

## Including competitive asymmetry in measures of local interference in plant populations

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**Summary.** Although considerable evidence exists that plant competition is generally asymmetric or “one-sided”, with larger plants having a disproportionate competitive effect on smaller plants, currently employed measures of local interference generally assume that competition is “two-sided”. We describe a simple measure of competitive asymmetry in which the effects of neighbors smaller than a focal individual are discounted by a constant factor, and include this variable in a composite measure of local interference. In this model competition varies between complete asymmetry (the effects of smaller plants are entirely discounted) and complete symmetry (the competitive effect of a neighbor is proportional to its size). The proposed method is applied to two natural populations and one experimental monoculture. In all cases an asymmetric model provides the best fit to the data. Completely two-sided models account for 26–39% of the variance in relative growth rate, while relatively one-sided models account for 44–57%. The increases in  $r^2$  values resulting from the inclusion of asymmetry are significant in the two cases in which the data permit randomization tests. Our results suggest that interference is completely asymmetric in a population of *Impatiens pallida*, a species with very low root allocation and a shallow crown, and somewhat less asymmetric in an experimental monoculture of *Ambrosia artemisiifolia* and a natural stand of *Pinus rigida*, cases in which competition for water and nutrient resources is likely to be of greater importance.

**Key words:** Asymmetric competition – Local interference – Neighborhood analysis – One-sided competition – Plant-plant interactions

Individual plants, as sessile organisms, interact primarily with their spatial neighbors. This realization has encouraged the development of a variety of neighborhood models of plant competition in which the performance of a focal plant is explained as a function of some measure of local interference (Mack and Harper 1977; Waller 1981; Schellner et al. 1982; Weiner 1982, 1984; Watkinson et al. 1983; Mithen et al. 1984; Silander and Pacala 1985; Pacala and Silander 1985, 1987; Penridge and Walker 1986; Goldberg 1987; Firbank and Watkinson 1987). Related studies which have examined the effects of plant density on size variability have suggested that interactions between plants are usually “one-

sided”, with large plants having a disproportionate effect on small plants (Weiner and Thomas 1986; Schmitt et al. 1987). The hypothesis that plant competition is generally asymmetric is also supported by studies in which plant performance is related to emergence time of seedlings: early emerging seedlings generally give rise to the largest plants in a population (Black and Wilkinson 1963; Ross and Harper 1972; Kasperbauer and Sutton 1977; Abul-Fatih and Bazzaz 1979; Naylor 1980; Howell 1981; Van Baalen et al. 1984; but see Wilson 1988). In spite of the apparent importance of asymmetric competitive interactions among plants, it has recently been observed that “neighbourhood models currently available disregard the importance of one-sided competition” (Firbank and Watkinson 1987 p. 316).

The term “symmetric” or “two-sided” competition has been used to describe two situations: (1) Absolute symmetry – contested resources are divided equally among competing individuals. For example, if local crowding is measured using positional information only (e.g. the number of plants within a certain radius, as in Pacala and Silander 1985, 1987) plants of different sizes are assumed to have numerically equal competitive effects. (2) Relative symmetry – neighbor influence is proportional to neighbor size (proposed by Ross and Harper 1972; used in neighborhood analyses by Weiner 1984; Firbank and Watkinson 1987; Goldberg 1987; Mitchell-Olds 1987).

Almost all studies of neighborhood competition have assumed either absolute or relative competitive symmetry because measures of local interference are based on positional information only, or are proportional to neighbor size. Two studies which do incorporate some aspect of competitive asymmetry are those of Firbank and Watkinson (1987), who include emergence time as a predictor of plant performance, and Penridge and Walker (1986), whose measure of local crowding includes a weighting factor proportional to the inverse of the size of the focal plant. No empirical study of neighborhood competition has explicitly modelled competitive asymmetry as a variable.

Firbank and Watkinson (1987) point out that two-sided models of neighborhood competition have been most successful in explaining differences in plant performance in desert and dune species. This is consistent with experimental studies which have suggested that competition for below-ground resources (water and soil nutrients) may be two-sided, while competition for light tends to be one-sided (Weiner 1986; Wilson 1988). However, plants generally compete for above- and below-ground resources simulta-

neously. Also, competition for any one resource may also not be completely symmetric or completely asymmetric. For example, competition for light may be less one-sided in plants with deep crowns if small plants shade large plants to some extent.

