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ORIGINAL ARTICLE

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Size-asymmetric competition and size-asymmetric growth in a spatially explicit zone-of-influence model of plant competition

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Abstract Size-asymmetric competition among plants is usually defined as resource pre-emption by larger individuals, but it is usually observed and measured as a disproportionate size advantage in the growth of larger individuals in crowded populations ("size-asymmetric growth"). We investigated the relationship between size-asymmetric competition and size-asymmetric growth in a spatially explicit, individual-based plant competition model based on overlapping zones of influence (ZOI). The ZOI of each plant is modeled as a circle, growing in two dimensions. The size asymmetry of competition is reflected in the rules for dividing up the overlapping areas. We grew simulated populations with different degrees of size-asymmetric competition and at different densities and analyzed the size dependency of individual growth by fitting coupled growth functions to individuals. The relationship between size and growth within the populations was summarized with a parameter that measures the size asymmetry of growth. Complete competitive symmetry (equal division of contested resources) at the local level results in a very slight size asymmetry in growth. This slight size asymmetry of growth did not increase with increasing density. Increased density resulted in increased growth asymmetry when resource competition at the local level was size asymmetric to any degree. Size-asymmetric growth can be strong evidence that competitive mechanisms are at least partially size asymmetric, but the degree of size-asymmetric growth is influenced by the intensity as well as the mode of competition. Intuitive concepts of size-asymmetric competition among individuals in spatial and nonspatial contexts are very different.

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Introduction

Competition from neighboring plants is one of the most important biotic factors limiting plant growth. Often, larger plants have a disproportionately larger effect in competition, suppressing the growth of their smaller neighbors (Begon 1984; Weiner 1990). This phenomenon is called "size-asymmetric competition" (Schwinning and Weiner 1998) or just "asymmetric competition," but it has also been referred to as "one-sided competition" (Kikuzawa 1999) or "dominance and suppression" (Schmitt et al. 1986). Size-asymmetric competition occurs when larger individuals pre-empt resources, making them unavailable to smaller individuals (Schwinning and Weiner 1998).

While size-asymmetric competition is usually defined in terms of resource pre-emption, researchers are just beginning to be able to measure resource uptake as a function of size in competing plants (Berntson and Wayne 2000; Hikosaka and Hirose 2001). Resource pre-emption by larger individuals is often inferred from the growth of larger vs. smaller individuals.

A simple way to do this is to analyze the relationship between growth and size among individuals within a crowded population over a period (Westoby 1982; Hara 1988). If the growth increment (absolute growth rate, AGR) of a plant is proportional to its size (Fig. 1a) or increases less than proportionately with plant size (e.g., Fig. 1b), there is no evidence for asymmetric competition. Such patterns are consistent with the fact that plant growth is sigmoidal. Size-asymmetric competition is the most likely explanation for those cases in which AGR increases more than proportionally with size within a crowded population (Fig. 1c; Thomas and Weiner 1989). Indeed, it is difficult to think of a reasonable

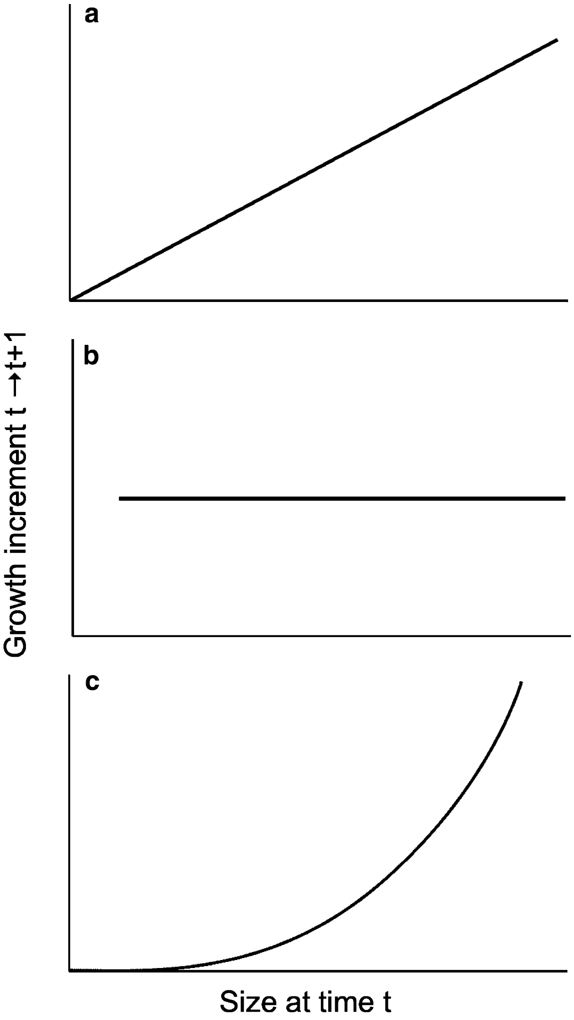

Fig. 1a–c If the growth increment (absolute growth rate, AGR) of a plant in a crowded population is proportional to its size (**a**) or if AGR increases less than proportionately with plant size (**b**), there is no evidence for size-asymmetric competition. An AGR that increases more than proportionally with size (**c**) is strong evidence for size-asymmetric competition (after Weiner 1990)

