figure 8B), DMFs become sigmoidal in shape with increasing density, as Westoby (1982) proposed for asymmetrically competing plants. This indicates that initially large plants are nearly unaffected by

neighbors, while initially small plants are more strongly inhibited than in the symmetric case. The greater the height differences between plants, the more non-linear is the DMF (results not shown).

In model 3 (Figure 8C), DMFs become convex with increasing density. One can interpret the DMFs as sigmoidal curves that are cut off on the right: large focal plants never approach the growth rates of large single plants, since they lack the power to completely suppress their neighbors.

Thus, in the non-spatial models, the three models generate unique DMFs at least at high density. In the spatial models this is different (Figure 9). The DMFs of the spatial models are more linear, in general. In model 1 (Figure 9A), the main effect of increasing neighbor density is to lower the y-intercept without greatly affecting the DMF slope. In model 2 (Figure 9B), the over-all slope increases with density, but the DMF is usually not sigmoidal, except at very high density. In model 3 (Figure 9C), the DMF is nearly linear, as in model 1, but the slope increases with density.

In the three spatial models the symmetry of competition cannot easily be distinguished by the DMF shape. The DMFs are most non-linear, if competition is strongly asymmetric, but under highly asymmetric competition there is also a large amount of scatter around the DMF regression curves (omitted from Figures 8 and 9, but shown in Figure 11). Thus, in practical application, non-linear trends in empirical DMFs may often not be significant. However, below I show that the response of linear DMF regression slopes to density are

characteristic of asymmetric competition. Furthermore, this density response is predictably different between models.

The density responses of the DMF slopes in spatial models

Figure 10 shows how the slope parameter of the linear regression DMF changes with density. The estimates are based on the same simulations that gave rise to Figures 5-8.

The density responses of the DMF slope estimates are quite distinct for the three models. In model 1, the DMF slope does not increase with density with the exception of a small increase at very low density. In models 2 and 3, the DMF slope increases substantially with density, but more slowly in model 3. In both models, the slope increase diminishes at high density.

The three models maintain their distinct density-responses under random variation in height, site, or spacing (Figure 10). Random variation tends to increase the DMF slope slightly at low density, and decreases the DMF slope slightly at high density. If there is random variation, the DMF slope decreases with density in model 1. Height variation, whether plant spacing is uniform or random, causes the greatest effect on the DMF slope.

The surprising robustness of the DMF slope estimates to different sources of random variation calls for an explanation. An example for the way in which DMFs vary between different sites is given for model 2 (Figure 11). The good site (high P_{max}) generates a slightly steeper DMF than the average site.

Conversely, the bad site generates a DMF with a slightly more shallow slope. The DMF generated from data for all three sites generates a DMF that is nearly indistinguishable from the DMF of the average site. The difference in the slope between the three sites is explained by differences in the duration and the intensity of competition. In the bad site all plants grow more slowly and start to interact later. In the good site all plants grow faster and interact sooner. If competition is asymmetric, this difference in the intensity of competition is reflected in the DMF slopes. Variation around some average site quality increases in the scatter around the DMF regression line, therefore, but has little effect on the DMF slope.

These results mean that if a population is distributed across a patchwork of sites with variable qualities, empirical DMFs estimated from small subpopulations can vary in slope according to the local site quality. However, empirical DMFs for the entire population should be similar to the DMF derived for a sub-population growing in an average site. Therefore, unless the site variation influences the sizes of seedlings, DMF regressions for populations sampled from a heterogeneous range should give a good indication for the average symmetry of competition between individuals.

DMFs as predictors of size structure in spatial models

Since final size structures respond greatly to random variation (Figures 4, 6, and 7), but DMF slopes do not (Figures 10 and 11), DMFs cannot be very

accurate predictors of size structure dynamics. Moreover, even in the absence of any other sources of random variation, except the sizes of neighbors, DMFs do not account for size structure very well. This is illustrated in Figure 12 for model 2.

In this example the DMF is sigmoidal (Figure 12A) and has a great amount of variation around it. This variation is not homoscedastic, but a function of size (Figure 12B). The variance of the relative growth increment corresponds to Hara's D-function (1984a, see **INTRODUCTION**). Variation is maximal in the intermediate seedling size range, just below the mean. The associated final size distribution appears bimodal on log scale (Figure 12C), just as Westoby (1982) assumed for sigmoidal DMFs (compare with Figure 1). However, the apparent sigmoidal curvature of the DMF does not suffice to explain the two modes in the size distribution. This is demonstrated in Figure 12D which shows the size distribution predicted on the basis of the regression DMF. It is not bimodal and looks quite different from the actual size distribution (Figure 12C). Thus, the two modes of the actual size distribution are explained, not by the average growth rates of plants with a certain size, but by the variation of their growth rates (Figure 12B). In particular, the two modes appear to be generated by the size variation of medium sized seedlings, which can become members of either the suppressed or the dominant sub-population.

If there is additional environmental variation the match between DMFs

and size structures is necessarily worse. Figure 13 gives an overview of the accuracy with which DMF slopes predict changes in size structures. This representation is equivalent to the one in Figure 2. In model 1, the DMF slope has virtually no predictive power, because the DMF slope is independent of density. In models 2 and 3 without site or height variation, and if plants are evenly spaced, variation increases faster with density than the DMF slope suggests. There is a positive correlation between the DMF slope and the change in relative variation throughout. With random spacing, the correlation between the DMF slope and the change in relative variation is also positive, except at high density in model 3. The change in variation is, however, much higher than predicted. This suggests that asymmetric competition contributes to size variation, even if the main source of variation is plant spacing. If sites vary, the correlation between the change in relative variation and the DMF slope is negative at low density, showing that asymmetric competition reduces size variation. On the other hand, the presence or absence of height variation does not affect the accuracy of the prediction very much.

DISCUSSION

These simulation results allow three general conclusions. First, there is no general relationship between the symmetry of competition, density and size structure. Second, at least in these simulations, there is a consistent difference in the density-dependence of empirical DMFs between symmetrically and

asymmetrically competing populations. The third conclusion follows from the first two: empirical DMFs do not in general predict size structure dynamics.

Size structure and the symmetry of competition

Many previous simulation results showed that symmetric and asymmetric competition have distinct effects on size structure (e.g. Aikman and Watkinson 1980, Ford and Diggle 1981, Firbank and Watkinson 1985). Asymmetric, but not symmetric competition 1) increases relative size variation in time, 2) increases relative size variation with density, and 3) has the capacity to produce extremely positively skewed or bimodal size distributions. The present study confirms these patterns (Figure 4 and 5). However, I show that they hold only in special cases, when key environmental factors (such as site quality and plant spacing) are held constant and when density is above a certain minimum.

Below a minimum density, relative size variation can decrease during growth, even though competition is asymmetric (Figures 5 and 6). The existence of a minimum density suggests that asymmetric competition must be strong enough to offset the tendency of plants to converge in size, before it can cause plants to diverge in size. I explain the reason for this pattern through growth rate analysis elsewhere (Schwinning 1994).

Increasing density under asymmetric competition does not always lead to an increase in relative size variation. If sites vary in quality and if density is low, relative size variation drops with density (Figure 6). This happens,

because weak asymmetric competition generates little variance in the relative growth rates of plants within neighborhoods, while it can greatly lower the variance in the average relative growth rates of plants between neighborhoods. If the variance reducing effect of competition outweighs the variance increasing effect of asymmetric competition, relative size variation decreases with density.

On the other hand, under symmetric competition relative size variation can increase with density. This happens if the spacing between plants is random, independent of whether other sources of variation act simultaneously (Figure 7). Random spacing introduces large differences in the use of space by individuals. Plants that occupy a large space (because the next neighbors are distant) receive more resource per unit biomass than plants that occupy less, a) because they self-shade less and, b) because they overlap less with other canopies. Plants develop differences in relative growth rates, not because some plants take a greater share of the resource from regions of overlap, but because some plants have more available space than others.

Random variation in the height of individuals does not affect size distributions very much if competition is asymmetric (Figures 4 and 6). This in agreement with Hara's (1986) result. If competition is symmetric, random height variation can lead to an increase of size variation with density, showing that random height variation is more important to generating size structure if competition is symmetric. Random height variation can lead to asymmetric resource division in the spaces of overlap, however, since the resource capture

advantage is assigned to seedlings irrespective of seedling biomass, large seedlings and small seedlings have equal average advantage.

As shown in other studies (e.g. Koyama and Kira 1956, Koch 1966) random variation of site and spacing, but not of plant height alone, generate positive skewness in populations and swamp any tendency for size distributions to become bimodal. This may explain why bimodal size distributions are easier to generate in models than to find in nature.

Empirical DMFs and the symmetry of competition

A link between the symmetry of competition and the shape of the DMFs has been assumed by several authors (e.g. Westoby 1982, Weiner 1990). Hara (1986a,b; 1992) characterized that link on the basis of allometric relationships and assuming spatially uniform competition for light. By the assumption of spatial uniformity, allometric height functions do not only define the symmetry of competition locally, within any section of the canopy, but define the symmetry of competition at the population level, as well. In this study, I relax the assumption of spatial uniformity and show that it is necessary distinguish between the local symmetry, i.e. the symmetry of competition in regions where plants overlap, and population-level effects of competition, expressed here in empirically derived DMFs.

In these simulations, empirical DMFs (on log scales) are adequately characterized by linear regressions in spatial models (e.g. Figures 9 and 11).

Nevertheless, this limited ability to characterize different DMFs suffices to distinguish the local symmetry of competition. If competition is symmetric, the DMF regression slope does not increase with density. If competition is asymmetric, it does. Size-independent sources of variation, such as variation in height, site, or spacing, have only minor effects on the DMF slope and do not alter the qualitative link between DMFs and the symmetry of competition.

The symmetry of competition does not, however, determine the sign of the DMF slopes (Figures 9 and 10). In these simulations, DMF slopes for symmetrically competing plants and for asymmetrically competing plants at low density are negative. This occurs because the DMFs of single plants are negative. Thus, the existence of a mechanism for resource pre-emption (e.g. the overtopping of small plants by larger plants) per se does not guarantee that large plants take up relatively more resource than smaller plants. In model 2, large plants shade neighbors in regions of canopy overlap, but are also be highly self-shaded. On the other hand, small plants are suppressed in regions of overlap, but are less self-shaded outside regions of overlap with a large neighbor. Therefore, large plants have lower relative growth increments between the seedling stage and maturity than smaller neighbors at low density, despite asymmetric competitive interaction.

A similar relationship might hold for below-ground competition for water. The ability to compete for water is linked to the rate with which plants extract water (Eissenstat and Caldwell 1988, Caldwell and Richards 1986). This rate

depends greatly on the density of the fine root system. However, a plant that has a high rate of water extraction lowers its own water availability the most. This necessarily link between the resource depletion imposed on neighbors and the self-imposed resource depletion is often overlooked. It may set a limit to the size inequality that can be generated through resource competition.

On the other hand, it is conceivable that DMFs for some single plant populations have positive slopes, perhaps because larger plants are better able to access resource-rich sites (e.g. light gaps in an understory environment, water stored in deep soil). In that case, symmetrically and asymmetrically competing plants would have positive DMF slopes. However, in all cases one would expect the DMF slope to increase only under asymmetric competition.

This robust link between the symmetry of competition and the density response of the DMF slope has important ecological and evolutionary consequences. The fitness of an annual plant correlates with the relative size of the individual with respect to the population average, rather than its absolute size (Wall and Begon 1985). The DMF slope is therefore a measure of individual fitness differences in the population. The fact that DMF slopes increase under asymmetric competition, indicates that large seedlings always profit from an increase in density by increasing their fitness, although their absolute sizes may decrease. The simulations show that this occurs independent of other variable factors influence plant growth, such as plant spacing and site quality variation.

How realistic are the density responses of the empirical DMFs generated by these models? The central assumption of the models is that at any time, all neighboring plants utilize intercepted light in exactly the same way. Thus, differences in the relative growth increments of neighbors are completely determined by differences in their leaf area based light interception. Of course, many other mechanisms could influence the growth rates of plants, and perhaps the DMF slopes. Could these factors influence the distinct density response of DMF slopes under asymmetric competition?

I showed elsewhere (Schwinning 1994) that at least some factors which interfere with the conversion of intercepted resource into biomass, such as the cost of maintenance and acclimation to low resource capture, have little effect on the dynamics of the size ratios of competitors, thus, on DMF slopes. However, there are many other plant responses which could possibly affect DMF slopes and their density responses. Many plants become taller and narrower with increasing density, by accelerating the growth of the main axis at the cost of reduced branching (Hara 1984b, Geber 1989, Weiner et al. 1990). They tend to shift leaf area upward in the canopy (Givnish 1982, Menges 1987). Shading tends to increase the efficiency for capturing light (Boardman 1977, Smith and Morgan 1983, Gutschick and Wiegel 1988), for example by increasing the leaf angular distribution and decreasing leaf thickness. Shading tends to increase the efficiency of light utilization, for example by decreasing leaf nitrogen (Field 1983).

These plastic responses can be interpreted as adaptations to better cope with a highly competitive environment and to increase the growth rates of small plants relative to the growth rates of plants lacking these adaptations. Thus, the density responses of real DMFs under conditions of competitive asymmetry may be weaker than expected on the basis of rigid models of resource division that do not allow for plastic plant responses (Geber, 1989). Since plastic responses to density are quite common in plants, one may speculate that highly asymmetric competition between conspecific even-aged annual plants is rarely found in nature. There is evidence that crowded monocultures of grass species are dominated by symmetric rather than asymmetric competition (Turner and Rabinowitz 1983).

DMFs as predictors of size structure

In contrast to Westoby's (1982) suggestion and Hara's (1986) simulation results, in these simulations the DMF do not predict changes in size structure very accurately (Figures 12 and 13). The present simulations demonstrate that environmental variation has a variety of effects on populations. Different sources of environmental variation interact with competition in different ways. Previous simulation studies of competition have often assumed a perfectly homogeneous environment. Most experimental studies have been performed on populations raised in greenhouse flats, creating exceptionally uniform atmospheric and soil environments. The view that the size structures of

crowded populations largely reflect the effects of resource competition has perhaps been biased by a shortage of experiments located in heterogeneous environments. In the light of recent ecological theory (e.g. Grubb 1977, Shmida and Ellner 1985, Chesson and Huntly 1988) suggesting that environmental heterogeneity plays a key role in stabilizing plant communities, it seems timely to address this issue in studies of competition at the individual plant level.

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LEGENDS

Figure 1. The effects of distribution-modifying functions (DMFs) on size distributions. The frequency distribution on the left indicates a normal initial biomass distribution. The graphs in the middle titled **A-E** represent DMFs with different shapes (see text for discussion). The frequency distributions on the right show the final biomass distributions as modified by the DMFs.

Figure 2. The change in relative variation as a function of the DMF slope and the standard deviation of the residuals. The standard deviation of the residuals is indicated next to the curves. The standard deviation of the initial biomass distribution is set to 1.

Figure 3. Final biomass frequency distribution for the three non-spatial models. Density is 3. Results are shown for 1000 individuals in 30 size classes.

Figure 4. Final biomass frequency distributions for the three spatial models. In all simulations, density is 25. Results are shown for 1000 individuals in 30 size classes. The density was chosen to match the average final biomass of the three non-spatial models. **A** (none): There is no other source of random variation besides initial

biomass. **B** (height): There is 15% normal random variation in the maximal height parameter H_{max} between individuals. **C** (site): There is 15% normal random variation in the site parameter P_{max} between neighborhoods. **D** (spacing): Interplant distances are Poisson-distributed.

Figure 5. Four univariate measures for variation as functions of density in the three spatial models without any other source of random variation besides initial biomass. Estimates are based on a sample size of 9000. The numbers next to the graphs correspond to the model type. The dotted line indicates the values for the initial biomass distribution. Values below the dotted line indicate that the corresponding measure of variation dropped between the beginning and the end of growth.

Figure 6. Four univariate measures for variation as functions of density in the three spatial models with random variation in two parameters, but uniform spacing. Estimates are based on a sample size of 9000. The solid lines (height) indicate the results with 15% normal random variation in the maximal height parameter H_{max} between individuals. The dashed lines (site) indicate the results with 15% normal random variation in the site parameter P_{max}

between neighborhoods. The numbers next to the graphs correspond to the model type. The dotted line indicates the values for the initial biomass distribution. Values below the dotted line indicate that the corresponding measure of variation dropped between the beginning and the end of growth.

Figure 7. Four univariate measures for variation as functions of density in the three spatial models with random variation in two parameters and random spacing. Estimates are based on a sample size of 9000. The solid lines (spacing) indicate the results with Poisson-distributed interplant distances, alone. The long-dashed lines (spacing+height) indicate the results with 15% normal random variation in the height parameter H_{max} between individuals. The short-dashed lines (spacing+site) indicate the results with 15% normal random variation in the site parameter P_{max} between neighborhoods. The numbers next to the graphs correspond to the model type. The dotted line indicates the values for the initial biomass distribution. Values below the dotted line indicate that the corresponding measure of variation dropped between the beginning and the end of growth.

Figure 8. DMFs for the three non-spatial models at three densities. A:

model 1. B: model 2. C: model 3. The DMFs are derived from calculating the mean relative growth increment (RGI) for specific values of ln(initial biomass) between -2.3 and -0.36. Scatter is omitted. Densities (d) are indicated next to the curves. d=1 corresponds to isolated plants that are not competing. There are no other sources of random variation besides initial biomass.

Figure 9. DMFs for the three spatial models at three densities. A: model 1. B: model 2. C: model 3. The DMFs are derived from calculating the mean relative growth increment (RGI) for specific values of ln(initial biomass) between -2.3 and -0.36. Scatter is omitted. Densities (d) are indicated next to the curves. d=1 corresponds to isolated plants that are not competing. There are no other sources of random variation besides initial biomass.

Figure 10. Linear DMF regression slopes (based on 9000 observations) as functions of density in the three spatial models under various sources of random variation. The numbers next to the graphs indicate the model type. The solid line (none) indicates the result with no other source of random variation besides initial biomass. The dashed lines indicate the results with the following additional sources of random variation: height = 15% normal variation in the

height parameter H_{max} between individuals, site = 15% normal variation in the site parameter P_{max} between neighborhoods, spacing = Poisson-distributed interplant distances, spacing+height = Poisson-distributed interplant distances and 15% variation in H_{max}, and spacing+site = Poisson-distributed interplant distances and 15% variation in P_{max}.

Figure 11. Three separate linear regression DMFs for three sites (dashed lines) and a DMF for the combined data for all three sites (solid line). Data are shown for the spatial model 2 at a density d = 25. In the 'good site' P_{max}= 1.5, in the 'average site' P_{max} = 2.0, and in the bad site P_{max} = 2.5. The regressions are based on 200 observations per site, but for clarity only 50 points per site are shown. The DMF with the greatest slope is generated in the 'good site' (open squares). The DMF with the intermediate slope is generated in the 'average site' (solid circles), and the DMF with the smallest slope is generated in the 'bad site' (open triangles).

Figure 12. Example of the predictive ability of an empirical DMF for the spatial model 2 at density d=25, uniform interplant spacing and no other source of random variation besides initial biomass. A: The DMF (solid line) as derived from calculating the mean relative

growth increment (RGI) for specific values of ln(initial biomass) between -2.3 and -0.36. The solid circles indicate 200 randomly chosen individuals from a normal initial biomass distribution. **B**: The variance of the RGI for specific values of initial biomass between -2.3 and -0.36. The arrow indicates the location of the absolute biomass mean. **C**: The actual final size distribution on a log scale based on 1000 individuals with normal variation in initial biomass. **D**: The final size distribution on a log scale for the same 1000 individuals as predicted by applying the DMF in Figure **A**.

