

## NEIGHBOURHOOD INTERFERENCE AMONGST *PINUS RIGIDA* INDIVIDUALS

JACOB WEINER

*Department of Biology, Swarthmore College, Swarthmore, Pennsylvania 19081, U.S.A.*

### SUMMARY

(1) Recent yearly bole growth of individual trees, as estimated from height and annual growth ring measurements, is considered as a function of the number, distance and size of neighbours in a young *Pinus rigida* stand in New Jersey.

(2) To measure the annual increase in tree bole volume, an allometric model of tree bole growth was developed. In the model, the cross-sectional area of annual growth rings is constant along the length of the bole, which is constructed as concentric ellipsoids. A complete ring profile of one individual tree is consistent with this model.

(3) Significant correlations between individual plant growth rate and several measures of local interference demonstrate that interference is occurring.

(4) The size of neighbours, estimated from height and girth measurements, was the most important single variable in the regressions on individual plant growth; the number and distance of neighbours was significant but of less importance. The angular dispersion of neighbours within 2 m did not make a significant contribution to the variation in individual tree growth.

(5) The results are consistent with a model in which the growth of an individual is inversely related to the total effect of interference, and the contribution of each neighbour to this effect is additive in proportion to its size and inversely proportional to the square of its distance.

(6) While the results show, as expected, that the effect of a neighbour decreases with its distance, they do not allow one to distinguish between alternative formulations with confidence. However, a modified version of the model in which the effect of a neighbour decreases with its distance always resulted in a slightly improved fit over the original formulation in which a neighbour's effect decreases with the square of its distance.

### INTRODUCTION

Interference is important in plant community structure, but its role is still mysterious. Interference is difficult to measure and most plant competition studies have focused on the mean performance of plants in relation to density (Harper 1961). However, density and mean plant performance obscure the variation which may be very large and of great importance. The behaviour and evolution of plant populations may be understood better if we study them at the level of the individual. For example, what are the determinants of individual growth and survival? Because of the immobility and phenotypic plasticity of plants, local variation is extremely important in determining whether a plant will survive, how large it will grow, and how many offspring it will produce. Interference from neighbours may be one of the most important sources of local variation.

Plants do not react to density *per se*, but to the proximity and behaviour of neighbours (Harper 1977). Therefore, it should be possible to look at a plant's performance as a function of the conditions of its neighbours, such as their size, distance, number, age, genotype and angular dispersion. There have been several attempts to begin this task. In glasshouse experiments, Mack & Harper (1977) were able to account for 32–69% of the variation in plant weight of individual dune annuals as a polynomial function of the size,

weight and angular dispersion of their neighbours. Hickman (1979) showed that the mean distance to the nearest four neighbours could account for 48–73% of the variation in size of small annual *Polygonum* spp. Waller (1981) found evidence for neighbours effects in several natural populations of *Viola* spp. Foresters have attempted to develop easily implemented models of competing trees based on overlapping 'influence zones' (Opie 1968; Bella 1971; Daniels 1976). Polygon areas around individual plants have been shown to correlate with plant performance in some cases (Mead 1966; Liddle, Budd & Hutchings 1982; Mithen, Harper & Weiner 1983). These studies have shown that specific formulations of neighbour conditions may account for a significant fraction of variation in plant size and thus suggest that it is possible to explain plant performance in terms of neighbour conditions. However, these formulations, with the exception of the polygon method, are generally without theoretical bases and do not represent attempts to build models of neighbourhood interference. Polygons may be an elegant representation of the two-dimensional area available to similar individuals, but it will be difficult to incorporate important variables such as neighbour size into polygon analyses and, therefore, it may prove useful in relatively few cases. Part of the difficulty is that there are so many potentially important variables and they are often confounded, making it difficult to distinguish between alternative formulations (Waller 1981). Models must be built in steps, starting from very simple formulations involving only a few variables. Empirical tests must be designed to minimize variation due to factors other than interference (e.g. spatial heterogeneity) and variables which we are not yet ready to interpret (e.g. genotypic differences). In an earlier study (Weiner 1982) I tested a simple model of neighbourhood interference in annual plants in which (i) the total effect of neighbours is inversely related to plant performance, (ii) the effect of neighbours is additive, and (iii) the effect of a neighbour decreases with the square of its distance. This model accounted for 80% of the variation in the seed production in two populations of the annual species of *Polygonum* studied by Hickman (1979).

In the present study, this model is expanded to include the variable of neighbour size and is tested with data from a young stand of *Pinus rigida* Mill.