One-sided competition implies that the effects of small plants on large plants are relatively discounted. If competition is completely one-sided, any neighboring plant which is incrementally smaller than a focal plant would have no effect at all on the focal individual's performance (e.g. Ford and Diggle 1981). In extreme two-sided competition (in the relative sense) a neighbor's competitive effect is proportional to its size, irrespective of whether the neighbor plant is larger or smaller than the focal plant. Viewing these two conditions as limiting cases, we propose a measure of local interference in which local interference is proportional to neighbor size, but devalued by a constant factor if the neighbor plant is smaller than the focal plant. This principle is widely applicable to any neighborhood model. In this paper we incorporate asymmetry in one previously developed model of neighborhood competition (Weiner 1982, 1984).

The following general equation was advanced by Weiner (1982) based on the reciprocal yield law (Kira et al. 1953; Holliday 1960; Harper 1977; see also Watkinson 1980):

$$R = R_m / (1 + W) \quad (1)$$

where  $R$  is the growth or reproductive output of an individual;  $R_m$  is the growth or reproduction of the individual in the same environment in the absence of neighbors; and  $W$  is the measure of interference. More generally, all neighborhood competition models predict that  $R$  decreases monotonically with  $W$ . In a previous analysis of neighborhood interference amongst *Pinus rigida* trees (Weiner 1984),  $W$  was defined as a function of the number, distance, and size of neighbors:

$$W = \sum_{i=1}^n k S_i d_i^{-2} \quad (2)$$

where  $k$  is the effect of a neighbor (an estimated constant which, by Eq. (1), must have units of distance<sup>2</sup> size<sup>-1</sup>);  $S_i$  is the size of the  $i$ th neighbor;  $d_i$  is the distance to the  $i$ th neighbor; and  $n$  is the number of neighbors within some distance of the focal plant. The measure of local interference we propose here differs from expression (2) in that the effect of neighbors which are smaller than the target plant is discounted by a factor  $(1 - A)$ , where  $A$  is our measure of competitive asymmetry. This approach entails the logical use of an "if-then" statement: if neighbors are smaller than the focal plant then their effect is discounted. The least artificial way to incorporate this notion into a mathematical expression is to use a step function within the summation, hence:

$$W = \sum_{i=1}^n \begin{cases} k S_i d_i^{-2}, & S_i \geq S_f \\ k S_i d_i^{-2} (1 - A), & S_i < S_f \end{cases} \quad (3)$$

where  $S_f$  is the size of the focal plant;  $A$  is an asymmetry coefficient which varies from 0 (completely symmetric competition) to 1 (completely asymmetric competition), and represents the degree to which the effects of relatively smaller neighbors are discounted; other variables are defined as

above. In this study  $S_i$  and  $S_f$  represent "initial" sizes measured at time  $t - 1$ , where a final measurement of plant size is made at time  $t$ . This approach avoids the circularity that exists in models which predict final sizes of focal plants as a function of final sizes of neighbors. Expression (3) uses a standard notation for step functions employed in the physical sciences (e.g. Arfken 1985).

Alternative estimates of  $W$  based on successive values of the asymmetry coefficient,  $A$ , may result in differences in the amount of variance in plant growth rate explained: an estimated "optimal" value of  $A$  can therefore be determined as that corresponding to the highest  $r^2$  value. This "optimal" value for  $A$  is our proposed measure of competitive asymmetry for the population.

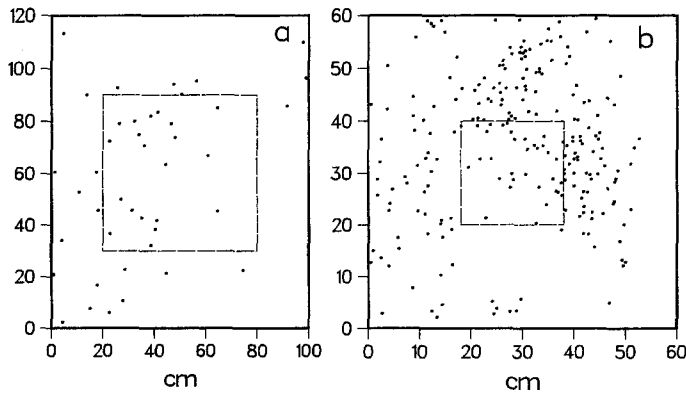
In the present study, we apply the method detailed above to data from two natural monospecific populations (*Impatiens pallida* and *Pinus rigida*), and one experimental monoculture (*Ambrosia artemisiifolia*). Our general hypothesis is that "optimal" values for the asymmetry coefficient ( $A$ ) will deviate from 0 in all cases. We also predict that neighborhood competition will be more asymmetric in *Impatiens pallida*, a species with very low allocation to root biomass and a shallow crown depth, than in the other two species, which have relatively greater root allocation and deeper crowns.