Figure 13. The change in relative variation as a function of the DMF slope for the three spatial models. All points are based on estimates from 9000 observations. **A**: model 1. **B**: model 2. **C**: model 3. Solid circles (none) indicate results with no other source of random variation besides initial biomass. Open squares indicate results with variation in initial biomass and Poisson-distributed interplant distances. Solid triangles indicate results with random variation in initial biomass and 15% normal variation in the maximal height parameter H_{max}. Open triangles indicate results with random variation in initial biomass and 15% normal variation in the site parameter P_{max}. In the last two cases spacing in uniform. The line indicates the change in relative variation if the DMF were

linear and exact.

Figure A1. Representation of a non-spatial neighborhood. This neighborhood has three individuals with heights H_1, H_2, and H_3. They define the heights of the canopy layers h_1, h_2, and h_3. All individuals cover the same ground area and leaf area is distributed uniformly within the canopies.

Figure A2. Representation of neighbor relationships in a spatial neighborhood. The ith plant in a neighborhood of 40 plants has two direct neighbors: i-1 and i+1. It partly overlaps with the two neighbors. The overlap (O_{iR} and O_{iL}) is determined by its own width (W_{iR} and W_{iL}), the widths of its neighbors (W_{i-1R} and W_{i+1L}), and the distances between neighbors (d_{iL} and d_{iR}). C_i is defined as the center region of plant i that does not overlap. Plant distances are defined as the original distances between seedlings. They remain constant throughout a simulation.

Figure 1.

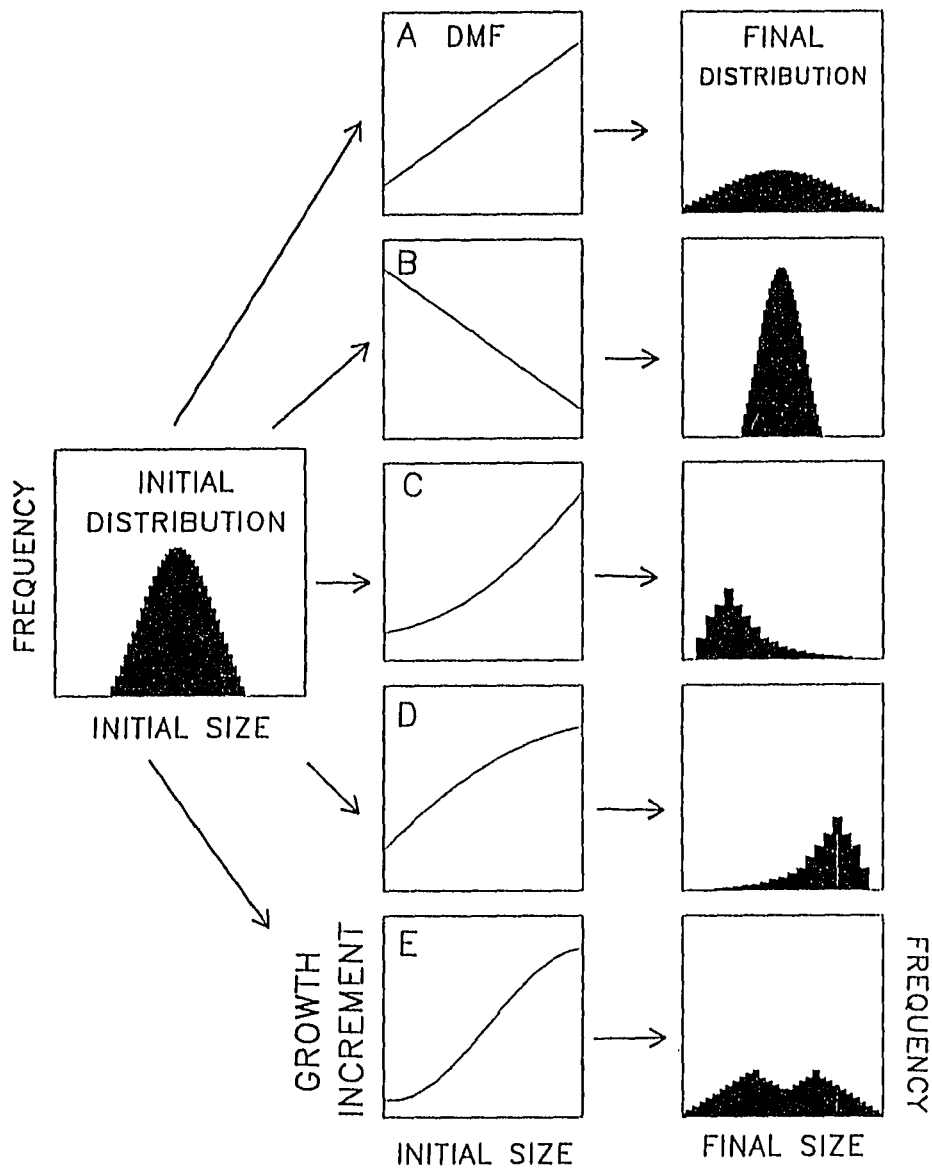
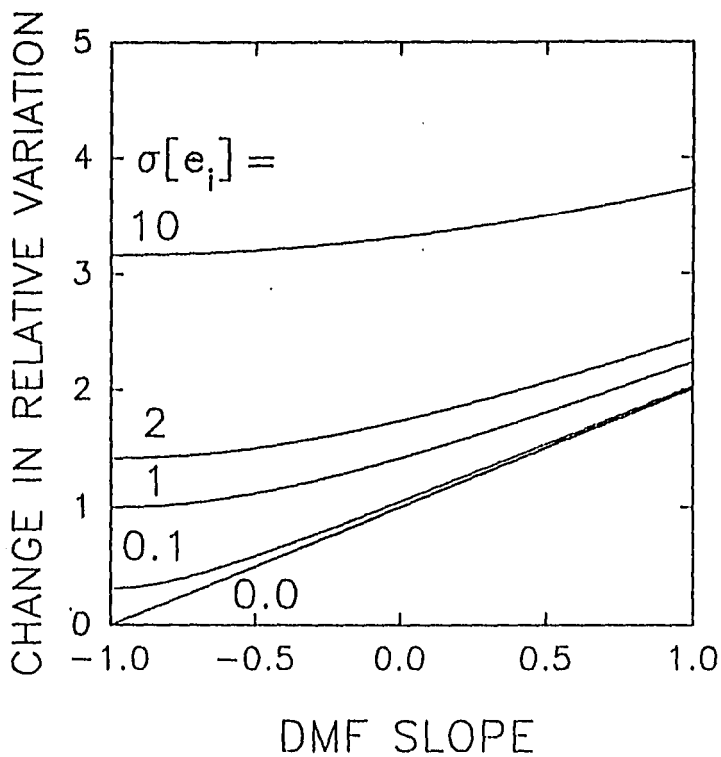

A DMF
FINAL DISTRIBUTION
B
C
D
E
INITIAL DISTRIBUTION
FREQUENCY
INITIAL SIZE
GROWTH INCREMENT
INITIAL SIZE
FINAL SIZE
FREQUENCY

Figure 2.


CHANGE IN RELATIVE VARIATION
DMF SLOPE
σ[e_i] =
10
2
1
0.1
0.0
0
1
2
3
4
5
−1.0
−0.5
0.0
0.5
1.0

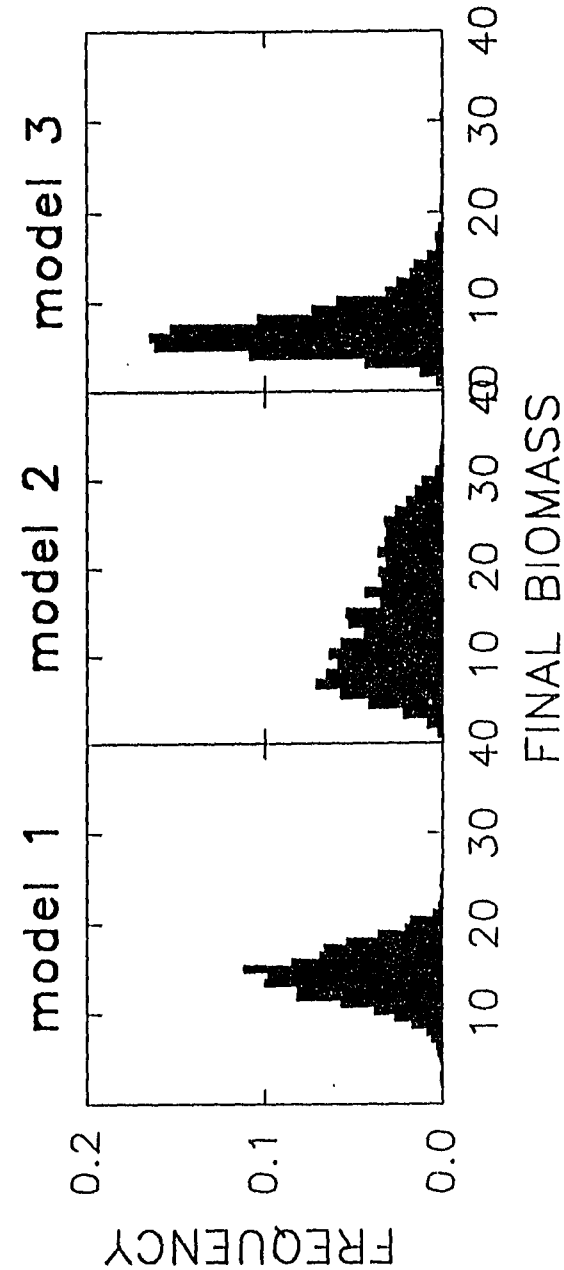

model 1
model 2
model 3
FREQUENCY
0.2
0.1
0.0
10 20 30 40
10 20 30 40
10 20 30 40
FINAL BIOMASS

Figure 3.

Figure 4.

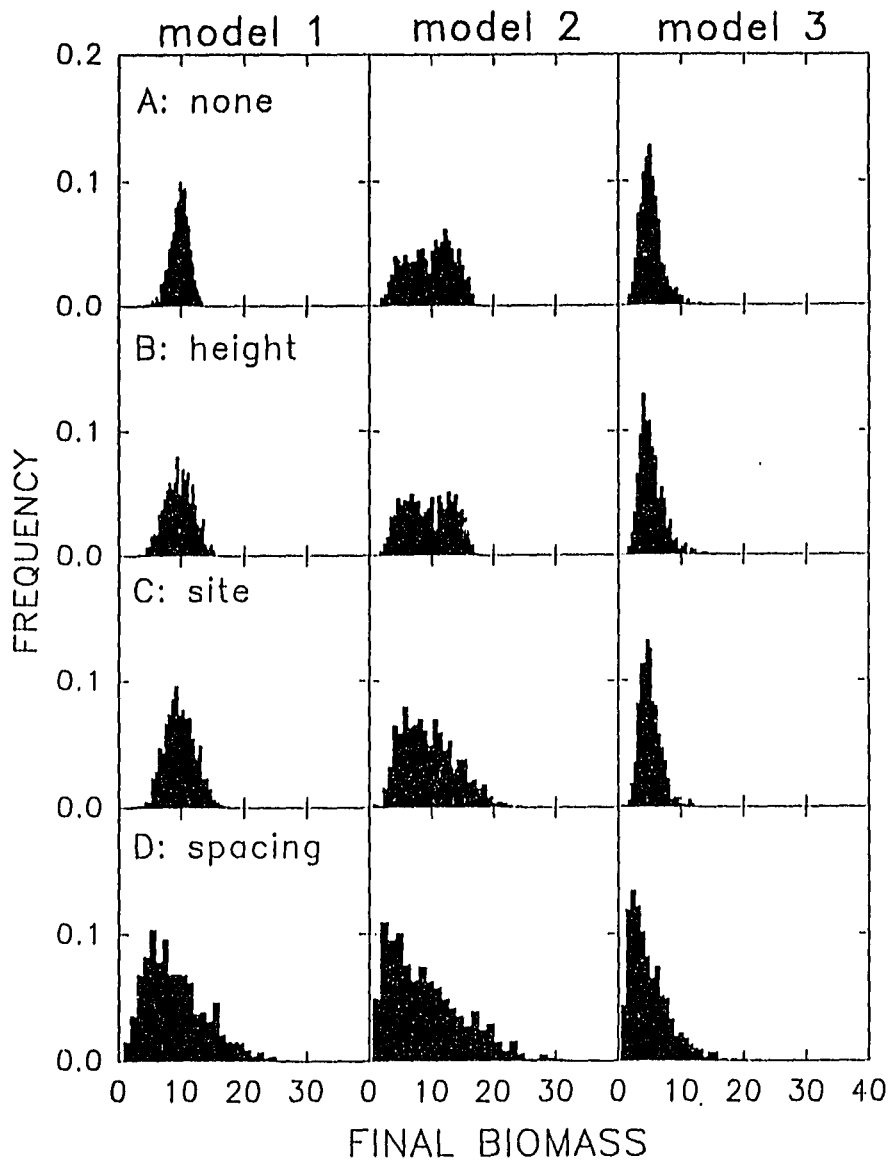

model 1
model 2
model 3
A: none
B: height
C: site
D: spacing
FREQUENCY
0.2
0.1
0.0
0 10 20 30 0 10 20 30 0 10 20 30 40
FINAL BIOMASS

Figure 5

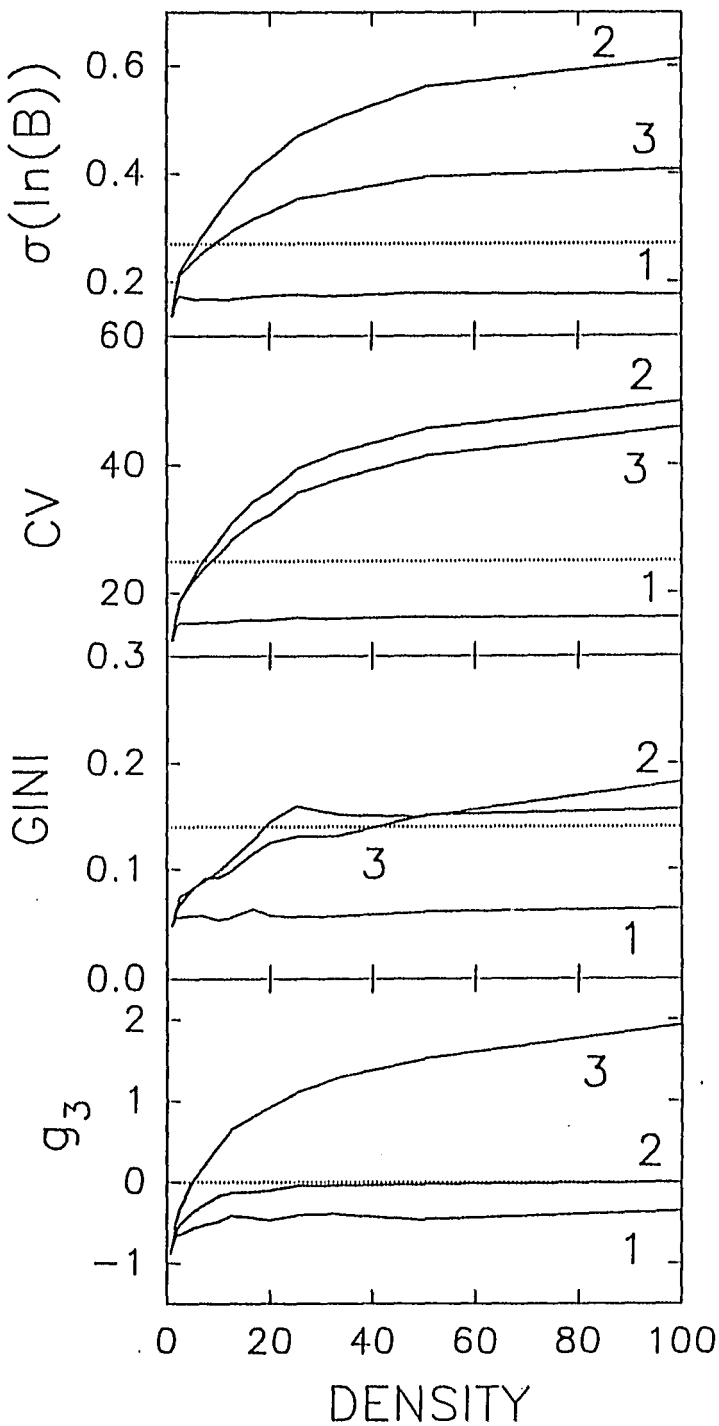

σ(ln(B))
0.6
0.4
0.2
2
3
1
60
CV
40
20
2
3
1
0.3
GINI
0.2
0.1
0.0
2
3
1
2
g3
1
0
−1
3
2
1
0
20
40
60
80
100
DENSITY

Figure 6.

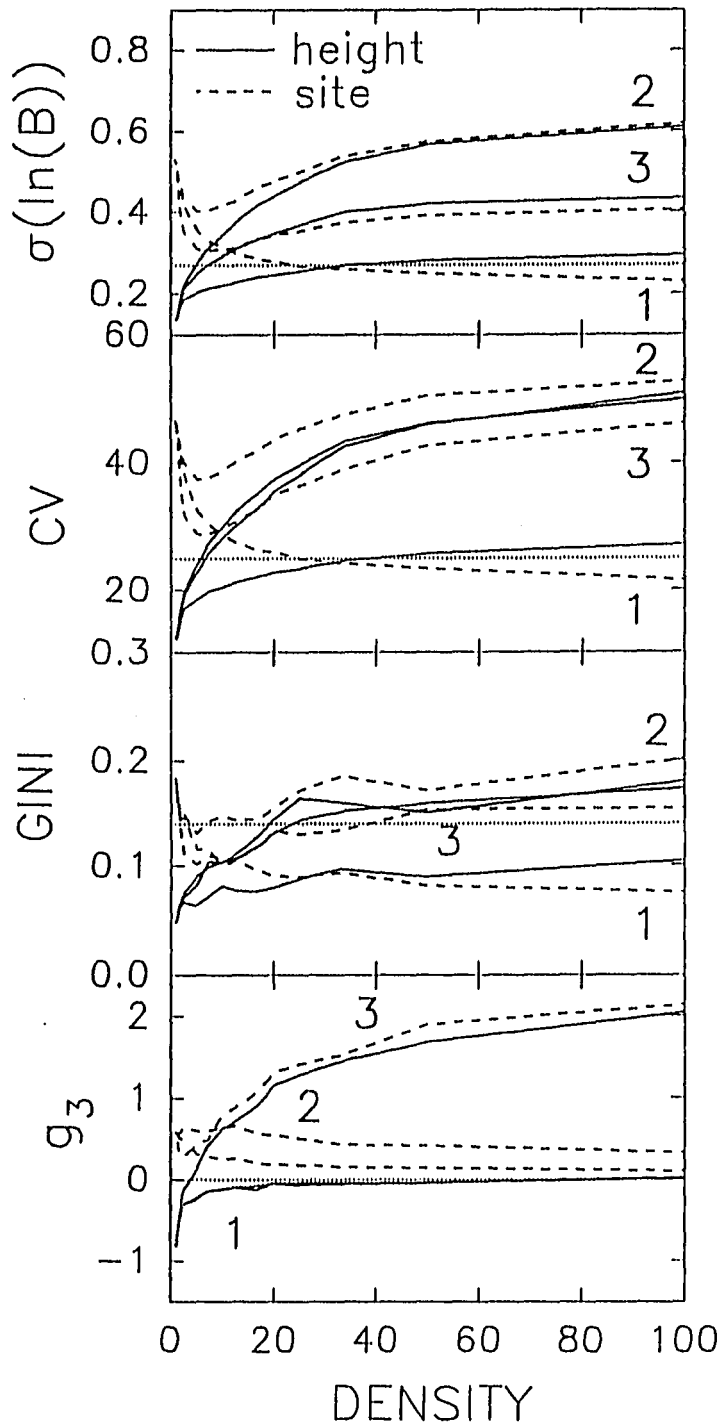

height
site
σ(ln(B))
0.8
0.6
0.4
0.2
2
3
1
60
CV
40
20
2
3
1
0.3
GINI
0.2
0.1
0.0
2
3
1
g_3
2
1
0
−1
3
2
1
0
20
40
60
80
100
DENSITY

Figure 7.