alternative hypothesis to explain such a pattern, in which larger plants have larger relative growth rates (RGR) than smaller plants under competition. Damgaard (1999) proposed using the degree of upward curvilinearity of the growth–size relationship as a measure of the size asymmetry of growth, and he developed a way to look at this relationship across several growth intervals by fitting coupled growth curves to individual plants. The method was used to show that the size asymmetry of growth increased with density in crowded populations of *Chenopodium album* (Damgaard et al. 2002).

The relationship between size-asymmetric competition and size-asymmetric growth is not clear, however. Is an increase in size-asymmetric growth due to some factor or treatment strong evidence for an increase in the size asymmetry of competition itself, or is the relationship between these two things more subtle? To address this question, we analyze the relationship between size-asymmetric competition and size-asymmetric growth in an individual-based, spatially explicit, semi-mechanistic, model of plant competition based on zones of influence (ZOI). We compare the "observed" asymmetric growth of simulated plants with a known degree of size-asymmetric competition for resources, and ask the following questions:

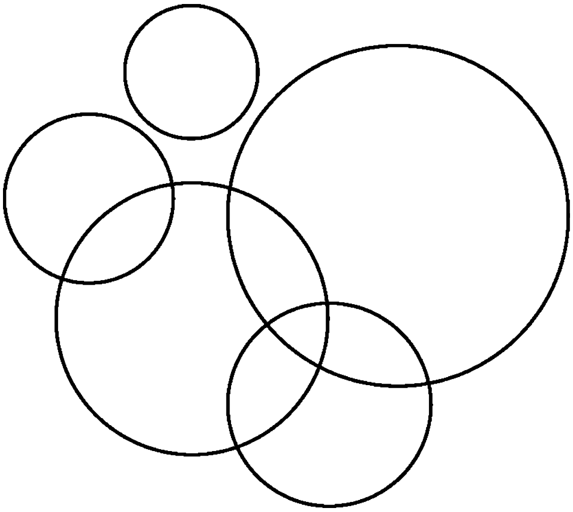

Fig. 2 Zone-of-influence model, in which a *circle* represents the area from which each of the five plants may extract resources. The plants divide resources in the overlapping area according to specific rules

(1). Does size-symmetric competition give rise to size-symmetric growth?
(2). Does an increase is the size asymmetry of competition result in a corresponding increase in the size asymmetry of growth?
(3). What is the interaction between density and size-asymmetric competition in determining size-asymmetric growth?

Methods

"Zone-of-influence" simulation model

"Zone-of-influence" models, in which plants grow, occupy space and compete for resources distributed in areas they overlap, have been popular in theoretical plant ecology because they are semi-mechanistic, conceptually simple, and seem to capture some essential aspects of spatial competition among individual plants (Gates and Westcott 1978; Wyszomirski 1983; Hara and Wyszomirski 1994; Wyszomirski et al. 1999; Weiner et al. 2001). In our ZOI model (Weiner et al. 2001), plants are three-dimensional but represented as circles in two dimensions (Fig. 2). The area a plant occupies, *A*, represents resources potentially available to the plant, and is allometrically related to the plant's biomass, B, as $A = c \times B^{2/3}$. A plant's potential growth, i.e., its growth if there are no neighbors, is sigmoidal. We chose the function

$$\frac{\mathrm{d}B}{\mathrm{d}t} = r\left(A - \frac{B^2}{B_{\max}^{4/3}}\right) = r\left(c \times B^{2/3} - \frac{B^2}{B_{\max}^{4/3}}\right). \quad (1)$$

where $B_{\max}$ is the maximum (asymptotic) plant mass, r is the initial (maximum) growth rate in mass per unit area occupied (in units of mass area^{-1} time^{-1}), and t is time. The gain term is proportional to the area occupied (West et al. 1999), while the loss term is proportional to the biomass squared, as in the widely used logistic growth equation (Hunt 1982).