## Methods

### Study species and experimental procedures

*Impatiens pallida* Nutt. is a common woodland annual found in eastern North America which characteristically forms even-aged, monospecific stands. Individuals within a 1 m<sup>2</sup> quadrat within a uniform, dense population in the Crum woods of Swarthmore College were tagged soon after emergence (15 April 1987). Height ( $h$ ) and diameter ( $d$ ) of individuals were thereafter measured twice (8 May 1987 and 3 June 1987). Above-ground plant dry mass ( $S$ ) of individuals at each measurement was estimated using a power function of the form  $S = ah^b d^c$  (where  $a$ ,  $b$ , and  $c$  are constants) fit using multiple linear regression of log-transformed variables. Since our neighborhood analyses are based on the log-transformed growth rates, we did not correct for bias (in estimation of arithmetic means) in any of the size estimation functions used in this paper (Baskerville 1972; Sprugel 1983). Harvested stands of similar density, canopy height, and height-diameter allometry were used to generate these prediction equations: in the first comparable stand, the equation explained 81% of the variance in log above-ground dry mass, in the second, 96%. After the third measurement the population was grazed by white-tailed deer, and the stems were harvested and the location of each individual mapped to the nearest mm. Crown diameters ranged up to approximately 40 cm; a 20 cm radius ("cutoff distance") was therefore used in determining individuals included as neighbors ( $n$  in Eq. 3). Plants in the peripheral 20 cm of the plot where used in the analyses only as neighbors (Fig. 1a).

*Ambrosia artemisiifolia* L. is an early successional annual and commonly a dominant species in recently abandoned croplands in eastern North America (Bazzaz 1974). Seeds of this species were soaked for 6 days to induce germination, and seedlings transplanted into a pre-mapped pattern in



**Fig. 1 a, b.** Maps of plant populations analyzed. **a** *Impatiens pallida* plot (natural population). **b** *Ambrosia artemisiifolia* plot (experimental monoculture). Plants used as focal individuals are located within the central square outlined for each plot. The planting pattern for *Ambrosia* was generated as a poisson cluster process (Diggle 1983)

a 60 cm<sup>2</sup> × 12 cm deep flat. The sowing pattern was generated as a poisson cluster process (Diggle 1983) with  $\mu=5$  and standard deviation 2.5 cm iterated to produce a density of 500 plants/m<sup>2</sup>. This procedure produced a clumped distribution (Fig. 1b) which gave a high variance in local density of plants and simulated the natural distribution of germinating plants more closely than a simple random distribution. As in the *Impatiens* plot, plants in the peripheral 20 cm of the plot were used only as neighbors. The experimental monoculture was grown in an environmental growth chamber under the following conditions: 18 h day length at 440  $\mu\text{Em}^{-2}$  PAR; 60–70% humidity; initial total nutrient concentrations of 0.15 g/l N, 0.30 g/l P, and 0.15 g/l K in a total of 30 l soil. Plants were watered every 2–3 days to maintain soil saturation. Height ( $h$ ), stem diameter ( $d$ ), and longest leaf length ( $l$ ) were measured after 16 days of growth, and plants were harvested soon after the onset of flowering to determine final above-ground dry mass after a total growing period of 60 days. Above-ground dry mass ( $S$ ) at the first measurement was estimated using the function  $S = ah^b d^c l^e$  (where  $a, b, c$  and  $e$  are constants), which was fit using a multiple linear regression of log-transformed variables measured for a second population. This second population was grown during the course of the experiment under the same conditions and for the same length of time. In this case the prediction equation explained 94% of the variance in log above-ground dry mass. A 20 cm cutoff-distance (for determining  $n$ ) was also used in analysis of the *Ambrosia* data set on the basis of the estimated extent of crown and root overlap in harvested plants.