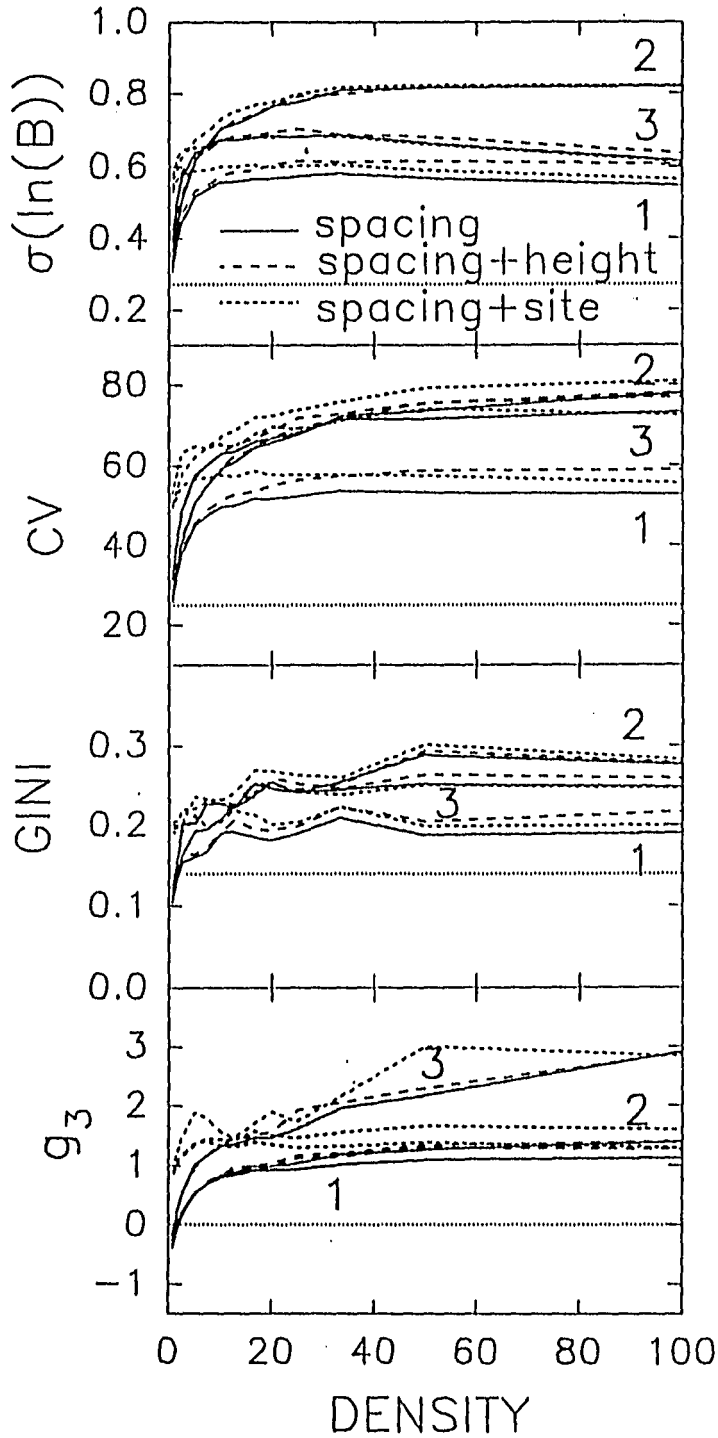

σ(ln(B))
CV
GINI
g_3
DENSITY
spacing
spacing+height
spacing+site
1.0
0.8
0.6
0.4
0.2
80
60
40
20
0.3
0.2
0.1
0.0
3
2
1
0
−1
0
20
40
60
80
100
1
2
3

Figure 8.

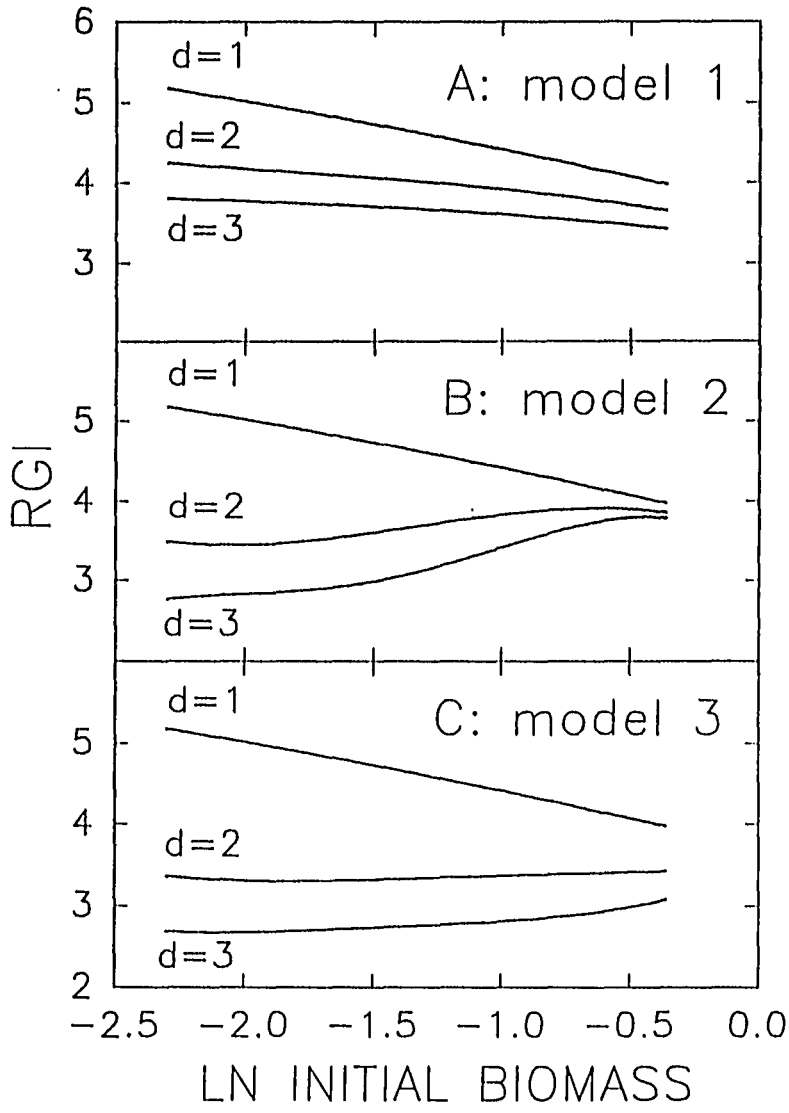

A: model 1
B: model 2
C: model 3
d=1
d=2
d=3
RGI
6
5
4
3
2
−2.5
−2.0
−1.5
−1.0
−0.5
0.0
LN INITIAL BIOMASS

Figure 9.

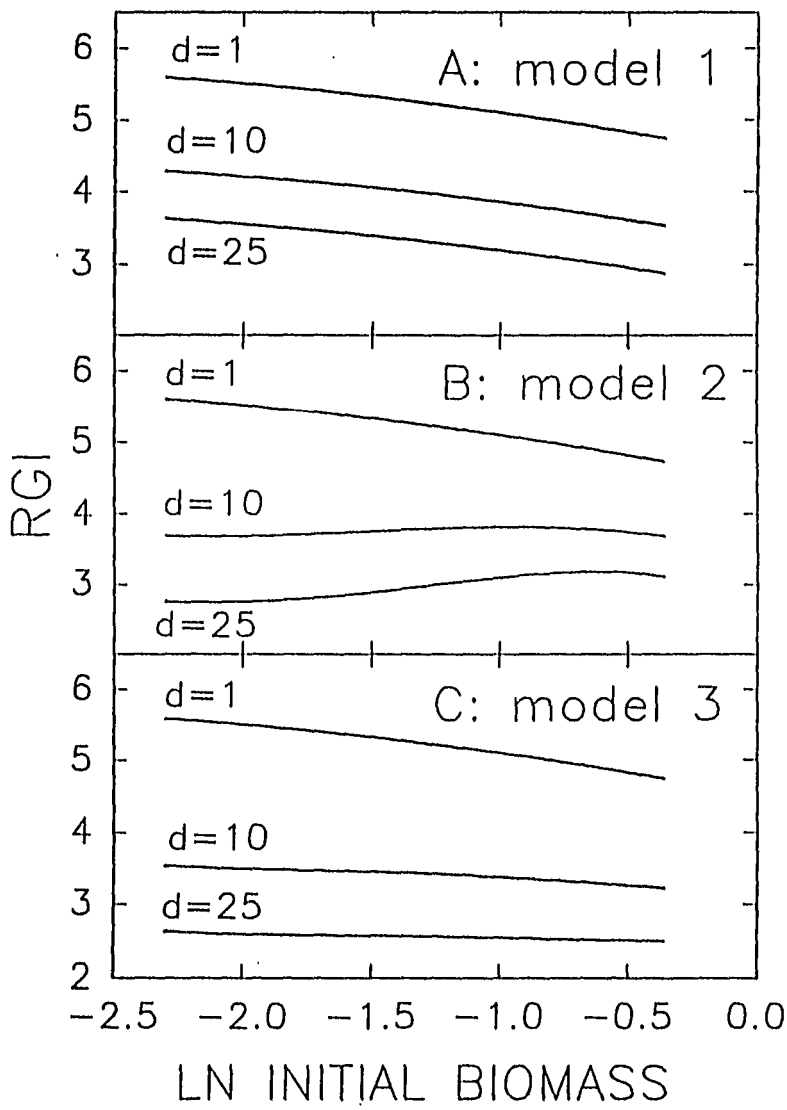

A: model 1
B: model 2
C: model 3
d=1
d=10
d=25
RGI
LN INITIAL BIOMASS
6
5
4
3
2
−2.5
−2.0
−1.5
−1.0
−0.5
0.0

Figure 10

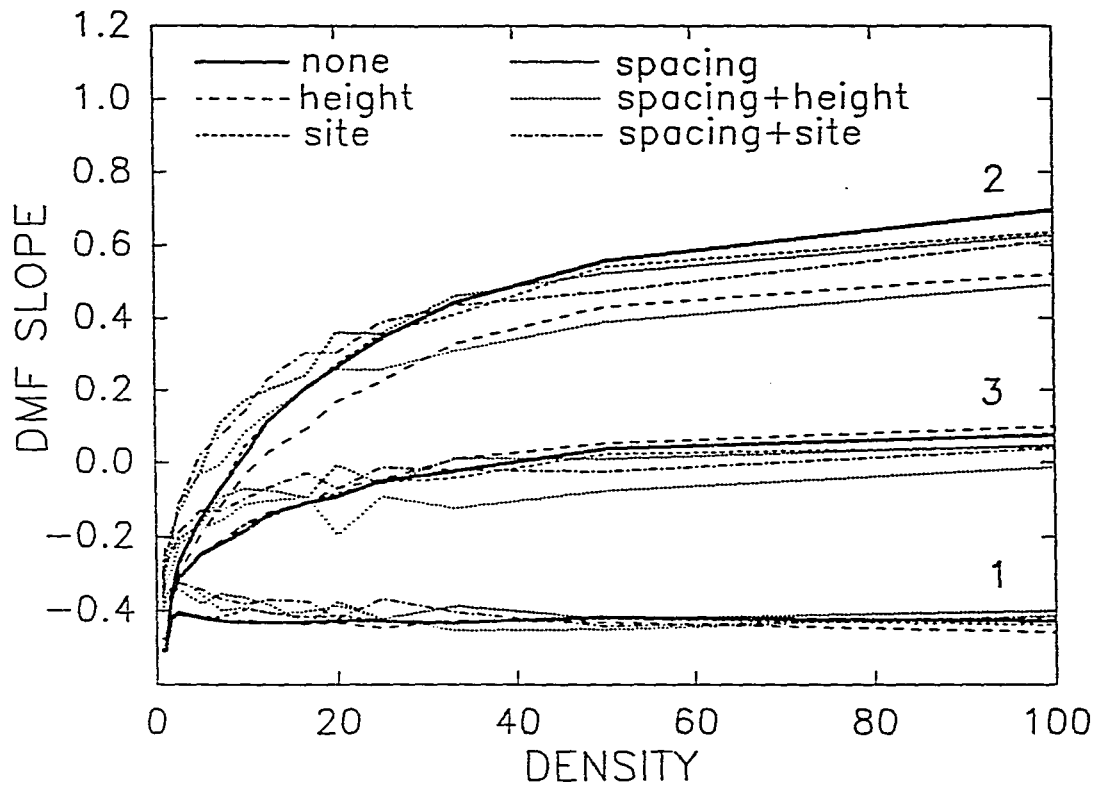
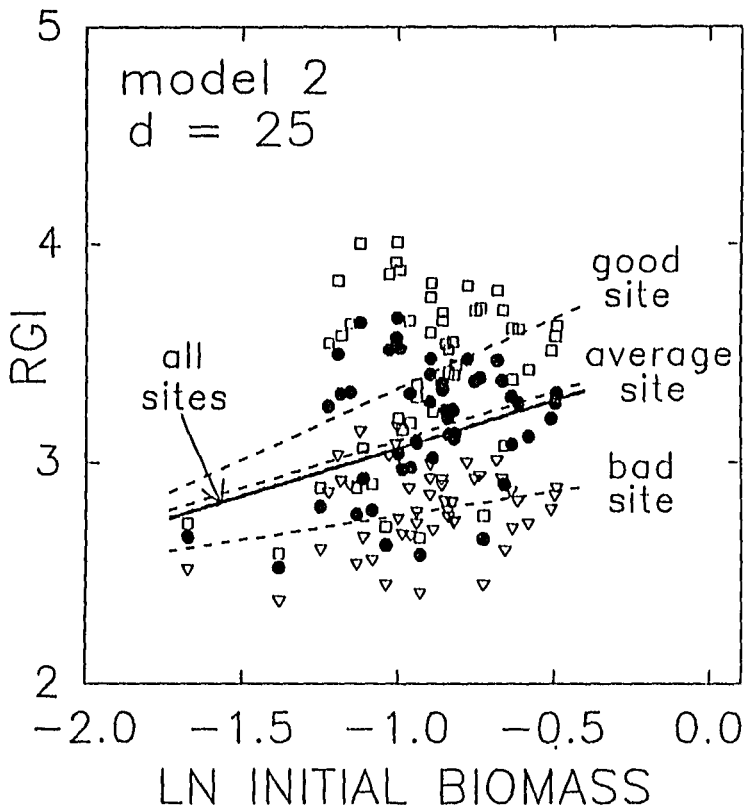

1.2
1.0
0.8
0.6
0.4
0.2
0.0
−0.2
−0.4
DMF SLOPE
none
height
site
spacing
spacing+height
spacing+site
2
3
1
0
20
40
60
80
100
DENSITY

Figure 11


model 2
d = 25
good site
average site
bad site
all sites
RGI
5
4
3
2
−2.0
−1.5
−1.0
−0.5
0.0
LN INITIAL BIOMASS

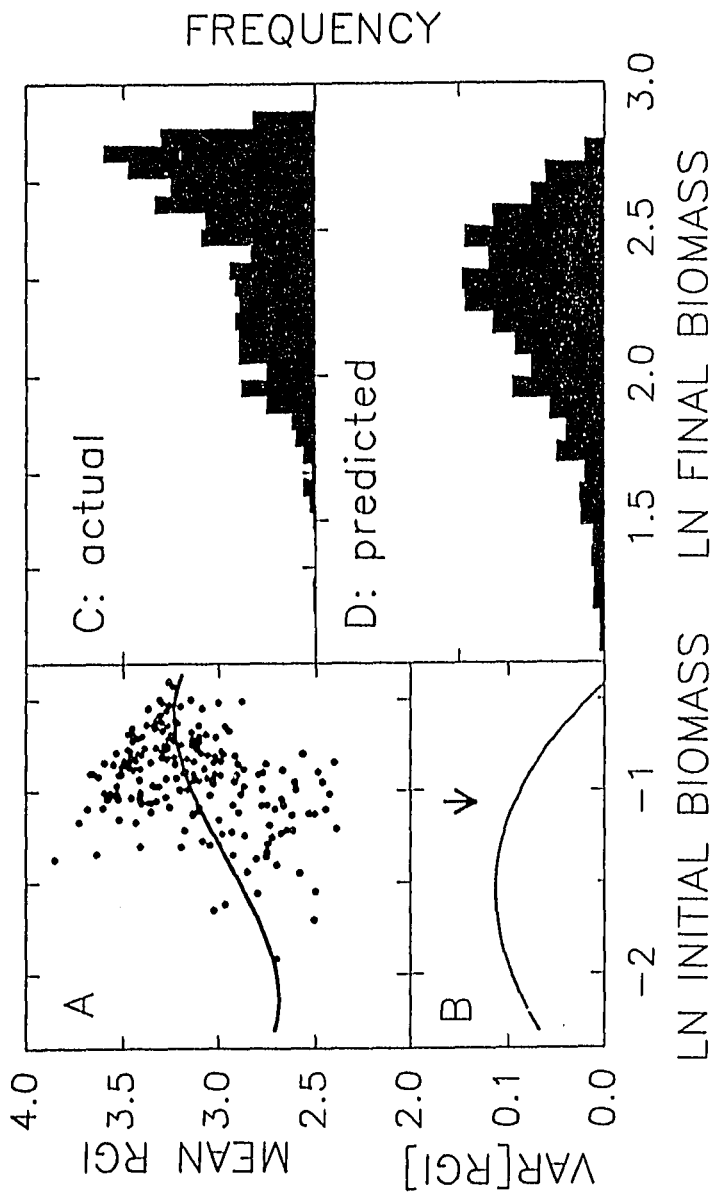

FREQUENCY
C: actual
D: predicted
A
B
MEAN RGI
VAR[RGI]
4.0
3.5
3.0
2.5
2.0
0.1
0.0
−2
−1
1.5
2.0
2.5
3.0
LN INITIAL BIOMASS
LN FINAL BIOMASS

Figure 12.

Figure 13.