When plants overlap, they compete for resources in areas of overlap. The effective area of a plant (A_{e}) is the area it covers (A) minus that part of the area lost to neighbors (A_{n}). A_{e} determines the realized growth rate of the plant during the next time interval:

$$\frac{\mathrm{d}B}{\mathrm{d}t} = r\left(A_{\mathrm{e}} - \frac{B^2}{B_{\max}^{4/3}}\right). \quad (2)$$

For simplicity when analyzing and interpreting the results, plants cannot have negative growth rates, but continue to live and maintain the maximum size they achieve. The degree of size asymmetry of competition is reflected in the rules for dividing the overlapping areas among the competitors. "Complete size asymmetry" (Schwinning and Weiner 1998) occurs when the largest individual obtains all of the resources in the area of overlap. In complete size symmetry, areas of overlap are divided equally among all overlapping individuals, irrespective of their sizes.

The model is not based on specific units of measure, but we describe it with real units to give a picture related to real plants. One hundred individuals are randomly positioned on a torus with variable area (either 100 cm × 100 cm, i.e., a plant density of 0.01 cm^{-2}, 50 cm × 50 cm, i.e., a plant density of 0.04 cm^{-2}, or 31.62 cm × 31.62 cm, i.e., a plant density of 0.1 cm^{-2}). There is random normal independent variation in initial sizes (B_0), initial RGR (r), and asymptotic sizes ($B_{\max}$). We chose mean parameter values that are reasonable based on previous work with the model and that are realistic for annual plants. The coefficient of variation for parameters was arbitrarily set to 10%. For r, mean (μ) = 1 mg cm^{-2} t^{-1}, standard deviation (σ) = 0.1; B_0—μ = 1 mg, σ = 0.1 mg; $B_{\max}$—μ = 20,000 mg and σ = 2,000 mg. The ZOI of plant i at time t is a circle on the torus with radius:

$$\sqrt{\frac{B_i(t)^{2/3}}{\pi}}. \quad (3)$$

The resources of a small area, $\mathrm{d}\Omega$, are distributed among the k plants where the ZOI areas overlap $\mathrm{d}\Omega$ according to a power function of the biomass of the plants (e.g., Wyszomirski et al. 1999). The available resources for the growth of plant i are obtained by adding over the entire ZOI area of plant i, Ω_i:

$$A_i(t) = \sum_{\Omega_i} \frac{B_i(t)^b}{\sum_j^k B_j(t)^b} \mathrm{d}\Omega, \quad b \geqslant 0. \quad (4)$$

The parameter b determines the degree of size-asymmetric competition due to the uptake of contested resources (Table 1). The parameter b was assumed to take the values 0, 0.5, 1, 2, 5 or ∞ in the simulations. When $b = \infty$, the largest plant that overlaps $\mathrm{d}\Omega$ gets all of the resources. The time step, $\mathrm{d}t$, was set to one day, and the simulation was stopped after 100 days, when most of the plants had stopped growing. For each combination of plant density and degree of size-asymmetric competition, three simulations were run.

"Coupled Richards growth" analytical model

Our goal in this study is to analyze the simulated growth data with an empirical growth model. Several sigmoidal or saturated growth models have been proposed to describe the growth of individual plants, e.g., Gompertz, and logistic growth models. The essential difference between these models is the size at which the plant experiences its maximum AGR (Seber and Wild 1989). The maximum AGR occurs at the point when the sigmoidal growth curve shifts from being convex to being concave (the inflection point). In the Richards growth model (Richards 1959; Vandermeer 1989; García-Barrios et al. 2001) this inflection point is modeled by a free parameter. The determination of the inflection point by a free parameter makes the Richards growth model relatively flexible and inclusive of the other sigmoidal growth models.

The Richards growth model describes the growth of individual plants quite well. Competition among individuals can be modeled by coupling the individual growth models, so the growth of the individual plants is constrained by the total biomass of the population. Even in a monoculture, individuals will differ in their time of germination, distance to nearest neighbor, genetic composition and microenvironment, and these differences will generate variation in plant size. One could start by treating such variations as random. But if the plant growth is limited by a resource that may be monopolized, e.g., light, then size-asymmetric competition will occur and the variation among plant sizes will increase over time and cannot be considered random.

The effect of size-asymmetric growth may be included in the Richards growth model by modeling individual plant growth as proportional to a power function of their size (Damgaard 1999; Damgaard et al. 2002; Schwinning and Fox 1995; Wyszomirski et al. 1999).

$$f(v(t), a) = \begin{cases} 1 & a = 0 \\ (v(t) + 1)^a - 1 & a > 0 \\ 1 \text{ or } 0 & a = \infty \end{cases} \quad (5)$$

where $v(t)$ is the size of plant i at time, and the effect of plant size on growth is summarized by a size-asymmetry parameter, a, which measures the degree of curvature of the size–growth relationship over the entire growth curve. It takes values between 0 and ∞ (Table 1).