*Pinus rigida* Mill. is a dominant tree in parts of the New Jersey Pine Barrens, which often forms monospecific, even-aged stands following fires (McCormack 1979). Here we re-analyze the data presented by Weiner (1984), from such a stand in Wharton State Forest, New Jersey. An allometric model in which annual growth is estimated as an ellipsoid shell is used to estimate volume increment from annual growth ring width for focal trees. Size of focal and neighbor trees is estimated as  $hc^2$ , where  $h$  is bole height and  $c$  is tree circumference at breast height. Trees were cored and measured in 1980. For the purposes of this analysis, we use the 1979 growth data, which has a relatively large mean annual increment, and for which the assumption for

neighboring trees that the size at the beginning of the growth period ( $S_{1979}$ ) equals the measured final size ( $S_{1980}$ ) has the greatest validity. Trees within 2 m were treated as neighbors, this value being greater than the maximum observed canopy spread. Further details of methods are given by Weiner (1984). Contrary to statements in Penridge and Walker (1986), this study was of a naturally-occurring monoculture, not a pine plantation.

#### Statistical treatment of neighborhood analyses

Treating each plant in a continuous plot as both a focal individual and a neighbor in an analysis of neighborhood competition violates assumptions of independence required by statistical tests of correlation or regression, since positional information for one plant is dependent on positional information for other plants (Fowler 1984; Mitchell-Olds 1987). For example, the distance of plant  $A$  to plant  $B$  must be equal to the distance of  $B$  to  $A$ . It does not necessarily follow that spurious correlations will result from a neighborhood analysis which relates some measure of plant performance to a measure of local interference; probabilities of either type I or type II errors (or both) could be affected.

Fisher's Method of Randomization provides a distribution-free test of association when observations are not independent, and is particularly suited to tests regarding effects of specific spatial distributions (Sokal and Rohlf 1981). As applied by Mitchell-Olds (1987) to neighborhood analysis, a null distribution of correlation coefficients (of log biomass and a measure of local interference) is generated by randomly assigning observed plant sizes to locations of individuals in the plot (without replacement); the null hypothesis is that a plant's size is unrelated to its spatial position. In this study we seek to explain relative growth rates of individuals as a function of local interference. Therefore, three sorts of information are associated with each plant: position, size at time  $t-1$  ( $S_{t-1}$ ), and relative growth rate (RGR) of individuals between time  $t$  and  $t-1$  ( $(S_t - S_{t-1})/S_{t-1}$ ). (Since we are using RGR as a descriptor of plant growth and there is no expectation that individual plant growth is exponential, this discrete measure of RGR is more appropriate than the estimated instantaneous rate.) Because there may be a negative relationship between RGR and  $S_{t-1}$  under a null hypothesis of no interaction between individuals (Hunt 1982), random assignment of both  $S_{t-1}$  and RGR to each position is the method we used to generate the null distribution.

Relative growth rate (RGR) is usually the most appropriate measure of plant performance for use in neighborhood analysis when plant size is incorporated into a measure of local interference. Neighborhood analysis using single measures of plant size at one point in time is problematic in that neighborhood conditions and plant size are not independent for a variety of statistical and biological reasons (see Mitchell-Olds 1987). Measurement of plant size for at least two points in time to yield some measure of growth is therefore mandated. Use of absolute change in size ( $\Delta S = S_t - S_{t-1}$ ) is problematic because the relationship of  $\Delta S$  to  $S_{t-1}$  (in the absence of interference) depends upon the stage of plant growth. Growth of individual plants is sigmoidal. In the exponential phase of growth a positive correlation between  $\Delta S$  and  $S_{t-1}$  is expected; if growth is approximately linear (near the inflection point of a sigmoidal growth curve), no association is expected; in the levelling-off

phase of growth a negative relation between  $\Delta S$  and  $S_{t-1}$  is expected. On the other hand, the relationship of RGR to  $S_{t-1}$  also depends on plant growth stage, but the expectations in this case are no association in the exponential phase, a negative linear relationship in the linear growth phase, and a decreasing exponential relationship in the levelling-off phase of plant growth. Therefore, a positive association between RGR and  $S_{t-1}$  is never expected under a null hypothesis of no local interference.