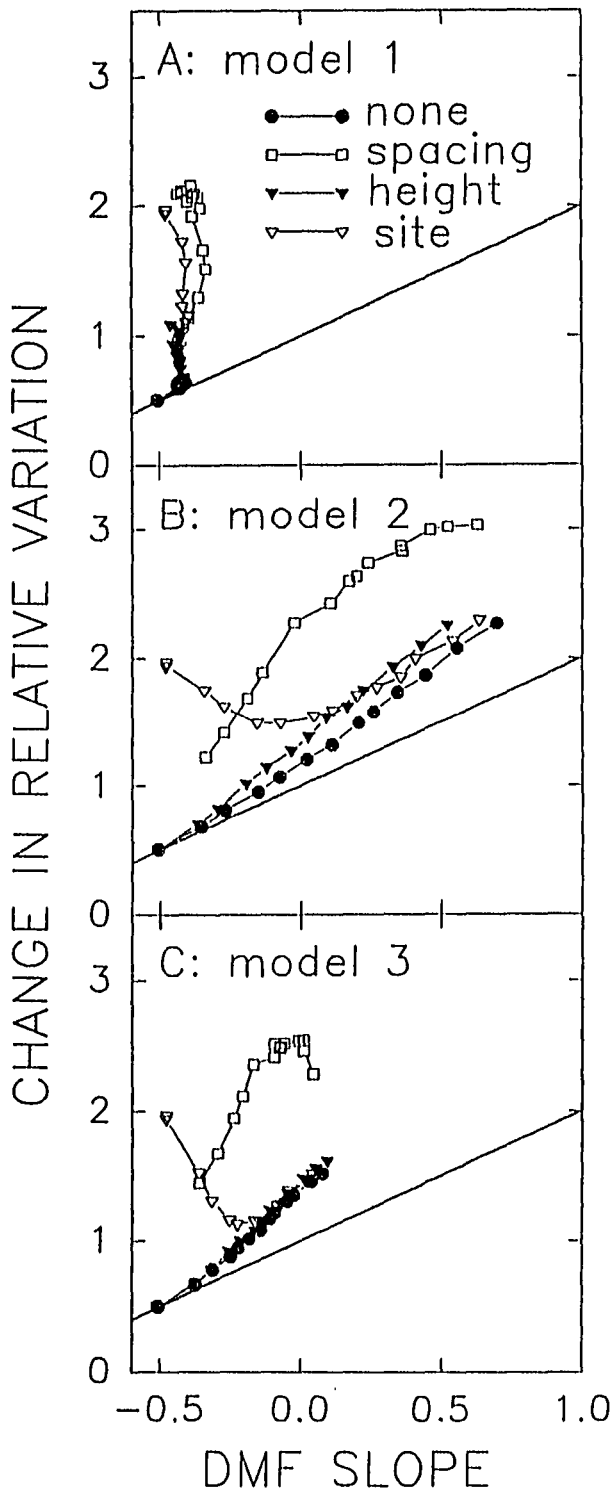

A: model 1
none
spacing
height
site
B: model 2
C: model 3
CHANGE IN RELATIVE VARIATION
DMF SLOPE
0
1
2
3
−0.5
0.0
0.5
1.0

Figure A1

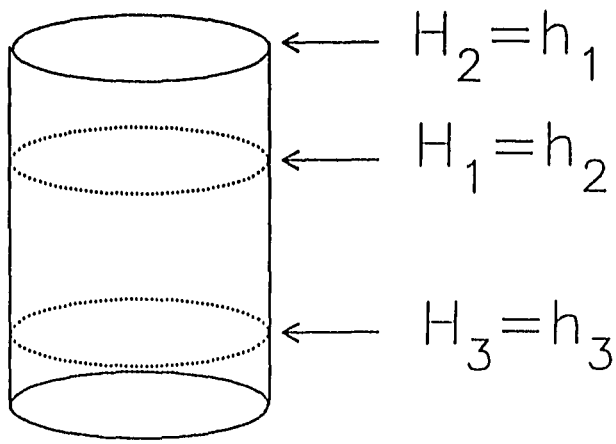
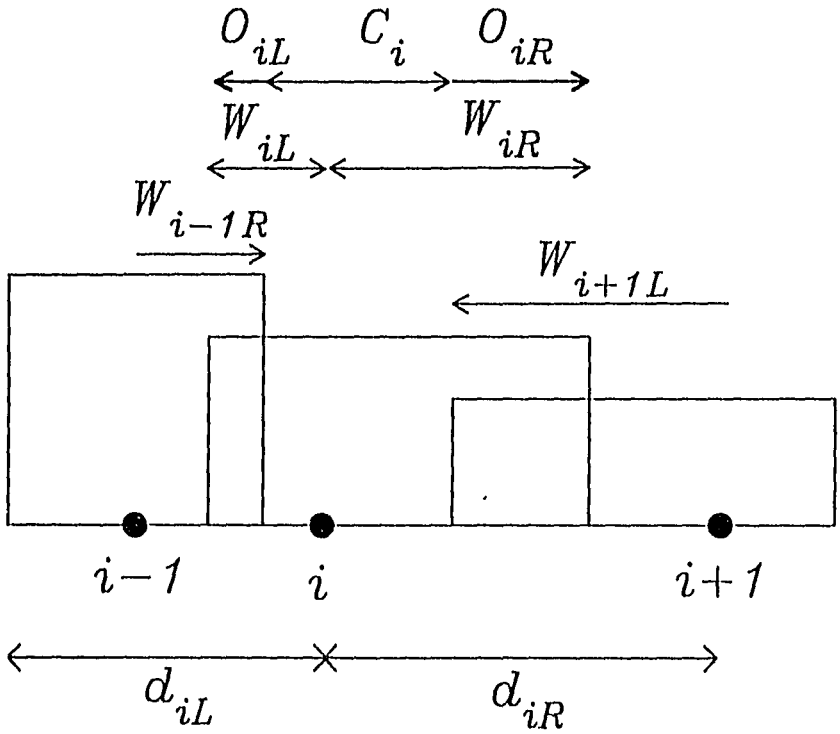


Figure A2



APPENDIX 1.

Symbols used in the spatial and the non-spatial models

Indices and parameters

Symbol	Meaning	Value
i	Plant index (i=1: focal plant).	
j	Canopy layer index (j=1: topmost layer).	
t	Day index.	1-50
p	Leaf area to total biomass ratio.	1
α	Biomass at which plant has half-maximal height.	10
β	Constant defining the height disadvantage of the focal plant in model 3.	0.5
ε	Light extinction coefficient.	0.1
P_{max}	Maximal daily photosynthetic flux in units of biomass/area.	constor random
H_{max}	Maximal height of a plant.	constor random

State variables

Symbol	Meaning
$B_i(t)$	Biomass of plant i. The initial condition is a normal random variable with mean 0.4 and standard deviation 0.1.

$H_i(t)$	Height of plant i.
$\tau(t)$	Timer variable that gradually lowers the growth rate of all plants synchronously in time.
$l_i(t)$	Total leaf area index of plant i across all layers.
$l_j(t)$	Total leaf area index of all plants in layer j.
$l_{ij}(t)$	Leaf area index of plant i in layer j.
$h_j(t)$	Height of the top of canopy layer j.
$Q_i(t)$	Proportion of the daily incident light flux density intercepted by plant i.
$Q_j(t)$	Proportion of the daily incident light flux density intercepted by layer j.
$Q_{ij}(t)$	Proportion of the daily incident light flux density intercepted by plant i in layer j.

Special symbols used in non-spatial models

Indices and parameters

Symbol	Meaning	Value
A_i	Constant ground area covered by the canopy of plant i.	1

Special symbols used in spatial models

Indices and parameters

Symbol	Meaning	Value
L,R	Indices referring to the two row directions: left, right.	
k	Width to biomass ratio as long as plants expand.	0.5
D	Depth of plant perpendicular to row direction.	1
W_{max}	Maximal plant width from center to periphery	2.5
$d_{iL(R)}$	Distance between the center of plant i and the center of the left (right) neighbor.	constor random

State variables

Symbol	Meaning
$W_{iL}(t)$	Width of plant i in row direction left (right) of center.
$C_{iL(R)}(t)$	Width of plant i in non-overlapping center.
$O_{iL(R)}(t)$	Width of plant i overlapping to the left (right) with neighbor.
$Q_{iC}(t)$	Proportion of the daily incident light flux density intercepted by plant i in the non-overlapping center.
$Q_{ijL(R)}(t)$	Proportion of the daily incident light flux density intercepted by plant i in layer j in the space of overlap to the left (right).

APPENDIX 2

General model assumptions

Plants in the non-spatial and spatial models grow by increments that are, in part, determined by their daily photosynthesis $P_i(t)$ and, in part, by age:

$$B_i(t+1) = B_i(t) + \tau(t)P_i(t) \ , \qquad \text{(A1)}$$

where $B_i(t)$ is the biomass of the ith plant at the beginning of day t, and $P_i(t)$ is the daily photosynthesis in units of biomass. τ is a function of time and determines the effect of age:

$$\tau(t) = 1 - \left(\frac{t}{50}\right)^2 . \qquad \text{(A2)}$$

This function reduces the daily photosynthesis as plants grow older. The function generates a sigmoidal growth curve that is typical for annual plants. It has the consequence that events that occur early in the growing season have a greater impact on the growth rates of plants than events that occur later. It is assumed that all plants in a population stop growing simultaneously at t=50. This may occur because photoperiodism regulates the development of all plants identically, because some weather event interrupts the growth of all plants at once, or in crop plants, because plants are harvested at some time. τ has no effect on the relative size distribution of plants, however, because all plants are affected in the same proportion.

$P_i(t)$ depends on the intercepted fraction of the daily incident light flux

density $Q_i(t)$ and the ground area A_i covered by its canopy.

$$P_i(t) = P_{max}\, Q_i(t)\, A_i(t) \ . \qquad \text{(A3)}$$

P_{max} is the maximal daily photosynthesis per unit ground area. It is set constant or varies randomly. Notice that the fraction of the maximal daily photosynthesis flux density is equal to $Q_i(t)$. This relationship was suggested by Charles-Edwards et al. (1986).

The canopy structure of a plant and its neighbors determines the fraction of the available light a plant intercepts. When plants overlap, light is divided between different individuals. In particular, height differences determine the proportion of available light each plant intercepts. Below, I describe three models which differ in the control of plant height:

MODEL 1: $H_1(t) = H_2(t) = \ldots = H_n(t) = c(t) H_{max}$, (A4)

where c(t) indicates that height may increase in time. However, since plants have the same height, or the same mean height, at all times, c(t) need not be specified.

MODEL 2: $H_i(t) = H_{max} \dfrac{B_i(t)}{B_i(t) + \alpha}$. (A5)

In model 2, height is a saturating function of biomass, where H_{max} is the maximal plant height and α is the biomass at which the height is half of H_{max}.

MODEL 3: $H_i(t) = H_{max} \dfrac{B_i(t)}{B_i(t) + \alpha}$ *if* $i \neq 1$ and (A6)

$$H_1(t) = \beta\ H_{max} \frac{B_1(t)}{B_1(t) + \alpha} \text{ where } 0 < \beta < 1.$$

In model 3, the plant with the index 1 (= focal plant) is assumed to be a different species or genotype from plants with indices 2 and above. For any given biomass, plant 1 is assumed to be smaller by a factor β than any of its neighbors.

Along with other model assumptions, which are laid out below, the three height assumptions form the basis for differences in competetive symmetry. In model 1, all plants have equal access to light, because biomass gives no height advantage. This is a symmetric model of competition. In models 2 and 3, larger plants have a competitive advantage, because they overtop smaller neighbors and pre-empt light. They are asymmetric competition models.

The structure of the non-spatial models

Non-spatial neighborhoods cover a constant ground area and the canopies of neighbors overlap completely. If plants have different heights (models 2 and 3) the canopy is structured into layers. For example, Figure A1 shows a neighborhood containing three plants. The height of the first canopy layer, h_1 is equal to the height of the tallest plant, H_2, in this case. The height of the next canopy layer, h_2, is equal to the height of second tallest plant, H_1. The height of the lowest canopy layer, h_3 is equal to the height of the shortest plant, H_3. Thus, there are always as many canopy layers as there are plants, unless some plants

have identical size. Layer 1, the top layer, is occupied solely by plant 2, layer 2 by plants 2 and 1, and layer 3, the bottom layer in this example, by all three plants.

The leaf area of all plants is uniformly distributed within the plant volume. Assuming there are n plants in the neighborhood, the leaf area index $l_{ij}(t)$ of the ith plant in the j'th layer is:

$$l_{ij}(t) = \frac{pB_i(t)}{A} \frac{h_j(t)-h_{j+1}(t)}{H_i(t)} \quad if \quad H_i(t) \geq h_j(t) \; and \; j<n \; , \qquad \text{(A7)}$$

$$l_{ij}(t) = \frac{pB_i(t)}{A} \frac{h_j(t)}{H_i(t)} \qquad if \quad j=n \; ,$$

$$l_{ij}(t) = 0 \qquad if \quad H_i(t)<h_j(t) \; .$$

p is the ratio of leaf area to total biomass and n is the number of plants in the neighborhood.

The leaf area index of a layer determines the fraction of light incident into the layer that is intercepted within it (Charles-Edwards et al. 1987). For the top canopy layer:

$$Q_1 = (1-e^{-\epsilon l_{j-1}}) \; , \qquad \text{(A8)}$$

and for all other layers:

$$Q_j = \left(1 - \sum_{k=1}^{j-1} Q_k\right) \left(1 - e^{-\epsilon l_j}\right) \; . \qquad \text{(A9)}$$

ε is the layer's extinction coefficient. I assume that the extinction coefficient is constant and identical for all layers.

Assuming also that the leaf angle distributions and the leaf spectral properties of plant canopies are identical and constant in time and space, plants divide the intercepted light within each layer in proportion to their leaf area indices:

$$Q_{ij}(t) = Q_j(t) \frac{l_{ij}}{l_j} , \qquad \text{(A10)}$$

where Q_{ij} is the fraction of the daily incident light flux density intercepted by the ith plant in the layer j and l_j is the total leaf area index in layer j. The total fraction of light intercepted by plant i on day t is the sum of fractions of light intercepted in each layer:

$$Q_i(t) = \sum_{j=1}^{n} Q_{ij}(t) . \qquad \text{(A11)}$$

For model 1, equations A7 through A11 can be simplified to

$$Q_i(t) = \left(1 - e^{-\varepsilon \sum_{i=1}^{n} \frac{pB_i(t)}{A}}\right) \frac{B_i(t)}{\sum_{i=1}^{n} B_i(t)} , \qquad \text{(A12)}$$

because there is only a single canopy layer.

The structure of the spatial models

The plants in one neighborhood are arranged in a row with variable

interplant distances. Each neighborhood contains 40 plants. To avoid edge effects, the last plant is the row is next neighbor to the first plant in the row. Thus, all 40 plants have two immediate neighbors: one to the "left" and one to the "right". Plant canopies are cubes with variable height H and width W along the row direction but constant depth D perpendicular to the row.

The distance between the ith plant center and the center of its left neighbor is d_{iL} and the distance to the center of its right neighbor is d_{iR}. Plants along the row are counted sequentially and counter-clockwise, so that $d_{iL} = d_{i-1R}$ and $d_{iR} = d_{i+1L}$. However, $d_{1L} = d_{40R}$, because the two row ends are connected. In general, the plant index 0 is equivalent with the index 40.

Seedlings expand along the row direction with a rate that is proportional to the rate of biomass accumulation:

$$W_{iL}(t) = kB_i(t) \text{ and} \qquad \text{(A13)}$$

$$W_{iR}(t) = kB_i(t) \ ,$$

where $W_{iL}(t)$ is the distance from the ith plant's center to its left perimeter, and $W_{iR}(t)$ is the distance from its center to the right perimeter. An example is given in Figure A2. Lateral expansion stops either when a) W_{iL} or W_{iR} reach W_{max}; or when b) W_{iL} reaches d_{iL} or W_{iR} reaches d_{iR}. Thus, a plant can overlap with maximally two other plants (the left and right neighbors) and nowhere do more than two plants overlap.

The canopy width that is overlapping with neighbors to the left and right are

(compare with Figure A2):

$$O_{iL}(t) = W_{iL}(t) + W_{(i-1)R}(t) - d_{iL} \text{ and } O_{iR}(t) = W_{iR}(t) + W_{(i+1)L}(t) - d_{iR} . \quad \text{(A14)}$$

Thus, the canopy width in the center that is not overlapping is

$$C_i(t) = W_{iL}(t) + W_{iR}(t) - O_{iL}(t) - O_{iR}(t) . \quad \text{(A15)}$$

Leaf area is distributed homogeneously in the canopy volume. The leaf area index is

$$l_i(t) = \frac{pB_i(t)}{D(W_{iL}(t) + W_{iR}(t))} , \quad \text{(A16)}$$

where p is defined as before and D is the constant depth of the canopy. The non-overlapping portion of the canopy is a single homogenous layer. The proportion of light intercepted by it, is therefore:

$$Q_i(t) = 1 - e^{-\epsilon l_i} . \quad \text{(A17)}$$

In the overlapping portion of the canopy to the left and right, the canopy is layered, if the neighbors have unequal heights (models 2 and 3). As in the non-spatial models, there are as many canopy layers as there are overlapping plants, in this case only two. For example, the height of the top layer to the left, $h_{1L} = H_i(t)$, if $H_i(t) > H_{i-1}(t)$, otherwise $h_{1L} = H_{i-1}(t)$. Thus, the light intercepted daily in the overlapping portion of the canopy is equal to the sum of the light interception in four layers: $Q_{i1L} + Q_{i2L}$ is the light interception in the top and bottom layers to the left, and $Q_{i1R} + Q_{i2R}$ is the light interception in the top and bottom layer on the right

side of plant i.

Light is divided across and within canopy layers as in the non-spatial models (equations A8 - A10), with the exception that this division occurs only in the region of overlap. For example, in the situation given in Figure A2:

$$Q_{i1L} = 0 \qquad \text{(A18)}$$

$$Q_{i2L} = e^{-\epsilon l_{i-1}\frac{H_{i-1}-H_i}{H_{i-1}}}\left(1 - e^{-\epsilon(l_i+l_{i-1}\frac{H_i}{H_{i-1}})}\right)\frac{l_i}{l_i+l_{i-1}}$$

$$Q_{i1R} = 1 - e^{-\epsilon l_i\frac{H_i-H_{i+1}}{H_i}}$$

$$Q_{i2R} = e^{-\epsilon l_i\frac{H_i-H_{i+1}}{H_i}}\left(1 - e^{-\epsilon(l_{i+1}+l_i\frac{H_{i+1}}{H_i})}\right)\frac{l_i}{l_i+l_{i+1}} .$$

For simplicity, Q and H are not represented as functions of time.

The total daily photosynthesis is therefore equal to the sum of the contributions from all 5 layers:

$$P_i(t) = P_{max}D\left(C_i(t)\, Q_{iC}(t) + O_{iL}(t)(Q_{i1L}(t)+Q_{i2L}(t)) + O_{iR}(t)(Q_{i1R}(t)+Q_{i2R}(t))\right). \qquad \text{(A19)}$$

APPENDIX C

AN ANALYSIS OF COMPETITIVE SYMMETRY IN FIELD GROWN POPULATIONS OF MILLET (PENNISETUM AMERICANUM) AND COWPEA (VIGNA UNGUICULATA).

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ABSTRACT

A previous simulation study by Schwinning (1994) showed that the symmetry of competition generates distinct density effects on empirical distribution-modifying functions (DMFs). Here we tested these predictions in a field experiment using the annual crop plants millet (Pennisetum americanum) and cowpea (Vigna unguiculata). In agreement with the simulation results, we found (1) that empirical DMFs were adequately represented by linear regressions on a log scale, (2) that the slope of the linear regressions increased with density under asymmetric competition, (3) that asymmetric competition did not determine the regression slope at any particular density, and (4) that size-independent sources of random variation, such as variation in site quality, obscured the density effect on size variability, but not on DMF slopes. Thus, we found the density response of DMF slopes to be a more reliable indicator for the symmetry of competition than the density response of size variability. The density response of millet DMFs may have been caused by asymmetric competition for light. However, there were other factors that influenced DMF slopes. We discuss these results in relation to the symmetry concept in ecological theory.