#### THE MODEL

In a previous study (Weiner 1982) the following general formulation was advanced, based upon the reciprocal yield law (Kira, Ogawa & Sakazaki 1953; Holliday 1960; Harper 1977) and similar to density dependence models developed independently by Watkinson (1980):

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

where:  $R$  is the growth or reproductive output of an individual;  $R_m$  is the maximum growth or reproductive output of an individual in the same environment, i.e. in the absence of neighbours; and  $W$  is the measure of interference. The measure of interference ( $W$ ) was defined in terms of the number and distance of neighbours:

$$W = \sum_{i=1}^n k d_i^{-2}$$

where:  $n$  is the number of neighbours;  $k$  is the effect of a neighbour (expressed as a constant); and  $d_i$  is the distance to the  $i$ th neighbour.

In the present study, the additional variable of neighbour size is included. It seems reasonable to start with the simplest hypothesis—the effect of a neighbour is proportional to its size. Thus

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

where  $S_i$  is the size of the  $i$ th neighbour.

## MATERIALS AND METHODS

The site chosen is a young *Pinus rigida* stand in the Wharton State Forest of the New Jersey Pine Barrens, U.S.A. (39°37'N, 74°37'W). The community is of the upland *P. rigida* type (McCormack 1979), and the soil is a sandy, highly leached, nutrient-poor podzol (Tedrow 1979). This community has several attributes which make it especially suitable for the study of neighbourhood interference. The uniform sandy substratum and low relief minimize abiotic spatial heterogeneity. The stand is monospecific and relatively even-aged; most trees are near to 20 years of age.

There are two major difficulties in studying neighbourhood interference which can be overcome if we use recent plant growth rather than size as the dependent variable.

(i) The size of a tree is a function of its age and past neighbourhood environments as well as of other variables. Previous neighbourhood regimes will be different from the present one due to the growth, death and recruitment of neighbours, and local interactions will have occurred on a different scale. To elucidate individual performance as a function of observable neighbour conditions, it would be better to look at recent plant performance, when neighbourhood conditions were not much different from the present.

(ii) Problems in analysis arise because it is not valid to use the size of neighbours as the independent variable and size of a subject individual as the dependent variable in regression analyses, since they are not independent. However, it is valid to use regression to look at the growth of subject individuals over a period of time as a function of the size of their neighbours at the beginning of this period. Current neighbour size is the size of a neighbour at the end of this period of growth, but if its increase in size over the period is small relative to its size at the beginning, the error introduced by using this current value will be small. In any case, the current size of a neighbour is highly correlated with its size in the recent past.

### *Allometric model of tree bole growth*

It was necessary to develop an allometric model of tree bole growth so that the increase in its volume could be estimated. This is possible through the use of methods developed in dendroclimatology (Fritts 1976). The work of Farrar (1961) suggests that the cross-sectional area of annual growth rings of pine trees growing in crowded stands is relatively constant along the height of the bole. That growth ring area is constant along the bole is also consistent with the 'pipe stem' allometric model of tree growth proposed by Shinozaki *et al.* (1964a, b). While these workers are concerned primarily with the relationship between the amount of photosynthetic and non-photosynthetic tissue in a tree, constancy of the cross-sectional area of functional xylem below the crown is a necessary corollary of the model if the pipe diameter is relatively constant. If the area of a growth ring is relatively constant along the trunk, it should be possible to estimate the annual bole volume increment from measurements of ring width, radius, and height.

To test the applicability of this idea, a growth ring profile was performed on a tree (number 31) of average size, from the centre of the plot. Yearly height increment in these conifers is marked by a whorl of branches, and this individual was cut into twenty stem length increments, one for each year's growth in height. Each of the segments was sectioned at its midpoint and smoothed with sandpaper. Measurements were made of the distance from the centre of the pith to the outer edge of each ring in three directions ( $120^\circ$  apart) under a dissecting microscope. Additional measurements determined that the outer edge of each growth ring was nearly circular, although the circles were usually eccentric with respect to the pith. The area of each circle could be calculated from the three measurements. Annual growth increment areas were determined by subtraction of inner circle areas from outer circle areas. Growth ring width measurements were also made and the three width measurements for each ring were averaged. A complete study of the growth increments for the four most recent years (1976–79) was performed on this tree. For each of the remaining forty trees, ring measurements using the same procedure were performed on cross-sections or cores at three heights: near the base (0.35 m above the ground), towards the middle (1.5 m above the ground) and in the centre of the crown (1 m from the top of the tree). At each height, measurements for the four most recent years of growth were made and four ring areas were determined for each of the three heights. The three areas for each year were averaged. This average growth ring area and the corresponding height measurement for that year were used to calculate the volume of the growth