Given these considerations, we examined the relationship of RGR to  $W$  in the following analyses. Several approaches to evaluating the tightness of this relationship are possible. Residuals of log RGR log  $W$  plots were balanced and homoscedastic across all species and all measures of  $W$ , so these analyses are presented. We computed the correlation coefficient ( $r$ ) between log RGR and log  $W$  for 11 values of  $A$  ranging from 0.0 to 1.0. Null distributions of correlation coefficients were generated by randomly assigning values of  $S_{t-1}$  and RGR to observed plant positions using 1600 replications for each test. All measured values were randomly allocated, but randomized correlation coefficients were calculated only on the basis of the focal plant positions in the center of the *Impatiens* and *Ambrosia* plots. Tests for significance of local interference effects were one-tailed ( $p$  = proportion of the null distribution greater than the observed value). We also constructed a null distribution of maximum differences in  $r^2$  values between the two-sided interference model ( $A=0$ ) and the one-sided model which gave the highest  $r^2$  for each randomized data set: observed differences in  $r^2$  are tested relative to this distribution. We could not conduct randomization tests for the *Pinus* data, since growth increments for non-focal individuals were not measured.

The completely asymmetric model ( $A=1$ ) implies that in any given pair of plants one individual is a neighbor and one a focal individual. Statistical assumptions of independence are therefore not violated in this case, though the observed values of plant sizes and the spatial distribution of plants will still likely produce null distributions of  $r$  or  $r^2$  that deviate from the expectations of parametric statistical theory. Variation in  $r^2$  values with  $A$  might therefore reflect both biological effects and statistical differences in degrees of independence. We have examined mean  $r$  and  $r^2$  values of our null distributions in order to estimate how much variation in observed values may be due to statistical artifacts of this sort.

The relationship of log RGR to log  $W$  was fit using principal components analysis (PCA), since neither variable is independent or can be assumed to have a residual variance of zero (Sokal and Rohlf 1981; see Weller 1987). Although functional (Model I) linear regression is commonly used to fit such functions, Model II regression is appropriate in neighborhood analyses where size is included in the measure of local interference.

## Results

No focal individuals died in either the *Impatiens* or *Ambrosia* populations over the course of the growth periods analyzed. Growth rates among individuals were, however, highly variable, RGRs ranging from 0.031 to 0.140 g·g<sup>-1</sup> day<sup>-1</sup> in *Impatiens* and 0.020 to 0.786 g·g<sup>-1</sup> day<sup>-1</sup> in *Ambrosia*. The proportional increases in stem volume for *Pinus* range

**Table 1.** Values of  $r^2$  for growth vs local interference relationships over a range of values of competitive asymmetry ( $A$ ), modelled using Eq. (1). Significance levels for *Impatiens* ( $N=20$ ) and *Ambrosia* ( $N=34$ ) are based on randomization tests (see text). Significance levels for *Pinus* ( $N=40$ ) are based on standard parametric tests for correlation. Arrows indicate the model giving the highest  $r^2$  value, and show (where possible) significance levels for the increase in explained variance over a completely two-sided model ( $A=0$ )

Competitive asymmetry ( $A$ )	$r^2$		
	<i>Impatiens pallida</i>	<i>Ambrosia artemisiifolia</i>	<i>Pinus rigida</i>
1.0	*→0.44**	0.46**	0.39**
0.9	0.42**	0.56***	0.43**
0.8	0.41**	*→0.57***	0.45**
0.7	0.39**	0.55***	→0.45**
0.6	0.37*	0.53***	0.44**
0.5	0.35*	0.50***	0.44**
0.4	0.33*	0.47***	0.43**
0.3	0.31*	0.45***	0.42**
0.2	0.29*	0.41***	0.40**
0.1	0.28*	0.39***	0.40**
0.0	0.26*	0.36***	0.39**

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

from 0.056 to 0.222 m<sup>3</sup>·m<sup>-3</sup>·yr<sup>-1</sup>. The effect of local interference on RGR was significant for every asymmetry value ( $A$ ) tested for each species (Table 1). The value of  $A$  giving the best fit for the *Impatiens* data was 1.0 (complete competitive asymmetry). The increase in  $r^2$  (of the best-fitting asymmetric model over a completely symmetric model) was 0.18, which was judged to be significant at  $p=0.038$  by the randomization test employed (Fig. 2; Table 1). In *Ambrosia*, the value of  $A$  resulting in the best fit was 0.8. The increase in  $r^2$  over complete competitive symmetry was 0.20, which was significant at  $p=0.049$  (randomization test) (Fig. 3; Table 1). At harvest, 48% of the *Ambrosia* individuals displayed symptoms of nitrogen and phosphorus deficiencies (chlorosis, reddening of leaf margins), suggesting the possible importance of nutrient competition. The value giving the best fit for the *Pinus* data was  $A=0.7$ , with an increase in  $r^2$  of 0.06. Randomization tests were not possible in this case, but by comparison with the other species this increase is probably not statistically significant (Fig. 4; Table 1).