Key Phrases: symmetric and asymmetric competition, population size structure, distribution-modifying functions, random environmental variation.

INTRODUCTION

Two types of resource competition have been recognized for plants: symmetric, or two-sided, competition and asymmetric, or one-sided competition (Ford and Diggle 1981, Turner and Rabinowitz 1983, Weiner and Solbrig 1984, Firbank and Watkinson 1985, Weiner 1990). In symmetric competition resources are distributed in proportion to biomass in regions where competitors overlap in space. In asymmetric competition larger plants capture a more resource per unit biomass in those spaces. These two forms of competition are thought to have distinct effects on population dynamics and community ecology. For example, some models of the dynamics of monocultures show that populations fluctuate under symmetric, but not under asymmetric, competition (Watson 1980, Thrall et al. 1989, Pacala and Weiner 1991, Silvertown 1991). Asymmetric competition stabilizes population dynamics in these models by preventing a large portion of individuals from falling below the reproductive size threshold at high density or by facilitating self-thinning. The role of asymmetric competition in community ecology is still unclear. Asymmetric competition may facilitate competitive exclusion by magnifying small initial size differences among seedlings into large reproductive differences (Smith and Huston 1989, Samson et al. 1992, Zobel 1992). Alternatively, asymmetric competition may facilitate species coexistence by reducing differences in the competitive effects among species (Fowler 1988, Kohyama 1992). The ecological and evolutionary significance of asymmetric resource competition is not well understood. In

addition, there is little direct evidence for how common asymmetric competition is in populations, and to what extent population structure is governed by competitive symmetry.

Direct evidence for competitive symmetry is difficult to obtain. It would consist of measuring resource partitioning and utilization between neighboring plants as a function of their size difference. This is time consuming, at the least, and often impossible, so plant ecologists have often relied on indirect evidence . Two forms of indirect evidence for competitive symmetry are commonly accepted: the density-dependence of size variability, and the shape of so-called distribution-modifying functions (DMFs), functions that describe the relationship between plant size and plant growth rates (Westoby 1982, Turner and Rabinowitz 1983, Hara 1984, Weiner and Solbrig 1984, Weiner 1986, Weiner and Thomas 1986, Weiner 1990).

Symmetric and asymmetric competition are thought to generate distinct density effects on population size structures. Several simulation models have shown that relative size variation in populations remains constant or decreases with density under symmetric competition, but increases with density under asymmetric competition (Ford 1975, Diggle 1976, Gates 1978, Aikman and Watkinson 1980, Ford and Diggle 1981, Firbank and Watkinson 1985, Weiner and Thomas 1986). However, simulation models have also provided counter-examples. For example, if plants are randomly spaced, relative size variation can increase with density under both forms of competition (Bonan 1988, Miller

and Weiner 1989, Bonan 1991). On the other hand, relative size variation can also decrease with density under both forms of competition (Schwinning 1994). These differences in the effects of competition are explained by the ways in which different sources of random variation interact with competition (Schwinning, 1994).

Distribution-modifying functions (DMFs) express the symmetry of competition on the scale of populations. Asymmetric competition, for example, is indicated by DMFs with sigmoidal shapes (Westoby 1982, Hara 1984) or functions that indicate the existence of a size threshold for growth (West and Borough 1983, Schmitt et al. 1987, Geber 1989, Thomas and Weiner 1989). Schwinning (1994) characterized DMFs as regressions of the log-transformed biomass increments between the seedling stage and maturity on the log-transformed seedling biomass. In models, these empirical functions had some remarkably consistent properties: (1) they were always adequately described by linear regressions, (2) they had negative slopes at low density, (3) they increased in slope with increasing density under asymmetric, but not under symmetric, competition, and (4) they were minimally affected by several sources of random growth rate variation. Thus, DMFs indicated the symmetry of competition in regions of canopy overlap through the density response of their slopes, but not through their shapes or the signs of their slopes.

Schwinning (1994) demonstrated these effects of competition for three competition models: symmetric competition between equal competitors (model

1), asymmetric competition between equal competitors (model 2), and asymmetric competition between unequal competitors (model 3). In all models competition was for light. In model 1, plant height was not correlated with biomass, so that larger plants did not, on average, intercept more light than smaller plants. In model 2, larger plants were taller and intercepted more light per unit biomass than smaller plants. Plants in model 2 were equal, in the sense that all plants had the same height-to biomass allometry. In model 3, DMFs were derived for a population of a rare short species or genotype competing against a tall resident population. Different sources of random variation were introduced, including site variation, random spacing and random height variation. In all cases, DMFs indicated the symmetry of competition through the distinct response of DMF slopes to increases in density. Thus, empirical DMFs appear to be ideal indicators for the symmetry of competition at the local scale.

We tested these simulation results in field experiments. We examined asymmetric competition among equal competitors (comparable to models 1 or 2) in one series of experiments, and asymmetric competition among unequal competitors (comparable to model 3) in another series of experiments. To construct empirical distribution-modifying functions and to follow size structure dynamics, we used plants that permitted non-destructive and accurate estimation of seedling biomass. We chose two large, fast-growing agricultural species, pearl millet (Pennisetum americanum) and cowpea (Vigna

unguiculata). Millet is a C4 cereal with a high light requirement, given enough water and soil nutrients. The cowpea variety (CB46) is shorter than millet and usually forms bushy canopies. We established pure millet stands to create conditions similar to models 1 or 2, and stands containing a single cowpea plant in otherwise pure millet to create conditions similar to model 3. We did not change the sources of random variation systematically, but relied on natural variation in the form of spatially variable soil properties.

MATERIALS AND METHODS

Location, environmental conditions, and cultivars

All experiments were conducted at the University of Arizona experimental farm in Tucson, Arizona in the months of June to October. Intense, short rainfall events are typical for southern Arizona in the months of July and August. However, rainfall timing and amount was highly variable between years (Table 1).

The field site was laser-leveled before planting in 1991, but not in 1990 and 1992. Consequently, there was less elevational heterogeneity in 1991 than in the other two years. The uneven soil surface caused differences in local soil moisture, particularly after rainfall or irrigation events.

Prior to planting, the soil was fertilized with 45 kg ha^{-1} fertilizer (16:20:0) to ensure non-limiting levels of nitrogen and phosphorus. Seed beds were elevated for furrow irrigation. The beds ran north-south and had a width of 50

cm. The center of the beds were approximately 1 m apart. Blocks were separated by high border rows to control the flow of irrigation water into blocks independently.

Pearl millet (Pennisetum americanum) cultivar "Custer" is a short, drought-tolerant and tillering cereal. Mature plants are about 1.2 m tall and have 1 to tens of tillers that develop fertile heads. Cowpea (Vigna unguiculata) variety CB46 is a bushy high-yielding legume. CB46 in monoculture develops a predominantly globular canopy, but in mixed culture with millet can produce branches with long internodes that spread laterally or up into the millet canopy.

Experiments 1 and 2 (1990,1991)

Experimental design

The experiments of 1990 and 1991 were large- scale experiments designed to generate DMFs of millet and cowpea plants, as well as to test for the average effects of seed size, density and block in an analysis of variance. The experiments conducted on millet and cowpea plants were analyzed separately. However, to maximize efficiency, the two experiments were performed on the same site. The basic experimental unit, called patch, consisted of a 3 m by 3 m area containing one millet and one cowpea focal plant (Figure 1). Only focal plants were analyzed. Millet focal plants were located in the middle of the center row. Cowpea focal plants were located in the same row 50 or 55 cm north of the millet focal plants. In the 'single plant' (S)

treatment, the two focal plants were the only plants within the patch. In the 'low density' (L) treatment, the focal plants were surrounded by other millet plants at a density of 50,000 plants ha^{-1}, equivalent to a within-row plant distance of 20 cm. In the 'high density' (H) treatment, the focal plants were surrounded by millet plants at a density of 100,000 plants ha^{-1}, equivalent to a within-row plant distance of 10 cm. In 1991, there was an additional 'intercropping' (I) treatment with millet and cowpea plants alternating within rows at a combined density of 100,000 plants ha^{-1}. At low and high density, and in the intercrop, cowpea focal plants were centered between two millet plants. In the intercrop, millet focal plants were centered between two cowpea plants.

Seeds of future focal plants were sorted by weight into three size categories. The weight categories for millet seeds were 5-6 mg (small), 9-10 mg (medium), and 15-16 mg (large). The weight categories for cowpea seeds were 160-180 mg (small), 190-210 mg (medium), and 220-240 mg (large). The average weight of non-focal millet seeds were 9.7 mg (CV = 34%) and for non-focal cowpea seeds was 190 mg (CV = 16%).

The experiments were blocked. There were 6 blocks in 1990 and 4 blocks in 1991. Blocks were bordered with a row of millet plants east and west, and by at least 3 m of millet north and south. Each block consisted of a checker-board of patches with randomly assigned treatments. In 1990, each block contained 10 single plant patches, 10 low density patches, and 10 high density patches. Of the 10 replicate patches in each block, 3 contained focal

plants from small seeds, 4 from medium seeds, and 3 from large seeds. In 1991, each block contained 15 single plant patches, 15 low density patches, 15 high density patches, and 15 intercropping patches. Within the 15 replicate patches per block, each seed size category was represented 5 times. The location of the seed size treatments was randomized independently for millet and cowpea seeds. In both years the number of patches per density treatment was 60 across the entire experiment.

Seeds were planted on June 20 in 1990, and on July 4 in 1991 into the center of the beds. At each planting location, 3-5 seeds were dropped and covered with about 1 inch of soil. Following planting, the field was irrigated to facilitate germination. Seedlings emerged three days after planting. After one week, prior to the first size measurement, all seedlings were thinned to one plant per planting location. Millet plants produced heads nearly simultaneously around August 1 in both years. First flowers were observed in cowpea around the same time. Some cowpea plants continued to flower into October, although flowers initiated after August produced only a small proportion of all seeds. Millet heads were sprayed with the biocide Diazenone and enclosed in brown wax-coated paper bags immediately after pollen dehiscence to protect the maturing seeds from insect and bird predation.

Natural rainfall was supplemented by furrow irrigation using reclaimed water, which supplied some additional nitrogen. After the initial irrigation, plants were irrigated as soon as the top 20 cm of soil appeared dry, or as millet plants

showed mild signs of water stress during the noon hour. Without any rain, irrigations were performed about every 10 days. Plants were irrigated four times in 1990 and in 1991 (Table 1).

Weeds were effectively eliminated from the field through manual weeding or, when possible, through mechanical cultivation. Millet and cowpea plants were attacked by insect larvae. As needed, plants were sprayed with biocide to suppress predation damage. In 1990, plants were sprayed two times and in 1991 three times.

Non-destructive measurements of all focal plant sizes were performed on both species approximately 1, 2, 3 and 4 weeks after planting (WAP), with the exception of millet in 1990 which was measured only three times. Millet above-ground biomass was estimated on the basis of a single index: the product of plant height, width of the widest leaf, and tiller number. This index was highly correlated with the oven-dried weight of millet shoots at each growth stage (r^2= 0.61 at 1 WAP, r^2 = 0.94 at 2 WAP, r^2 = 0.96 at 3 WAP, r^2 = 0.88 at 4 WAP). In cowpea, the area of single trifoliate leaves was highly and linearly correlated with the product of the widest width and the length of the terminal leaflets. The oven-dried weight of cowpea shoot was estimated on the basis of measuring the dimensions of all leaves (r^2 = 0.97 1 to 2 WAP, r^2= 0.99 3 to 4 WAP).

Focal plants were harvested in late September of 1990, and early October of 1991. At that time, all millet plants had fully matured and all but the largest cowpea plants had stopped producing new pods. Reproductive biomass

(millet heads, cowpea seeds) was separated from vegetative shoot biomass. Vegetative biomass of both species was oven-dried and weighed. Millet heads were air-dried counted and weighed. Cowpea seed pods were air-dried, then seeds were removed, counted and weighed. The percentage of seed loss, due to seed predation, was estimated visually. In millet, this was done by evaluating the percent of the head surface not covered with seeds, and in cowpea by evaluating the percent of empty spaces in pods.

Analyses

Focal plants were excluded from statistical analysis using the following criteria: 1) if a focal plant did not emerge or died at any time, 2) if a nearest neighbor of a focal plant did not emerge or died at any time, or 3) if a cowpea focal plant showed a growth anomaly that stunted the main shoot axis. Focal plants were excluded from analyses of reproductive yield only if seed loss due to predation appeared to be greater than 50%. Mortality was usually low and mostly caused by root damage, not by a self-thinning mechanism. The growth anomaly in cowpea was observed at a small frequency in all years and may have been caused by a viral infection.

The experimental structure was a blocked two-way factorial design with population type (S, L, H, and I) and seed size (small, medium, large) as main effects. ANOVA was performed on untransformed seedling biomass. The hypothesis of normal distribution of biomass could not be rejected in most

cases; however, within-group variances were unequal. Therefore, the results of ANOVA have to be considered conservative estimates. ANCOVA was performed on the log-transformed biomass of seedlings and mature plants following Silk (1980).

To increase the ability to discriminate regression slopes and measures of relative variation, we relied on bias-corrected bootstrap confidence intervals (Dixon 1993), based on 1000 pseudo-values. We called a difference between two statistics significant, if the 90 percentile bootstrap confidence intervals did not overlap. Confidence limits based on bootstrapping were slightly narrower than confidence limits based on the normal distribution. In most cases, both significance tests had the same outcome. However, in a few instances, a comparison indicated no difference based on the parametric method, but a significant difference based on bootstrapping.

As measures of relative variation, we used the coefficient of variation (CV) and the Gini coefficient (GINI) (see Weiner and Solbrig 1984).

Experiment 3 (1992)

Experimental design

Experiment 3 served to determine the symmetry of competition in millet populations directly by estimating the size-dependence of light interception at low and high density. Low and high density were defined as in Experiments 1 and 2.

The field site was randomly divided into 3 high density and 3 low density blocks. Field preparation was as in 1990 (no laser-leveling). Planting was June 26. 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.

Pairs of plants in Experiment 3 were harvested destructively two times during the season. Each time, at most one representative of each pair was randomly selected in each block. The first harvest was between July 17 and 19, about three weeks after planting. A 3-dimensional radial grid of thin wire was constructed around each plant, centered on the position of the main tiller at soil level. The grid consisted of planes formed of concentric rings. In the plane, the rings increased in diameter by 10 cm. The outermost ring had a diameter of 40 cm. These planes were stacked at 10 cm distance above one another. The topmost plane was 60 cm above the ground. Thus, the grid divided canopies into central cylinders with 10 cm diameter and height, and ring elements with 5 cm width and 10 cm height. Once the grid was constructed, leaves were carefully clipped from the top down and the outside in. Leaf area from different ring segments was measured separately, using a Delta-T Devices Ltd. digital image analyzer. After the entire leaf area of a plant had been determined, the combined above ground biomass was oven-dried and weighed.

The second harvest was August 1 and 2, approximately five weeks after planting. This time, only pairs of unequal size (LM, LS, and MS) were harvested. 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 topmost plane was 80 cm above the ground.

Estimation of individual light interception

To estimate the light interception of individual plants, we used a simple light interception model 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 canopy element with random angular distribution, (2) leaf transmittance is 10%, (3) the incidence angle of direct light is perpendicular to the ground, and (4) contributions to light interception from diffuse sources are ignored.

The leaf area of two plants forming a focal pair was mapped into a three-dimensional, grid-based coordinate system, spaced at their true distance. To both sides of the focal pair, more canopies were mapped into a row with the same inter-plant distances (20 cm at low, 10 cm at high density). They formed the neighborhood of the focal pair. The neighborhood plants were represented by randomly selected canopies of other measured medium-sized plants. Neighborhoods to the "left" and "right" of the focal pair were constructed

symmetrically. This was done to reduce variation in light interception for any other reason than the differences in the leaf area distribution of the focal pair. We assumed no overlap of canopies across rows, as was the case for the field plants.

The cells of the coordinate system were 1 cm by 1 cm in the plane, and 10 cm in height, for the first harvest. For the second harvest, cells had the dimensions 2 cm by 2 cm in the plane, and 20 cm in height. For each cell, the total leaf area index (the ratio of leaf area to ground area), and the leaf area contributed by each plant of the focal pair was determined. Total light interception within each cell was estimated 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 was then partitioned among the focal plants and their neighbors in proportion to their leaf area within each cell. Finally, the light interception for the two plants in the focal pair was determined by summing across the contributions from all cells in the three-dimensional grid.

Thus, the estimate of light interception took into account canopy overlap and vertical leaf area distribution. If plants overlapped greatly, plants with more leaf area near the canopy top intercepted more light. If canopies did not overlap much, height differences between plants did not matter much.

This simple light interception model did introduce some bias with respect to the symmetry of competition. Since light was supplied strictly from the top

down, the effect of height differences between plants was maximal. In reality, since millet was planted in rows, some light was intercepted from the sides as well. Lateral light interception reduces the effect of height differences on light capture. In the extreme, if the incidence angle of light had been horizontal, height differences would have not mattered at all. Thus, asymmetry was probably overestimated by this light interception model.

RESULTS

1. Environmental differences in the years 1990 and 1991

Though the experiments of 1990 and 1991 were managed and controlled similarly, the uncontrolled influence of weather introduced some important differences. In 1990 the conditions were very conducive to even germination and good seedling establishment. In 1991, the planting of seeds was followed by rainfall (Table 1). This led to crusting of the soil surface and obstructed the emergence of millet seedlings. About 10% of all millet focal plants had to be excluded from the analysis, because the focal plants or their immediate neighbors failed to establish (see **METHODS**). The remaining seedlings were more variable in size. The emergence of the larger cowpea seedlings was not impeded by soil crusting.

In the first two weeks of growth, soil moisture was higher in 1991 than in 1990, because of the additional rainfall and a lower air temperature. This may have facilitated seedling growth in 1991. In the subsequent weeks there was

substantially more rainfall in 1990 than in 1991. In the fourth and fifth week of growth in 1990, plants were visibly water-logged, indicated by yellowing of the leaves. Water logging was not uniform across blocks, because of elevational heterogeneity of the field site.

2. Millet Analyses

Size variation

Reproductive biomass was highly and linearly correlated with the vegetative biomass at harvest, independent of density or population composition. The r^2 for the regression of reproductive biomass on vegetative biomass was 0.95 in 1990 and 0.89 in 1991. Therefore, our results concerning the vegetative biomass of mature plants can be extended to reproductive yields.

Table 2 summarizes the mean and variation in the biomass distribution of millet plants two weeks after planting and at final harvest. For simplicity, we refer to individuals at two weeks after planting as 'seedlings' and to individuals at final harvest as 'mature plants'. Seedlings were slightly larger in 1991 than in 1990, probably because of more moderate environmental conditions during the first two weeks of growth in 1991 (Table 1). In both years, mean seedling biomass was not significantly different between populations. This indicates that plants had not begun to interact two weeks after planting. At maturity, single and high density millet plants were larger in 1990 than in 1991, indicating that 1990 was a better year for millet. Mean biomass decreased with population

density in both years, proving that millet plants at low and high density and in the intercrop were competitively suppressed. In the intercrop (1991), average millet biomass was intermediate between low and high density plants, and significantly greater than in the high density treatment, showing that the competitive effect of cowpea neighbors on millet focal plants was smaller than the competitive effect of conspecifics (see experimental design in Figure 1).