Assume a monoculture of n competitively interacting plants of variable size. The growth of plant i at time t may be expressed by n coupled differential equations (Damgaard et al. 2002),

$$\frac{\mathrm{d}v_i(t)}{\mathrm{d}t} = \begin{cases} \dfrac{\kappa}{1-\delta} f(v_i(t),a)\left(\left(\dfrac{1}{nw}\displaystyle\sum_{j=1}^{n} v_j(t)\right)^{\delta-1} - 1\right), & \delta \neq 1 \\ \kappa f(v_i(t),a)\left(\log(nw) - \log\left(\displaystyle\sum_{j=1}^{n} v_j(t)\right)\right), & \delta = 1 \end{cases} \tag{6}$$

where $v_i(t)$ is the size of plant i at time t, and w is the *average* plant size at the end of the growing season. The initial growth rate is $(\kappa a)/(\delta - 1)$, and the saturating term $\left(\left(\frac{1}{nw}\sum_{j=1}^{n} v_j(t)\right)^{\delta-1} - 1\right)$ or $\left(\log(nw) - \log\left(\sum_{j=1}^{n} v_j(t)\right)\right)$ if $\delta = 1$, measures the decrease in individual plant growth due to the size and competitive effects of the n interacting plants. The saturation term, which is equal for all n plants at a given time, reduces as the plants grow and when $\Sigma_{j=1}^{n} v_j(t) = nw$ the saturation term equals 0 and growth stops.

Sampling and statistical methodology

We sampled all 100 plants every 10 days over the 100 simulated days. The individual-based Richards growth model (6) cannot be solved in the general case. Consequently, in order to fit the growth model to the simulated growth data, the growth models were solved numerically for each set of parameter values used in a maximum likelihood fitting procedure using the NDSolve routine of Mathematica (Wolfram 1999). In order to ensure that the parameters are strictly positive, the growth models were reparameterized (exp[κ], exp[a], exp[w]); however, all results are reported after parameter values were transformed back.

To avoid autocorrelated errors (Seber and Wild 1989), the growth model (6) was fitted to the growth increments. The residual variance in the growth increments was homogenized with log-transformation, and after transformation of both the growth model and the simulated growth data, the residuals were approximately normally distributed. The maximum likelihood estimates of the parameter values were found using the FindMinimum routine of Mathematica (Wolfram 1999).

The maximum likelihood estimates of the empirical growth models were analyzed using an analysis of variance with the fixed factors: (a) degree of asymmetric competition and (b) plant density (SAS Institute 2001).

Results

The Coupled Richards growth model (6) could be fitted to the simulated plant growth data in all the simulations. The maximum likelihood estimation of the degree of asymmetric growth in the simulated plants depended on the degree of asymmetric competition used in the ZOI model and the plant density (Table 2; Fig. 3).

The degree of asymmetric growth was always higher than 1. When the degree of asymmetric competition was 0, the size asymmetry of growth was still slightly above 1

Table 1 Comparison of definitions and associated parameters values for the degree of size-asymmetric competition in the zone-of-influence (ZOI) simulation model (b), and the degree of size-asymmetric growth (a) in the Coupled Richards growth model

	Definitions	
	Size symmetry of resource competition in ZOI simulation model (b)	Size symmetry of growth in Coupled Richards growth model (a)
Complete symmetry	All plants share contested resources equally, irrespective of their size. $b = 0$	All plants have the same absolute growth rate irrespective of their size. $a = 0$
Partial size symmetry	Uptake of contested resources increases with size but less than proportionally. $b < 1$	The growth rate is less than proportional to the size. $0 < a < 1$
Perfect size symmetry	Uptake of contested resources is proportional to size. $b = 1$	The growth rate is proportional to the size. $a = 1$
Partial size asymmetry	Uptake of contested resources increases with size and larger plants receive a disproportionate share. $b > 1$	The growth rate is more than proportional to the size. $a > 1$
Complete size asymmetry	Limiting case where only the very largest plants get all the contested resources. $b = \infty$	Limiting case where only the very largest plants are growing. $a = \infty$

The degree of size-asymmetric competition in the ZOI simulation model is defined in terms of the rules for dividing up resources in overlapping ZOI. The degree of size-asymmetric growth in the Coupled Richards model is defined by the observed growth advantage that larger plants show. Terminology after Schwinning and Weiner (1998)