Bias in  $r^2$  values due to statistical artifacts (non-independence) was relatively small in all cases. Average  $r^2$  values for the 22 null distributions used in the randomization tests (calculated as the square of the average  $r$ ) ranged from 0.0001 to 0.0476. Within this range higher values were associated with relatively symmetric models.

## Discussion

Our results confirm the prediction that relatively one-sided models of neighborhood competition account for more variance in plant growth than do two-sided models in our sample of one experimental and two natural monocultures. While the three species analyzed all displayed relatively asymmetric competition, they differed somewhat in the estimated degree of competitive asymmetry. These differences may be a result of both species-specific differences in allometry and resource allocation, and of site-specific differences in resource availabilities.

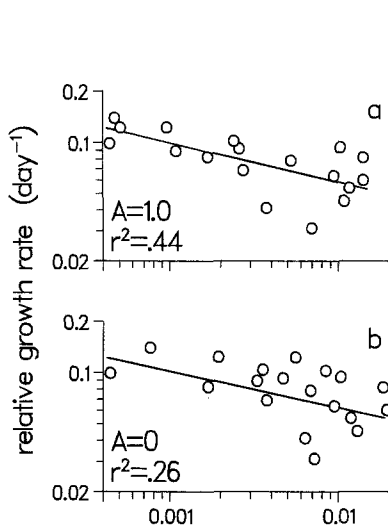


Fig. 2 measure of interference ( $\text{g m}^{-2}$ )

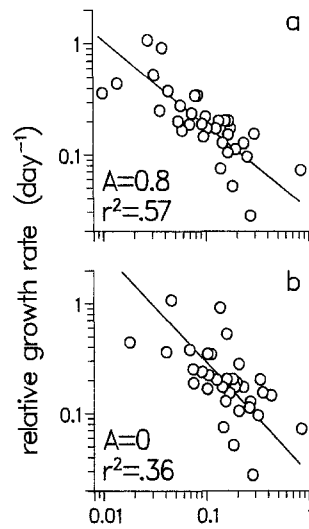


Fig. 3 measure of interference ( $\text{g m}^{-2}$ )

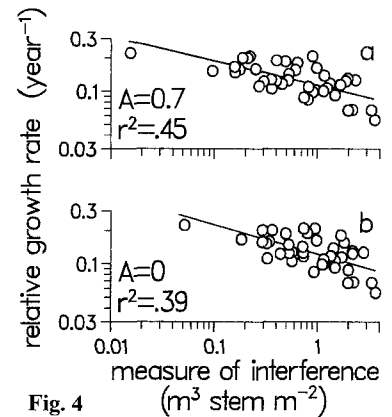


Fig. 4 ( $\text{m}^3 \text{ stem m}^{-2}$ )

Fig. 2a, b. The relationship between log relative growth rate and log  $W$  for the *Impatiens pallida* population. a Best-fitting asymmetric model ( $A=1.0$ ). b Completely symmetric model ( $A=0$ ). Fitted lines are calculated as the first principal axis

Fig. 3a, b. The relationship between log relative growth rate and log  $W$  for the *Ambrosia artemisiifolia* monoculture. a Best-fitting asymmetric model ( $A=0.8$ ). b Completely symmetric model ( $A=0$ ). Fitted lines are calculated as the first principal axis

Fig. 4a, b. The relationship between log relative growth rate and log  $W$  for the *Pinus rigida* population. a Best-fitting asymmetric model ( $A=0.7$ ). b Completely symmetric model ( $A=0$ ). Fitted lines are calculated as the first principal axis

In the *Impatiens pallida* population, the “optimal” model was one in which the effects of smaller neighboring plants were completely discounted ( $A=1.0$ ). Completely asymmetric competition in *I. pallida* may be due to two aspects of its growth form: (1) This species has very low root allocation, limiting possibilities for root competition. (2) In dense populations,  $\sim 90\%$  of the plant’s leaf area is distributed in the top 10% of the plant’s height (Weiner and Thomas, unpublished data), suggesting that smaller plants cannot shade leaves of larger plants.