Relative variation, as expressed by the CV and the GINI coefficient of biomass was greater among 1991 seedlings than among 1990 seedlings, probably because of the emergence problems in 1991. The bootstrap confidence intervals indicated differences in the variability of seedling populations within years, as well. We do not know the source of this variation. CV and GINI for mature single plants differed between years at low and high density, although the differences were small. In both years, relative variation was greater for high density plants than for single plants. However, variation in mature low density plants was not intermediate. In 1990, mature low density plants were as variable as mature high density plants, while in 1991 they were as variable as mature single plants. Variability among the intercropped plants of 1991 was intermediate between low and high density plants.

During growth, relative variation dropped significantly for single and low density plants in 1991, and increased significantly for low and high density in 1990. For all other populations, changes in relative variation were insignificant.

Thus, in both years relative size variation was greater among mature

high density plants than among mature single plants. Relative size variation increased during the growth of high density plants only in 1990.

Empirical DMFs

Figure 2 and Table 3 show the regression results for the empirical DMFs of millet plants. There were no detectable non-linear trends in the data. In both years, single plants had negative slopes and the DMF slopes for high density plants were significantly greater than for single plants. The DMF slope was negative for all density levels in 1991 and positive only for high density in 1990 (Table 3). In 1990, the DMF slopes for low and high density plants were similar, and in 1991 the DMF slopes for low density and single plants did not differ. In the intercropped millet population, the DMF slope was intermediate between the DMF slope for low and high density populations, corresponding to the intermediate level of competition experienced by these plants (Table 2). There is a close correspondence between the results for the change in variation and the DMF slope (compare Tables 2 and 3). For example, mature high and low density plants have similar biomass variability in 1990, when these two populations also have similar DMF slopes. In 1991, mature single and low density plants have similar biomass variability, and the DMF slopes for these two populations are also similar.

3. Cowpea Analyses

Size variation

For cowpeas, the r^2 for the linear regression of reproductive biomass on vegetative biomass was 0.96 and in 1991 and 0.83 in 1991. Consequently, our results concerning the vegetative biomass of cowpea plants can be extended to reproductive yields, just as for millet.

Like millet seedlings, cowpea seedlings were larger in 1991 than in 1990 (Table 4). Within years, high density cowpea seedlings were slightly, but significantly smaller than low density cowpeas in 1990 and all other treatments in 1991. This may indicate that millet seedlings had begun to suppress cowpea seedlings in high density two weeks after planting. High density seedlings were only slightly smaller, however, than other seedlings. Mature single plants were much smaller in 1991, suggesting that 1990 was a better year, not only for millet but also for cowpea. Mature cowpea plants in high density were smaller, however, in 1990 than in 1991. This may have been the consequence of more intense competition from millet neighbors in 1990. Focal millet plants were larger at high density in 1991 than in 1990 (Table 2). In 1991, cowpea plants were larger in the intercrop than in low density, though they had equal distances from the immediate millet neighbors in both populations (Figure 1). This may have been the consequence of suffering less competition from millet neighbors. Focal millet plants were smaller in the intercrop than at low density (Table 2).

Relative variation of seedling biomass not significantly different between years with only one exception (low density). In 1991, there were small significant differences in the seedling size variation between some populations. Relative size variation of mature plants was significantly greater in 1990 across all populations, perhaps because the severity of water-logging varied across the field. In 1990, the relative variation of mature plants was not significantly different between populations, but in 1991 there were some differences. Based on GINI, single plants in 1991 had a slightly lower, but significant, size variation than all other populations. Based on CV, single plants were significantly different only from high density plants.

During the interval between seedling stage and maturity, relative biomass variation increased substantially in all cowpea populations in both years and all treatments. The relative size variation of mature high density populations was significantly greater than the relative size variation of single plant populations only in one year.

Empirical DMFs

Figure 3 and Table 5 show the DMF regression results for cowpea populations. As for millet, there were no non-linear regression trends. The DMF slope for single cowpea plants had a negative slope in 1991, but a positive slope in 1990 (Table 5). The DMF slopes of high density plants were significantly greater than the DMF slopes for single plants in both years. In

1990, the DMF slopes of low density and high density plants were similar, while in 1991 the DMF slopes of low density and single plants did not differ. This pattern follows the pattern found in millet DMFs (Table 3). However, the differences in the DMF slopes between populations of single plants and high density populations appeared to be larger for cowpea than for millet plants. In 1991, the DMF slope for cowpea plants in intercrop was no different from the slope for high density plants, even though their average biomass in this treatment was greater than in the low density treatment (Table 4).

4. DMF slopes as predictors of changes in relative variation

If DMFs were exact and not just regression functions, they would predict changes in the size structure of populations exactly (Westoby 1982, Schwinning 1994). However, they are far from being exact, as the low r^2 values in Tables 3 and 5 indicate. Figure 4 illustrates the degree to which the change in relative variation of plant size is explained by DMF slopes. The dotted line is the hypothetical relationship, if the DMF were linear and explained 100% of the change in relative variation. The more removed the data points are from the dotted line, the greater is the contribution of the regression residuals to the change in relative size variation. Since the data points for millet are close to the dotted line, millet experienced little size-independent growth rate variation. Millet DMF slopes, though small, were well correlated with the change in relative variation. In 1990, the data points for millet were more removed from

the dotted line, indicating that size-independent sources of variation had a greater impact on plant growth in 1990 than in 1991. Non-uniform water-logging was most likely responsible for the additional variation. In contrast, cowpea plants experienced a great amount of size-independent variation. Cowpea DMF slopes were high, but uncorrelated with changes in relative variation.

5. Site effects on the DMF slopes

The additional size-independent variation of 1990 (Figure 4) generated significant block effects. About 20% of the residual variation in the DMF regressions of both species could be attributed to block effects in an analysis of variance. We used these block effects to examine how site differences affected DMF regressions.

Differences between blocks can alter the DMF y-intercepts, slopes, or both. If they do, then the degree of determination in the DMF regression can be improved by adding block-specific parameters to the regression model (Silk 1980). We compared the degree of determination of four different regression models (Table 6): M1 was the original 2 parameter model of Tables 3A and 5A, M2 was a 7 parameter model in which DMFs had block-specific y-intercepts but one common slope, M3 was another 7 parameter model in which DMFs had block-specific slopes but one common y-intercept, and M4 was the full 12 parameter model in which DMFs had block-specific y-intercepts and

slopes.

In both species and at all densities, with the exception of millet populations at high density, M2 and M3 accounted for a significantly greater fraction of the total variation than the simple model M1. Unfortunately, we were not able to distinguish the performances of models M2 and M3, probably because the within-block sample sizes were too small (10 plants or less). The full model M4 performed significantly better than the reduced models M2 and M3 only for low density millet plants. This indicates that low density millet populations had significantly different DMF slopes and y-intercepts between blocks. Bootstrap confidence intervals for the regression slopes of the full model (M4) did indicate significant slope differences between some blocks in all populations, except in high density millet.

Schwinning's (1994) simulation results showed that DMF slopes are affected by site quality. To test this possibility, we tried to link the differences in the DMF regression slopes of M4 to block quality. To obtain a density-independent index for block quality, we ranked blocks by the average final biomass of the target plants for each density. The most productive block was ranked 6 and the least productive block was ranked 1. Then, we averaged these ranks across all three densities. Block quality was estimated in this way independently for both species. We did not find significant correlations between the DMF slope and the average block rank in either species at any density. To increases the power of the test, we combined data from all three densities and

tested if the differences between block-specific DMF slopes (of M4) and the common slopes (of M2) could be related to block quality. In millet, we did not find a significant correlation with block quality in this way either. In cowpea we did (Figure 5). As in the simulation models, the differences between the block-specific DMF slopes and the common slopes tended to be greater in high quality than in low quality blocks.

These results suggest that site quality can affect the slopes of empirical DMFs. However, in each block and for both species in 1990, the density effects on DMF slopes tended to be consistent: with one exception (in cowpea), populations of single plants had the lowest DMF slopes in every block (results not shown). This may explain why the density effects on DMF regression slopes were significant even for the simplest regression model M1 (Tables 3 and 5), although the populations were sampled from a spatially heterogeneous environment.

6. The mechanism of the density effect in millet.

Millet plants have a strong potential for self-limitation (illustrated by negative DMF slopes); but the tendency for self-limitation is countered by crowding (DMF slopes increase with density). Schwinning's (1994) simulation results showed that crowding can oppose the effect of self-limitation on DMFs if competition is asymmetric. Here we ask whether asymmetric competition for light also explains the effect of density on the slope of millet DMFs.

Three weeks after planting, the leaf area index of millet plants was positively correlated with biomass, but was low for plants of all sizes. This means that all plants self-shaded very little. Therefore, the estimated (see **METHODS**) light capture per unit biomass was size-independent (Figure 6). Because there were no differences in the average light capture at low and high density, there was probably no competition for light. Light capture should not affect DMF slopes during the first three weeks of growth, therefore. Empirical DMFs for the second week of growth were negatively sloped, however, except for single plants in 1991 (Table 7). In the third week of growth, DMF slopes were zero or positive in 1990, and negative in 1991. This size-dependence of the relative growth increments must have been caused by factors other than light interception.

Five weeks after planting, leaf area index had increased and was still correlated with biomass (Figure 7A). At the same time, larger plants at high density tended to be taller than smaller plants (Figure 7B). In low density, foliage height was not significantly correlated with biomass. We estimated that larger plants captured significantly more light per unit biomass than smaller plants at high density, but not at low density (Figure 8A). The difference in the light capture between immediate neighbors was also significantly different from zero at high density, but not at low density (Figure 8B). This indicates that the reduced light capture of smaller plants at high density was caused by competition. Thus, competition for light around the fifth week of growth was

asymmetric at high density, and symmetric at low density.

Provided that growth was light-limited at that time, the DMF of a high density population would have acquired positive slope by the fifth week of growth, while the DMF slope of low density plants would have not been affected by light capture. Thus, a density effect on the DMF slope would have been generated. Unfortunately, we could not test this prediction against empirically determined DMFs for that interval. Instead, we determined empirical DMFs for the interval between the fourth and the twelfth week of growth (Table 7). During this interval, DMF slopes were negative in both years. High and low density populations had significantly different slopes only in 1991. Thus, our results are inconclusive: asymmetric competition for light may have played a role in generating the density effect in 1991, but failed to do so in 1990.

7) Determinants of initial size.

Above we showed that seedling size can have a substantial influence on the reproductive success of individuals. Thus, a large portion of the fitness of individuals is determined in the first few weeks of growth. What are the factors that determine seedling growth during this time? We examined three possible factors: site variation (between blocks), seed size, and density in an analysis of variance (Table 8). Density had no significant effects on seedling sizes in this analysis. However, bootstrap analysis did indicate that single cowpea seedlings were significantly bigger than high density seedlings in 1991 (Table 4).

In millet, large seeds gave rise to significantly larger seedlings (Figure 9A). In 1991, when germination was impeded by soil crusting, seed size was much more important than in 1990 in both species (Table 8). Seed size effects in cowpea were significant only in 1991, when seedlings from small seeds were smaller than seedlings from medium and large seeds (Figure 9B).

In both species, block explained a greater portion of the total variation in both years (Table 8). Blocks affected the mean seedling biomass of millet and cowpea seedlings similarly in 1991, but not in 1990 (Figure 10).

DISCUSSION

The two species in these experiments experienced quite different competitive conditions. Millet competed against conspecifics. Since millet is a tillering grass species, plant individuals had a limited potential for lateral canopy expansion. Since they must increase leaf area index with biomass (Figure 7A), they self-shade strongly, particularly towards the end of the growing season. The potential of large plants to shade and suppress smaller neighbors was small even at high density (Figure 8). Nevertheless, we found, based on measurements of canopy structure, that asymmetric competition for light is possible among millet plants.

In contrast, cowpea plants competed directly with millet neighbors and were overtopped for most of the growing season. The average light level near cowpea canopies was well below the saturating light level of sunlit leaves

(personal observation). Thus, cowpea plants experienced highly asymmetric competition for light.

Schwinning (1994) simulated both intra- and interspecific asymmetric competition using simple neighborhood-based growth models. In all simulations in which competition was modelled as spatially explicit, DMFs were adequately described by linear relationships. Although asymmetric competition promoted non-linear relationships between the average relative growth increments of seedlings and their log biomass, it also increased the variance of the relative growth increments. Consequently, non-linear trends in DMF regressions could not be detected with reasonable sample sizes. In the present experiments, empirical DMFs were adequately described by linear regressions as well.

In the simulations, the DMFs of single plants had negative slopes, because large plants were more limited through self-shading than smaller plants. In the present experiments, negatively sloped DMFs were observed in single millet plants in both years, and in single cowpea plants in 1991. In 1990, single cowpea plants had a DMF with positive slope.

In the simulations, DMF slopes always increased with density if competition was asymmetric. However, asymmetric competition did not always generate positively sloped DMFs. In the present experiments, the DMF slopes of high density populations were significantly greater than the DMF slopes of single plant populations for both species in both years (Tables 3 and 5). However, the DMFs of high density millet populations were positive only in

1990. In addition, the DMF slope increased significantly with density even when the DMF slope for single plant populations was positive, as for cowpea in 1990. The DMF slopes for low density plants were not intermediate, however.

In the intercrop, which was not modeled in Schwinning's (1994) simulations, the DMF slope of millet was intermediate between high and low density (Table 3). The average biomass of mature millet plants was also intermediate between high and low density (Table 2). Thus, in intercropped millet, the DMF slope reflected the average level of competitive suppression. The DMF of intercropped cowpea had a slope similar to the slope of the high density DMF (Table 5). However, the average biomass of mature intercropped plants was intermediate between single and low density plants (Table 4). Thus, in intercropped cowpea, DMF slopes were not simply correlated with the average level of competitive suppression.

Schwinning's (1994) simulations showed that DMF slopes had a simple response to density and were minimally affected by genetic or environmental random variation, but that measures of size variability had complex density-responses that depended on the particular form of random variation. Without any sources of random variation but seedling biomass variation, relative size variation increased with time and density under asymmetric, but not under symmetric, competition. In that case, the density response of the DMF slope and of relative size variation indicated the action of asymmetric competition equally well. On the other hand, if there were additional forms of random

variation, density effects on relative size variation were often indistinguishable under symmetric and asymmetric competition. In the present experiments, we found examples for both kinds of conditions. Relative size variation in millet plants changed little between the seedling stage and maturity (Table 2). Most of the change could be explained through the effect of seedling size (Figure 4). In contrast, relative biomass variation of cowpea populations increased greatly during growth (Table 4) and only a small part of that increase could be explained through the effect of seedling size (Figure 4). In millet, density affected the DMF slope and the relative biomass variation significantly in both years (Tables 2 and 3). In cowpea, density affected DMF slopes significantly in both years, but relative biomass variation only in 1991 (Tables 4 and 5). Thus, the simulation results were confirmed by demonstrating that increase in the DMF slopes between single plant and high density populations was a consistent indicator of asymmetric competition, when size structure was not. We do not know, however, why the DMF slopes of low density populations were not intermediate.

Variation in site quality is one of the factors that can contribute to the relative size variation of mature plants without greatly affecting DMF slopes. In the simulations, DMF slopes were robust to site variation for two reasons. First, differences in site mostly affected the y-intercept of the DMF. Second, good sites and bad sites affected DMF slopes in opposite ways, and their effects were consistent for all population densities. Thus, the net effect of site variation

on DMF regression slopes canceled almost entirely, and merely increased residual variation. As a result, the DMF slope for a population inhabiting a range of different sites was similar to the DMF slope for the portion of the population inhabiting the average site. In the present experiments, the DMF regression residuals exhibited significant block effects for both species in 1990. In millet, block differences could not be linked to site quality, but in cowpea there was indication that DMF slopes increased with block quality. This result seems reasonable: since cowpea populations competed highly asymmetrically and formed skewed distributions, a large portion of the population's total biomass was contributed by a few large individuals. Site quality was, therefore, largely a measure for how well large individuals did. Good sites simply increased the growth rate differences between small and large seedlings and increased the DMF slope concurrently. We may have failed to detect a positive correlation between site quality and the DMF slopes for millet because intraspecific competition was only weakly asymmetric.

The effect of light capture and other factors on millet DMFs

In the simulation models, light interception was the only size-dependent influence on plant growth rates. In the present experiments, we found that certain environmental conditions may also have had the capability of generating size-dependence of relative growth rates.

Based on a simple light interception model, we concluded that light

capture was not limited by crowding during the first three weeks of growth (Figure 6). However, empirical DMFs for this interval did indicate that growth was size-dependent (Table 7). DMFs for the second week of growth had negative slopes with only one exception, indicating that, in general, small plants had a growth rate advantage over large plants. Populations of single plants had significantly lower DMF slopes than low or high density populations. It is possible that this difference was caused by differences in the below-ground resource status of single plants and plants at high and low density. This implies that plants were already competing at high and low density, but that competition had not yet generated significant differences in above-ground seedling biomass at the end of the second week (Table 2). In the third week of growth, the DMFs of all populations were zero or positive in 1990, and negative in 1991 (Table 7). The weather may have been responsible for these differences. In 1990, the third week of growth was quite rainy, with moderate temperatures (Table 1). Single plants grew, on average, 80-fold during this week. In 1991, the third week of growth was dry and the temperature was high (Table 1). Single plants grew only 23- fold, on average. Whatever accelerated the growth of millet plants in 1990 must have been more beneficial to larger than to smaller plants. It is possible that small plants were more susceptible to the inhibitory effects of water-logging, while large plants may have gained from the improved water supply.

Thus, environmental conditions can determine how the relative growth

rates of seedlings depend on their sizes. Since growth is usually fastest at this time, these effects can greatly influence the DMFs for the entire growth interval between the seedling stage and maturity. Indeed, it appears that the positive slope of high density millet DMFs for the entire growth interval in 1990 (Table 3) was generated in the third week of growth, since all other intervals had negative DMF slopes (Table 7). In contrast, all measured intervals had negatively sloped DMFs in 1991, and DMFs for the entire growth period were also negatively sloped. Thus, the difference in the sign of DMF slopes for high density populations in 1990 and 1991 was probably generated during the third week of growth through differences in the weather.

In the simulation models, growth rates were always limited by light interception, thus asymmetric light division always increased the DMF slope. In the present experiments, populations went repeatedly through cycles of high and low soil moisture and changed the degree to which growth was light limited.

On the basis of morphological evidence, we estimated that light division was asymmetric at high density, and symmetric at low density about five weeks after planting (Figure 8). The degree of asymmetry may have been overestimated due to our model assumptions (**METHODS**). Nevertheless, we can conclude that there was at least a small difference in the symmetry of light division between the two density levels. If plant growth rates had been light-limited during that time, such differences would have generated a density effect

on the DMF slopes. The DMF slopes for the last interval of growth and the entire interval were significantly different between low and high density in 1991, but not in 1990 (Table 2 and 7). The environmental conditions in fifth and sixth week of growth were quite different between those years. In 1990, rainfall was heavy in both weeks (Table 1) and plants were quite water-logged. In 1991, the soil was tilled to improve aeration in the fifth week of growth and was irrigated in the sixth week. Thus, the prerequisites for light-limited growth were ideal in 1991, and minimal in 1990. These differences in the environmental conditions may have been responsible for the differences in the responses of millet DMFs to high and low density between years.