Table 2 Analysis of variance of the maximum likelihood estimates of the degree of size asymmetry of growth in the Coupled Richards growth model as a function of the density and the degree of size asymmetry of competition in the zone-of-influence model

Source	*df*	Mean squares	*F* value	$P > F$
A: degree of size asymmetry of competition	5	0.612	494.92	< 0.0001
B: plant density	2	0.192	155.24	< 0.0001
$A \times B$ interaction	10	0.0400	32.36	< 0.0001
Error	36	0.001237		

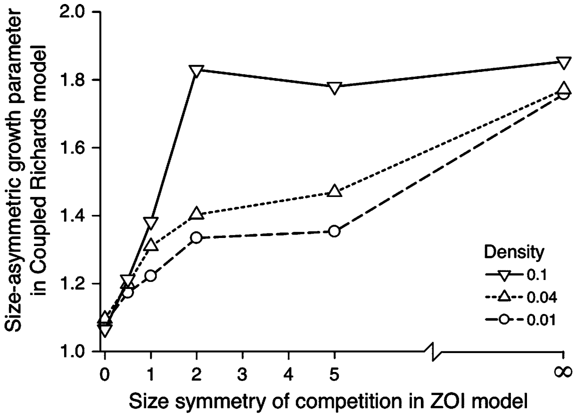

Fig. 3 Average maximum likelihood estimates of the degree of size-asymmetric growth in the simulated plants plotted against the degree of asymmetric competition used in the zone-of-influence model at different plant densities

(Fig. 3). The degree of asymmetric growth increases significantly with density except when competition is completely symmetric.

The estimated degree of asymmetric growth did not correspond closely to the degree of asymmetric competition under which it was simulated (Fig. 3). A relatively low degree of size-asymmetric competition gave rise to a high degree of size-asymmetric growth when the density was high.

Discussion

While size-asymmetric competition may be the primary cause of size-asymmetric growth in crowded plant populations, the quantitative relationship between these two processes is not straightforward. In the ZOI model simulations, size-asymmetric competition interacts with density to determine the degree of size-asymmetric growth. When competition of space was size-symmetric, growth was almost size-symmetric, and the very slight degree of growth asymmetry observed did not increase at higher densities. The size asymmetry of growth increased with density when competition was partially or completely size-asymmetric. Therefore, while size asymmetry of growth among competing plants may be strong evidence for the occurrence of size-asymmetric competition, the extent of size-asymmetric growth is not a reliable measure of the degree of size-asymmetric competition. While the effects of size-asymmetric competition increase with density (Damgaard et al. 2002), one cannot conclude that one or more competitive mechanisms themselves become more asymmetric at higher densities. The local distribution of contested resources among competing individuals of different sizes interacts with density to determine the population-wide distribution of resources among individuals of different size. The effects of density on size-asymmetric growth appear to be most important at intermediate levels of size-asymmetric competition, which may be the most realistic.

The observed degree of growth asymmetry is a function of both the degree of asymmetric competition and the intensity of competition, and the latter can be as or more important than the former. Density increases the effects of competitive size asymmetry on growth because it increases the intensity of competition.

Complete competitive symmetry (equal division of contested resources) at the local level results in a very slight size asymmetry in growth, even though equal division of contested resources represents an extreme form of size-symmetric competition (Weiner et al. 2001). This may be due to a small inherent advantage for larger individuals in a ZOI model: when a large individual overlaps a small individual, the area of overlap is a smaller fraction of the larger individual's area (Schwinning and Weiner 1998). It is important to note, however, that the slight size asymmetry of growth under complete competitive asymmetry did not increase with increasing density. Our results support the original (Weiner 1985; Weiner and Thomas 1986), but still controversial (Huston 1986; Bonan 1991; Weiner et al. 2001) contention that an increase in size inequality in populations grown at higher densities can be considered to be evidence that competition is partially size asymmetric. We conclude that a high level of size-asymmetric growth within a crowed population is strong evidence for the occurrence of size-asymmetric competition, even though the former is not a good measure of the strength of the latter.

Many of our results are due to the inclusion of space in the simulation model. Size-asymmetric competition is usually defined in terms of division of contested resources among competing individuals, but without reference to space: larger individuals obtain a disproportionate share of contested resources (Weiner 1990). When competition is local, the ability of larger individuals to monopolize contested resources is very limited, because only local resources can be monopolized. Even very large plants cannot pre-empt resources from plants that are not their neighbors. In a ZOI model, plants compete only for resources in areas of overlap. As density or mean plant size increases, so does the fraction of accessed resources that are contested.

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