*Ambrosia artemisiifolia* has a much higher root:shoot ratio and a deeper crown structure over all environmental conditions than does *Impatiens*. *Ambrosia* also displays a relatively high growth response to increased soil nutrient levels (Parrish and Bazzaz 1976). Under the moderate nutrient treatment of the experiment, symptoms of an apparent nutrient deficiency were found in 48% of the plants by the end of the 10-week growing period. The “optimal” model for this species was one in which the effects of smaller neighbors were discounted by 80% ( $A=0.8$ ). While this is a lower asymmetry value than *Impatiens*, competition was much more one-sided than might be expected given the apparent importance of nutrient limitation in the experimental monoculture.

*Pinus rigida* is another species in which competition might be expected to be largely two-sided. The species is found in well-drained, sandy soils of very low nutrient status and water potential, and the trees possess relatively deep crowns, facilitating mutual shading between individuals of all sizes (Weiner 1984; McCormack 1979). However, the “optimal” competition model for the *Pinus rigida* stand was also a relatively asymmetric one ( $A=0.7$ ).

In the above analyses, maximum distance for inclusion of neighbors was chosen *a priori* on the basis of the observed canopy spread in each population. In the measure of inter-

ference employed, the effect of a neighbor decreases exponentially with distance; therefore,  $r^2$  values are expected to reach a plateau with increases in the “cutoff-distance” within which plants are counted as neighbors. Analyses of the *Impatiens* and *Ambrosia* data sets in which both  $A$  and the cutoff distance were simultaneously varied in determining  $W$  showed that: (1) the *a priori* cutoff distances used occurred within this plateau region, and (2) the “optimal” values for  $A$  were not affected by choosing different cutoff-distance values (Thomas and Weiner, unpublished data).

The relatively high degree of competitive asymmetry observed in the *Ambrosia* and *Pinus* monocultures has several potential explanations, which are not mutually exclusive. (a) In spite of the importance of nutrient and water limitations of plant growth, competition for light structures interactions between plants. In *Pinus rigida*, for instance, most growth occurs when soil moisture content is high, and during these times light may be a limiting resource (Weiner, unpublished data). Similarly, nutrient competition may alter the speed, but not the form, of competitive interactions operating at the level of individual plants, whereas competition for light determines the form of the interaction (Morris and Myerscough 1984). (b) Mutual shading of plants does not alter the asymmetric character of competition for light since photosynthetic activity is concentrated in the uppermost leaves of the plant, and changes in light availability due to shading are most pronounced in the transition from canopy to sub-canopy of the stand. (c) There is one-sided competition for below-ground resources. In the New Jersey Pine Barrens, for example, the larger *Pinus rigida* individuals do, thus gaining a disproportionate share of the available water. Physiological measurements coupled with experimental manipulation of the environmental conditions of suppressed plants are necessary to test these hypotheses.

In general, differences in competitive asymmetry are expected to exist under different environmental conditions and over the course of stand development.

The ability of neighborhood analysis to detect competitive interactions or to determine the "importance" of neighborhood competition, or both, depends upon the quality of the measure of local interference used. Concluding that local interference is not important on the basis of low or non-significant  $r^2$  values is risky because such inference rests on the assumption that the relevant components of neighborhood conditions have been adequately measured. For instance, Primack et al. (1985) tentatively concluded that variation in girth increments of Moraceous trees in Sarawak may be due largely to variation in soils, local disturbance, and plant genotype, since correlations between growth rate and the mean distance to the three closest neighboring trees are generally non-significant and account for less than 9% of the variation in annual diameter increment. Other studies of trees in tropical rain forests have generally yielded similar results (e.g. Lowe and Walker 1977; Crow and Weaver 1977; but see Clark and Clark 1987). Use of measures of local interference which incorporate more information regarding neighborhood conditions, and which structure this information in a manner which is most relevant to conditions experienced by focal trees, might produce a quite different interpretation of neighborhood interactions in tropical forests. The results of the present study and related work (Weiner and Thomas 1986) suggest that competitive asymmetry should be included in efforts to detect and measure plant interference in natural systems.

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