In summary, empirical DMFs are not only influenced by density in conjunction with asymmetric competition, but also by abiotic environmental factors. Yearly variation in the weather can alter whether abiotic factors influence the DMF slope positively or negatively. This means that the frequently observed advantage of large seedlings (Ross and Harper 1972, Fowler 1988) is not necessarily caused by asymmetric competition. Conversely, the failure to find an initial size advantage does not prove that competition is symmetric. However, an increase in DMF slopes with density should indicate asymmetric competition, as long as abiotic influences on DMF slopes are density-independent. Differences in the weather pattern can alter the symmetry of competition between years simply by changing the timing of periods of predominant light limitation.

Competitive symmetry

Several important ecological hypotheses have been linked to the concept of competitive symmetry, such as population dynamic stability (Watson 1980, Pacala and Weiner 1991, Silvertown 1991) and coexistence in mixed populations (Zobel 1992, Kohyama 1992). This is appealing because of the generality of the concept and its implications. However, we believe that the concept of competitive symmetry has not been examined sufficiently. The present study illustrates the difficulties involved with evaluating competitive symmetry and its effects on populations.

In general, direct evidence for the symmetry of resource division is very difficult to obtain. In the present study, we estimated the division of light between individual plants. Although we did find evidence for unequal division of light in millet populations at high density, we did not know if growth was light limited during this stage of development.

Because of these difficulties, indirect indicators of competitive symmetry are often preferred over the direct evidence (Kuriowa 1960, Ford 1975, Hara 1986, Weiner and Solbrig 1984, Weiner and Thomas 1986, Firbank and Watkinson 1987). This study confirmed Schwinning's (1994) simulation result which demonstrated that the dynamics and the density-dependence of relative size variation may often be insufficient evidence for the symmetry of competition. As simulations predicted, we found that the density-dependence of empirically derived DMFs indicates the symmetry of competition better than

does the density-dependence of relative size variation. Moreover, our study suggests that it may be useful to classify competitive symmetry on a continuous, rather than a qualitative scale. Schwinning (1994) showed that the more asymmetric the competitive interaction, the greater the density-response of the DMF slope. For future theoretical development of the symmetry concept, it may prove useful to collapse competitive symmetry into a continuous variable. Our experimental results suggest that this can be useful, even if spatial variation introduces local variation in the DMF slope.

Application of the symmetry concepts in ecological theory has often been built on several implicit assumptions that may not be true. One assumption is that competitive symmetry is a fixed characteristic of communities. This assumption may have generated the hypotheses that asymmetric competition facilitates competitive exclusion (Smith and Huston 1989, Samson et al. 1992, Zobel 1992). Our results indicate that the symmetry of competition may vary from year to year, depending on the timing of resource limitations imposed by the environment. Variation only in the rainfall pattern, not necessarily the total rainfall, can influence the symmetry of competition greatly. Thus, the relationship between competitive exclusion and the symmetry of competition may not be simple.

Another assumption is that asymmetric competition determines the fate of small seedlings. Thus, species or genotypes with consistently smaller than average seedlings should suffer from asymmetric competition (Aikman and

Watkinson 1980). This assumption may have generated the hypothesis that selection should eliminate consistent seedling size differences (Solbrig 1981, Thomas and Bazzaz 1992). However, small seedlings need not necessarily suffer suppression, even if competition is asymmetric. First, annual plants may commonly be self-limited more than neighbor-limited once they become large. In that case, small plants may be able to decrease the size difference that was previously established (Newberry and Newman 1978, Wilson 1988). Second, abiotic sources of negative size-dependent growth rate variation, may eliminate the effect of asymmetric resource division.

In conclusion, we think that the symmetry concept is a useful generalization. However, we need to refine our knowledge about competitive symmetry in field populations before we can incorporate this concept into a larger theoretical framework. When and where populations compete asymmetrically, how symmetry interacts with environmental variation, and what consequences it has on population structure are the questions that need to be addressed in future field experiments.

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Table 1: Weather patterns in three experimental years. AVG T_{max} indicates the average of all daily maximal temperatures during the interval. PRECIP indicates the total precipitation during the interval. T indicates that only traces of rainfall were recorded, IRG indicates an irrigation.

	1990		1991		1992	
	AVG T_{max} (C)	PRECIP (cm)	AVG T_{max} (C)	PRECIP (cm)	AVG T_{max} (C)	PRECIP (cm)
WEEK 1	43	0 IRG	37	0.33 IRG	39	0 IRG
WEEK 2	41	T IRG	38	0 IRG	39	0.46 IRG
WEEK 3	33	3.99	38	0.03 IRG	36	2.72
WEEK 4	35	3.71	37	1.14	39	0.08 IRG
WEEK 5	37	4.81	39	T	37	0.08
WEEK 6	38	0	37	1.85 IRG	37	4.86
WEEKS 7-8	35	3.51 IRG	38	3.20	39	2.16
WEEKS 9-12	36	2.90 IRG	34	0.69	35	3.71

TABLE 2. **Millet biomass mean and variation of seedlings (SDL) and mature plants (MAT).** Variation is indicated by two measures of relative variation, the coefficient of variation (CV), and the Gini coefficient (GINI). The experimental populations (POP) were single (S), low density plants (L), high density plants (H), and intercropped plants (I).

		MEAN (g)			CV			GINI		
YEAR	POP	SDL	MAT		SDL	MAT		SDL	MAT	
1990	S	0.12 aY	338.4 aY	*	47 aY	38 a		0.20 aY	0.21 a	
	L	0.11 aY	86.4 b	*	30 bY	45 bY	*	0.13 bY	0.24 abY	*
	H	0.11 aY	52.3 cY	*	27 bY	45 bY	*	0.13 bY	0.25 bY	*
1991	S	0.36 aY	266.8 aY	*	56 abY	33 a	*	0.31 abY	0.19 a	*
	L	0.36 aY	84.4 b	*	48 acY	33 aY	*	0.27 acY	0.18 aY	*
	H	0.35 aY	59.3 cY	*	59 bY	62 bY		0.33 bY	0.33 bY	
	I	0.38 a	71.8 d	*	45 c	39 c		0.25 cY	0.22 c	

Different lower case letters indicate significant differences between populations within one year. Y indicates a significant difference across years within the same population type. * indicates a significant change during the interval. A difference between two statistics is considered significant if their bias-corrected 90 percentile bootstrap confidence limits do not overlap.

TABLE 3. DMF regressions for millet. Corresponding graph in Figure 2. The y-intercept (INTCPT), the slope (SLOPE), the r^2, and the numbers of observations (OBS) for linear regression DMFs in two experimental years (1990 and 1991). The experimental populations (POP) were single (S), low density (L), high density (H), and intercropped plants (I).

YEAR	POP	INTCPT	SLOPE	r^2	OBS
1990	S	6.91	-0.48a	0.1840	60
	L	7.10	0.23b,0	0.0159	58
	H	6.82	0.32b	0.0430	59
1991	S	5.99	-0.60a	0.6276	57
	L	4.81	-0.63a	0.5304	51
	H	4.61	-0.22b	0.1172	50
	I	4.79	-0.45c	0.3217	50

Same letter as subscript indicates no significant difference in slopes between populations in the same year. 0: indicates no significant difference from zero. A difference was called significant if the 90 percentile bootstrap confidence intervals did not overlap.

TABLE 4. Cowpea biomass mean and variation of seedlings (SDL) and mature plants (MAT). Variation is indicated by two measures of relative variation, the coefficient of variation (CV), and the Gini coefficient (GINI). The experimental populations (POP) were single (S), low density (L), high density (H), and intercropped plants (I).

		MEAN (g)			CV			GINI		
	POP	SDL	MAT		SDL	MAT		SDL	MAT	
1990	S	0.77 abY	60.4 aY	*	10 a	66 aY	*	0.05 a	0.36 aY	*
	L	0.78 aY	6.4 b	*	9 aY	74 aY	*	0.05 a	0.39 aY	*
	H	0.76 bY	3.9 cY	*	9 a	72 aY	*	0.04 aY	0.37 aY	*
1991	S	1.02 aY	36.5 aY	*	10 ab	44 aY	*	0.06 ab	0.24 aY	*
	L	1.03 aY	6.9 b	*	11 aY	51 abY	*	0.06 aY	0.29 bY	*
	H	1.00 bY	5.4 cY	*	10 b	51 abY	*	0.05 bY	0.29 bY	*
	I	1.02 aY	8.1 d	*	9 b	54 bY	*	0.05b	0.29 b	*

Different lower case letters indicate significant differences between populations within one year. Y indicates a significant difference across years within the same population type. * indicates a significant change during the interval. A difference between two statistics is considered significant if their bias-corrected 90 percentile bootstrap confidence limits do not overlap.

TABLE 5. DMF regressions in cowpea. Corresponding graph in Figure 3. The y-intercept (INTCPT), the slope (SLOPE), the r^2, and the numbers of observations (OBS) for linear regression DMFs in two experimental years (1990 and 1991). The experimental populations (POP) were single (S), low density (L), high density (H), and intercropped plants (I).

	POP	INTCPT	SLOPE	r^2	OBS
1990	S	4.68	2.11a	0.0665	56
	L	2.87	4.04b	0.2380	55
	H	2.52	3.98b	0.2790	53
1991	S	3.46	-0.96a	0.0260	56
	L	1.76	-0.46a,0	0.0071	57
	H	1.54	1.36b	0.0520	57
	I	1.91	1.35b	0.0558	53

Same letter as subscript indicates no significant difference in slopes between populations in the same year. 0: indicates no significant difference from zero. A difference was called significant if the 90 percentile bootstrap confidence intervals did not overlap.

TABLE 6. Comparison of regression models for cowpea and millet in 1990. M1: 2 parameter model (one slope, one intercept), M2: 7 parameter model (one slope, one intercept per block); M3: 7 parameter model (one intercept, one slope per block) ; M4: 12 parameter model (one slope per block, one intercept per block). There are 6 blocks in both experiments. The experimental populations (POP) were single (S), low density (L), high density (H), and intercropped plants (I).

		SLOPES:			
	POP	M1 (r^2)	M2 (r^2)	M3 (r^2)	M4 (r^2)
MILLET 1990	S	-0.48 (0.18)a	-0.56 (0.59)b	-0.36 to -0.67 (0.58)b	-0.77 to 0.32 (0.63)b
	L	0.23 (0.02)a	0.56 (0.27)b	0.32 to 0.55 (0.25)b	-0.62 to 2.82 (0.52)c
	H	0.32 (0.04)a	0.49 (0.20)a	0.39 to 0.57 (0.19)b	0.16 to 1.32 (0.22)a
COWPEA 1990	S	2.11 (0.07)a	1.36 (0.20)b	0.99 to 2.73 (0.19)b	-7.35 to 2.37 (0.26)b
	L	4.00 (0.24)a	5.17 (0.40)b	2.38 to 5.37 (0.36)b	1.34 to 15.46 (0.49)b
	H	4.00 (0.28)a	4.52 (0.56)b	2.04 to 5.16 (0.52)b	2.43 to 10.11 (0.61)b

The r^2 values for the models are indicated below the slope values in brackets. Same letters indicate no significant difference in r^2 between models.

TABLE 7. DMF slopes of millet for episodes for two experimental years (1990 and 1991). The experimental populations (POP) were single (S), low density (L), high density (H), and intercropped plants (I).

		DMF SLOPE	
		1990	1991
second week	S	-0.21a	-0.10a,0
	L	-0.46b	-0.54b
	H	-0.39b	-0.63b
third week	S	0.45a	-0.12a
	L	0.04a,0	-0.23b
	H	0.49a	-0.25b
fourth twelfth week	S	-0.59a	-0.65a
	L	-0.33b	-0.56a
	H	-0.24b	-0.30b

Same letters indicate no significant differences between the slopes of populations in the same year. 0 indicates no significant difference from zero.

TABLE 8. Analysis of variance for initial seedling sizes for two experimental years (1990 and 1991). Analysis was performed on untransformed data. The percent values represent the sums of squares (SS) in percents of the total sums of squares.

A: MILLET	1990		1991	
	SS	p	SS	p
DENSITY	0.0029	0.3421	0.0031	0.9501
SEED SIZE	0.0178 (6%)	0.0018	1.2323 (21%)	0.0001
BLOCK	0.0683 (23%)	0.0001	0.2620 (4%)	0.0387
BLOCK x DENSITY	0.0184	0.1995	0.1696	0.4742
SEED x DENSITY	0.0015	0.8884	0.0924	0.5519
SEED x BLOCK	0.0122	0.5266	0.2764	0.1770
BLOCK x DENSITY x SEED SIZE	0.0111	0.9875	0.2918	0.6472

B: COWPEA	1990		1991	
	SS	p	SS	p
DENSITY	0.0081	0.4135	0.0314	0.1910
SEED SIZE	0.0086	0.3909	0.0921 (5%)	0.0088
BLOCK	0.1693 (20%)	0.0001	0.1065 (6%)	0.0121
BLOCK x DENSITY	0.0281	0.7983	0.1300 (7%)	0.0374
SEED x DENSITY	0.0239	0.2701	0.0460	0.3034
SEED x BLOCK	0.0333	0.6948	0.0992	0.1116
BLOCK x DENSITY x SEED SIZE	0.0729	0.7095	0.1635	0.1501

LEGENDS

Figure 1: Planting pattern in the experimental units, called patches. Circles represent the center location of millet plants and diamonds the center location of cowpea plants. Focal plants are drawn solid. Patch dimensions are 3 m by 3 m. Rows are 1 m apart.

Figure 2. Millet DMFs for single plants (S), low density plants (L), high density plants (H), and in intercrop (I) in two experimental years (A: 1990, B:1991). B_M is the biomass in vegetative dry weight (g) at maturity. B_S is the estimated biomass in the same unit at the seedling stage, two weeks after planting. Regression parameters are presented in Table 3.

Figure 3. Cowpea DMFs for single plants (S), low density plants (L), high density plants (H), and in intercrop (I) in two experimental years (A: 1990, B: 1991). B_M is the biomass in vegetative shoot dry weight (g) at maturity. B_S is the estimated biomass in the same unit at the seedling stage, two weeks after planting. Regression parameters are presented in Table 5.

Figure 4. The relationship between the change in relative variation and the DMF slope for millet (M) and cowpea (C) populations in two experimental years (1990 and 1991). The change in relative variation is shown as the ratio of the standard deviation of log biomass for mature plants ($LN(B_M)$) over the standard deviation of

log biomass for seedlings ($LN(B_S)$). Biomass is in units of vegetative shoot dry weight (g). The dashed line shows the expected relationship if the DMF was exact and linear. For further explanation, see text.

Figure 5. The DMF slope deviation (Δ DMF SLOPE) as a function of block quality for cowpea in 1990. The DMF slope deviation is the difference between the block-specific DMF slope of model M4 and the common slope of model M2. Block quality is represented as the average rank of mean focal cowpea plant size across three density levels. Solid circles represent single plant populations, open triangles low density populations, and solid triangles high density populations. For further explanation, see text.

Figure 6. The estimated relative light interception (LN(B/L)) of millet plants as a function of log biomass (LN(B)) three weeks after planting. Biomass (B) is the vegetative shoot dry weight (g). Light interception (L) is the estimated whole plant light interception in relative units.

Figure 7. Allometric relationships in millet plants five weeks after planting. A: The relationship between leaf area index (LAI) and biomass. B: the relationship between average foliage height (HEIGHT) and biomass. Average foliage height is the leaf area-weighted height of the canopy.

Figure 8. A: the estimated relative light interception (LN(L/B)) as a function of log biomass (LN(B)) five weeks after planting. Biomass (B) is the vegetative shoot dry weight (g). Light interception (L) is the estimated whole plant light interception in relative units. B: The estimated difference in the relative light interception of plant pairs ($LN(L_1/B_1)$-$LN(L_2/B_2)$) as a function of their relative biomass difference ($LN(B_1)$-$LN(B_2)$). B_1 is the biomass in vegetative shoot dry weight (g) of the larger plant, B_2 that of the smaller plant in a pair. L_1 is the estimated whole plant light interception in relative units of the larger plant, L_2 that of the smaller plant in a pair. The dotted lines indicate the average differences in relative light interception.

Figure 9. The seed size effect on average seedling biomass across all blocks and densities in millet (A) and cowpea (B) in two experimental years (1990 and 1991). Seed size categories are specified in **METHODS**.

Figure 10. Correlation between the block average millet and cowpea seedling biomass (B_S) in two experimental years (1990 and 1991). Seedling biomass is the estimated shoot dry weight (g).

Figure 1

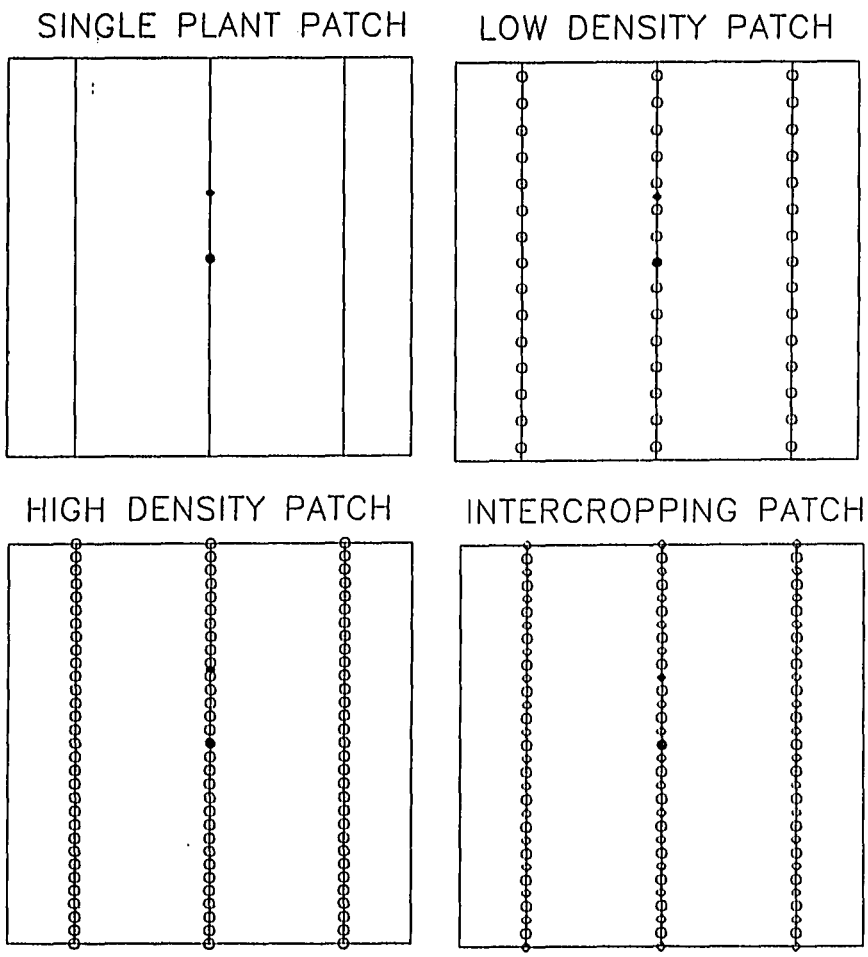

SINGLE PLANT PATCH
LOW DENSITY PATCH
HIGH DENSITY PATCH
INTERCROPPING PATCH

Figure 2

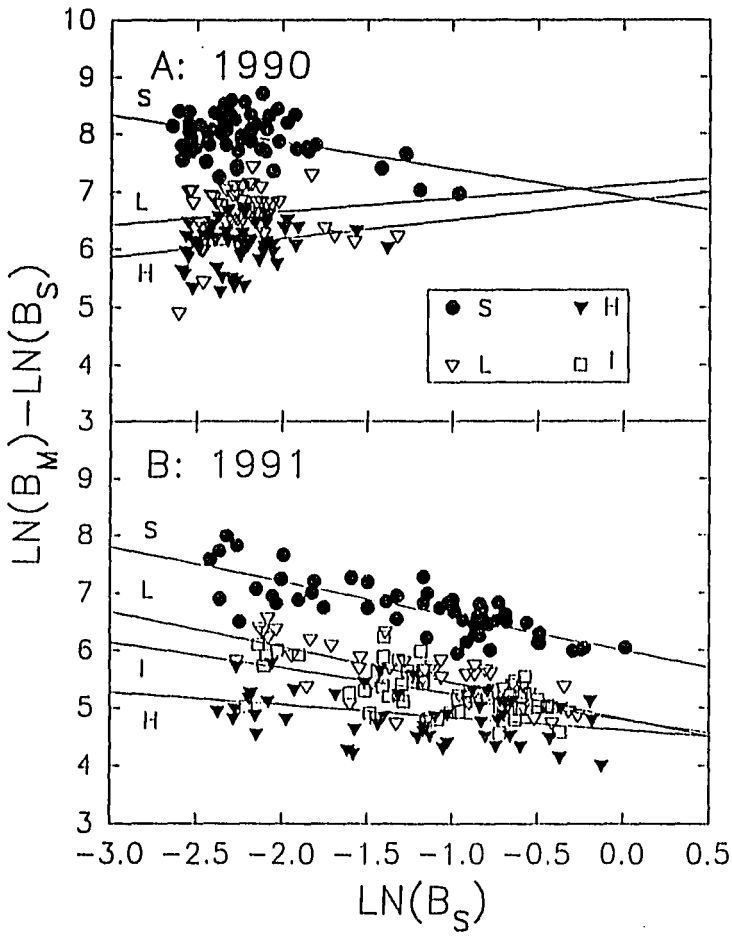

A: 1990
B: 1991
S
L
I
H
LN(B_M)−LN(B_S)
LN(B_S)
10
9
8
7
6
5
4
3
−3.0
−2.5
−2.0
−1.5
−1.0
−0.5
0.0
0.5

Figure 3

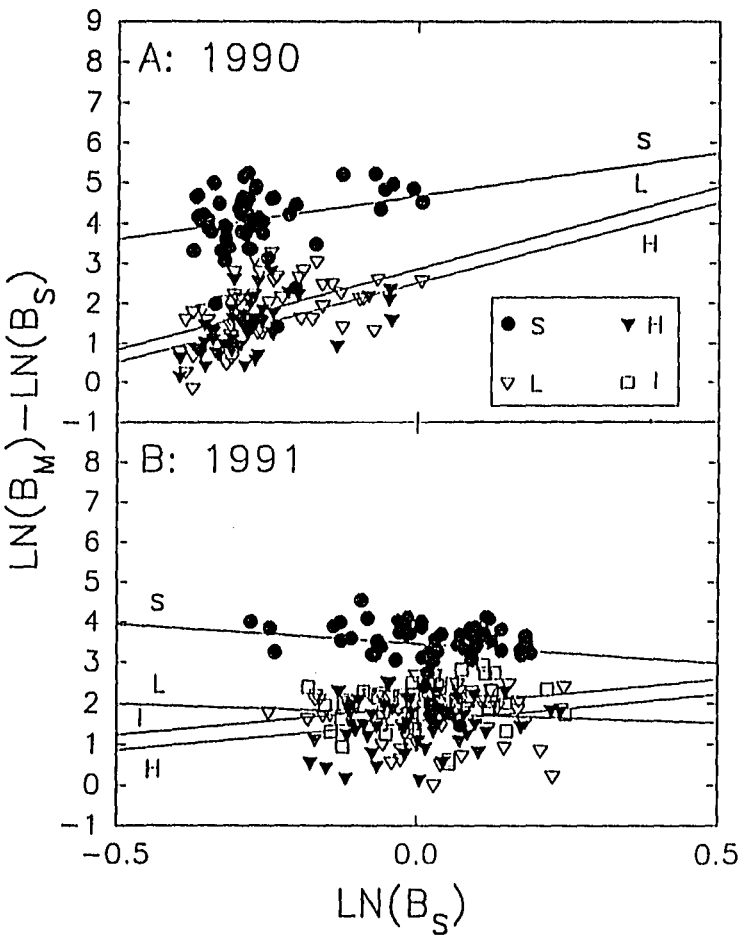


Figure 4

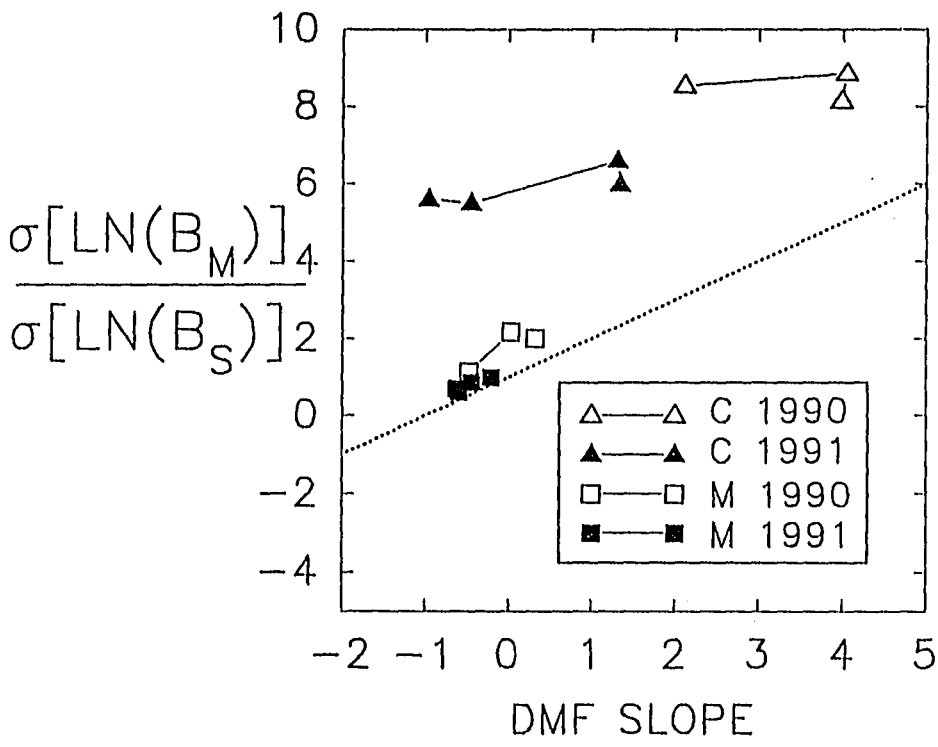

10
8
6
4
2
0
−2
−4
σ[LN(B_M)] / σ[LN(B_S)]
−2 −1 0 1 2 3 4 5
DMF SLOPE
C 1990
C 1991
M 1990
M 1991

Figure 5.

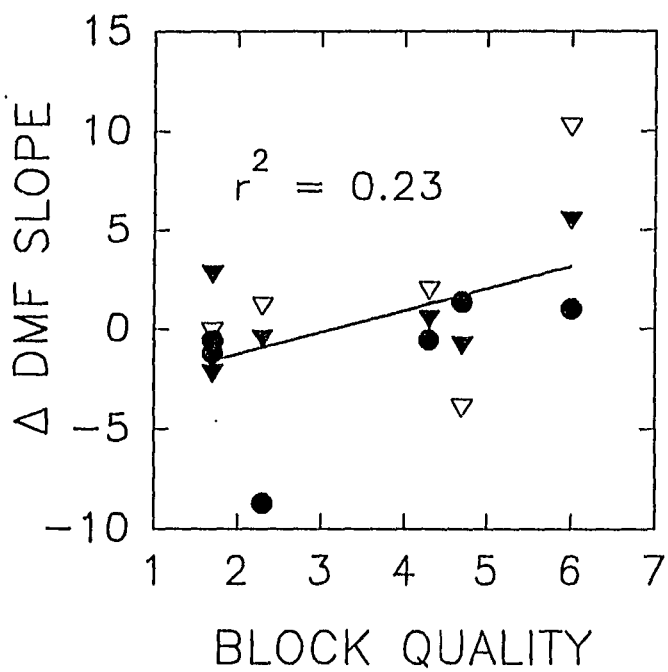


Figure 6

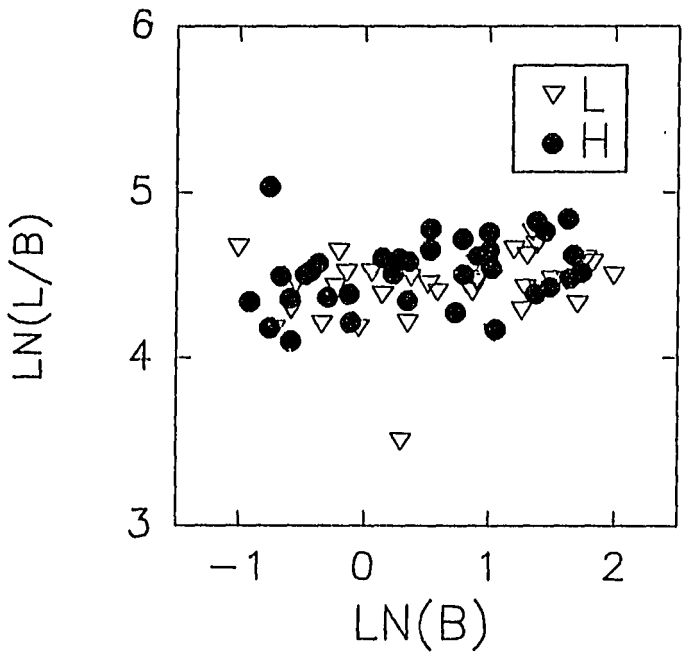


Figure 7

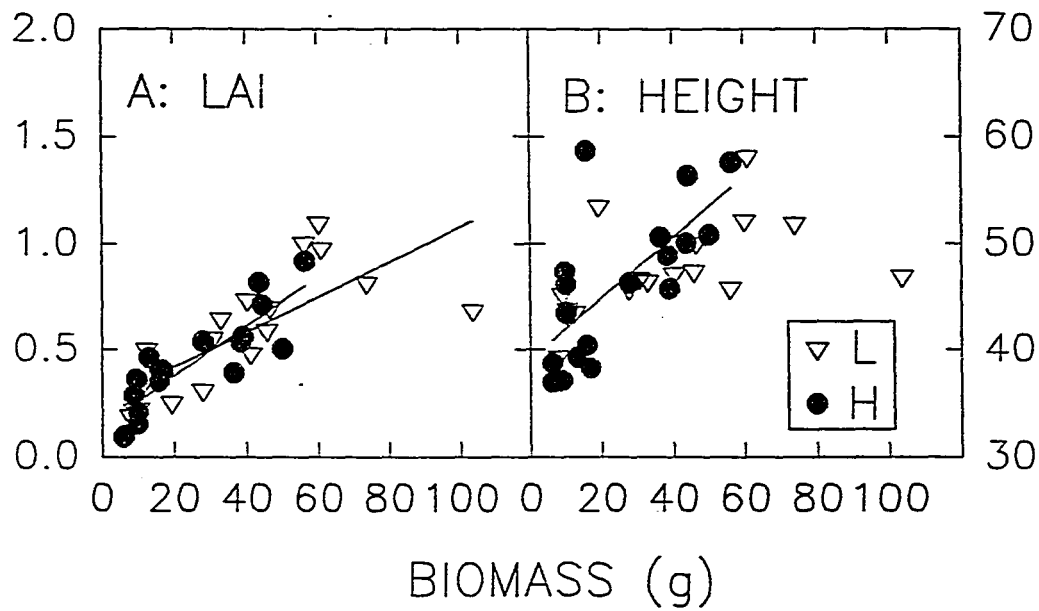

A: LAI
B: HEIGHT
2.0
1.5
1.0
0.5
0.0
70
60
50
40
30
0 20 40 60 80 100 0 20 40 60 80 100
BIOMASS (g)
L
H

Figure 8.

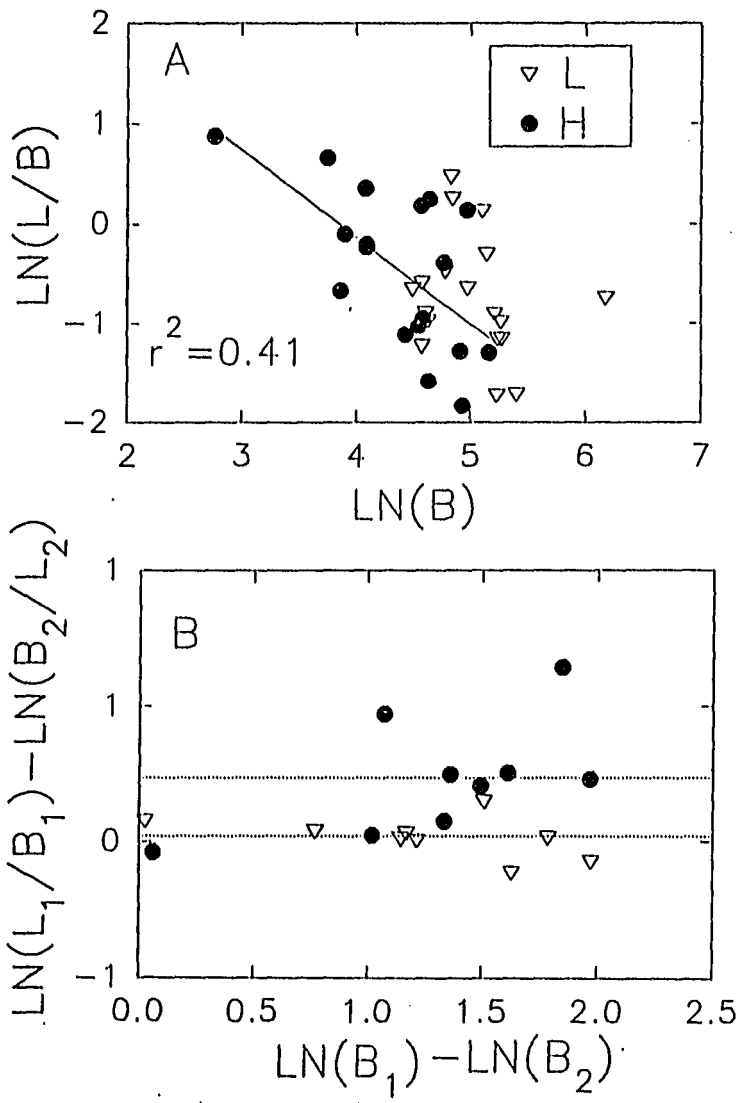


Figure 9.

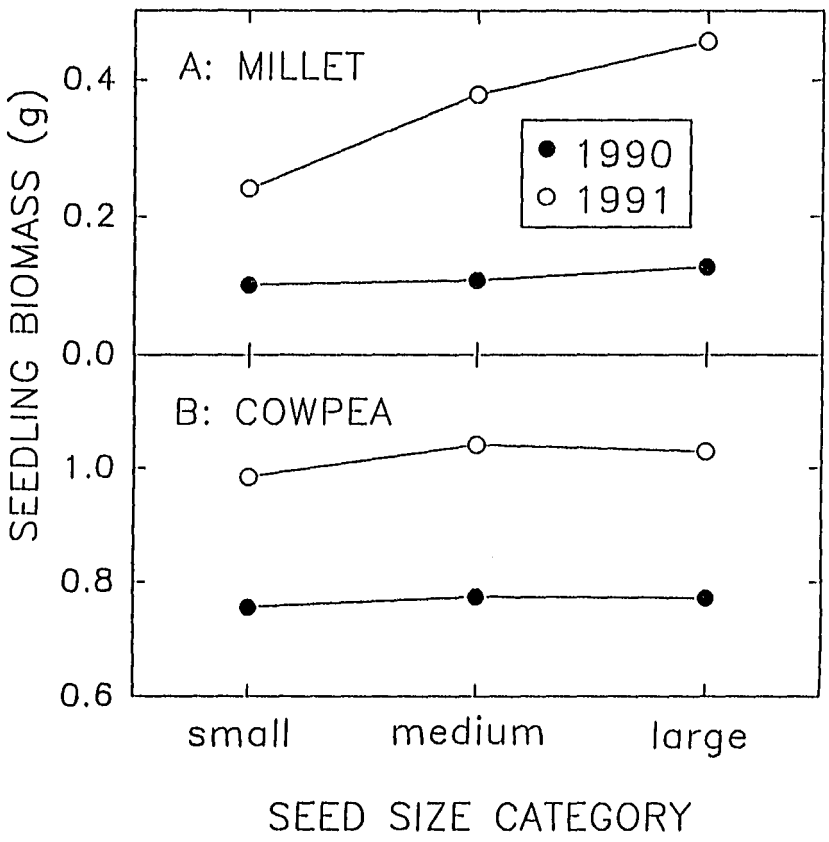
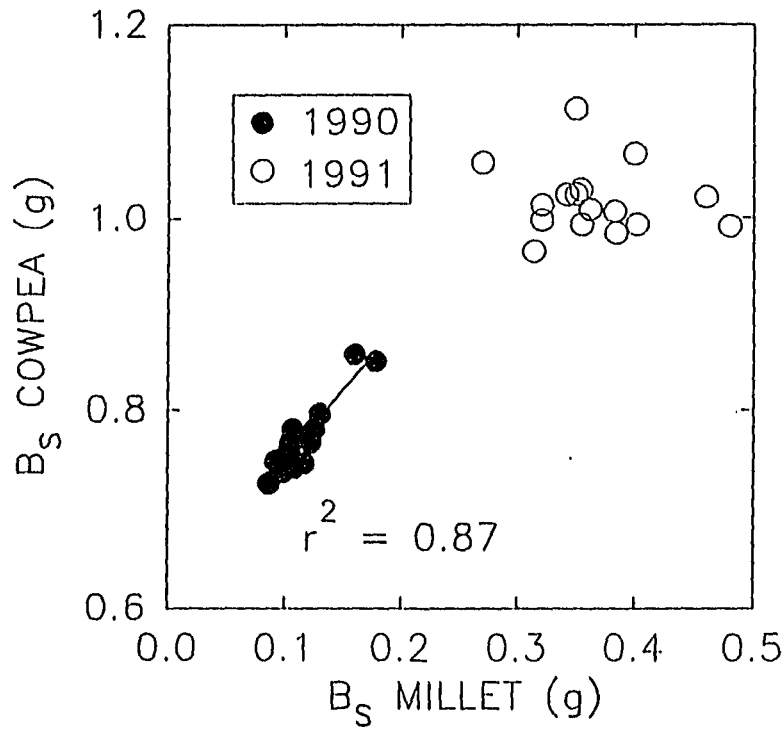

A: MILLET
B: COWPEA
1990
1991
SEEDLING BIOMASS (g)
0.4
0.2
0.0
1.0
0.8
0.6
small
medium
large
SEED SIZE CATEGORY

Figure 10.


1.2
1.0
0.8
0.6
0.0
0.1
0.2
0.3
0.4
0.5
1990
1991
r^2 = 0.87
B_S COWPEA (g)
B_S MILLET (g)