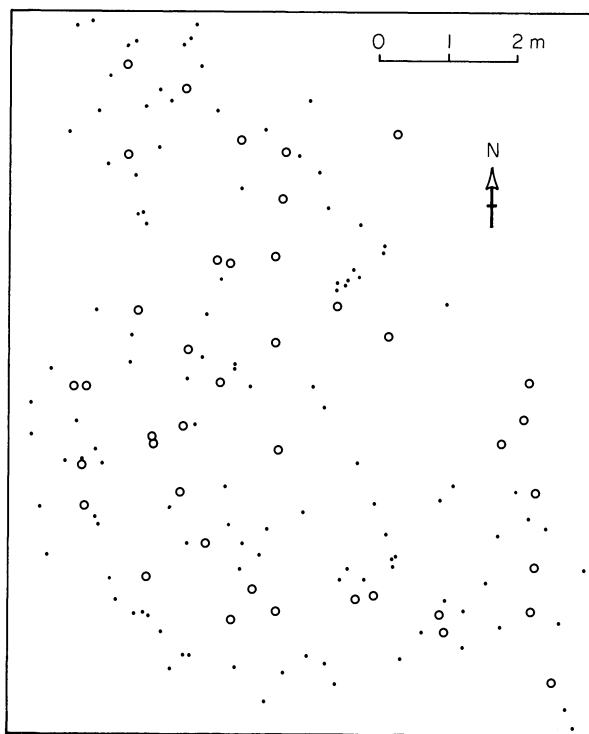


FIG. 1. Map of the study area in the New Jersey Pine Barrens, a monospecific stand of *Pinus rigida*. Circles represent subject trees; other trees are represented by points.

increment through the use of the ellipsoid model described below in Results. Bole volume before the 1976 growing season was determined in the same manner from the height and bottom cross-sectional area before the 1976 growth increment. The relative growth rate for an individual, defined as the proportional increase in bole xylem volume for that year, was used as a measure of individual performance.

### *Subject and neighbour trees*

The New Jersey Pine Barrens are subject to frequent fires. In burned *Pinus rigida* communities, individuals regenerate by stump sprouts. After a few years, one of the sprouts from a stump usually dominates and the others die, but often several will survive to produce an individual with several boles. All the trees in the study area were mapped (Fig. 1) and considered as neighbours, but only those which were not connected with other boles (i.e. did not originate from the same stump) and were between the ages of 17 and 21 years were chosen for analysis. The first constraint was applied to reduce the probability of two 'individuals' sharing a common root system and resources. The second was to avoid age-dependent variation in growth rate.

A neighbour was defined as any tree within 2 m of a subject individual; this was beyond the maximum distance of canopy spread. In addition to mapping, the height ( $h$ ) and trunk girth ( $c$ ) at 0.35 m above ground level were measured and used to estimate neighbour size (size  $\propto h \times c^2$ ). To ensure accuracy, the distance to each neighbour from each of the forty-one subject individuals was measured.

Statistical analyses were performed with Statistical Package for the Social Sciences (SPSS) programs.

## RESULTS

### *Allometric model*

Figure 2a displays the average width of the most recent (1979) year's growth ring as a function of the height at which it was measured for tree number 31. As in Farrar's (1961) study, ring width is greatest in the crown area. However, this increase in ring width is associated with a decrease in the circumference of each ring as the bole narrows. As in Farrar's study the annual growth ring area is relatively constant along the bole (Fig. 2c). The results for the previous 3 years are shown in Fig. 2b, d-f. Despite significant variation in yearly growth, presumably due to climatic variation, the assumption that annual growth ring area is constant along the bole, except for the top few sections, is supported by these results.

The constant annual growth ring area along the bole leads to an allometric model of growth in which the bole is viewed as a series of concentric, similar ellipsoids. The cross-sectional area between two such ellipsoids is the same at any height. Above the inner ellipsoid the cross-sectional area of the outer ellipsoid decreases linearly with height. The volume of an ellipsoid is  $(\text{area} \times \text{height})^2/3$ . Figure 3 shows the radii of the circles from the centre to the outer edge of the 1979 and 1976 growth rings as a function of height for tree number 31. The ellipsoid model fits the data very well except at the very top of the bole. While it is not clear whether this allometric model is generally applicable to other species or individuals of different ages, it provides a reasonable method of estimating tree bole growth in this population.

*Neighbourhood interference in Pinus rigida*

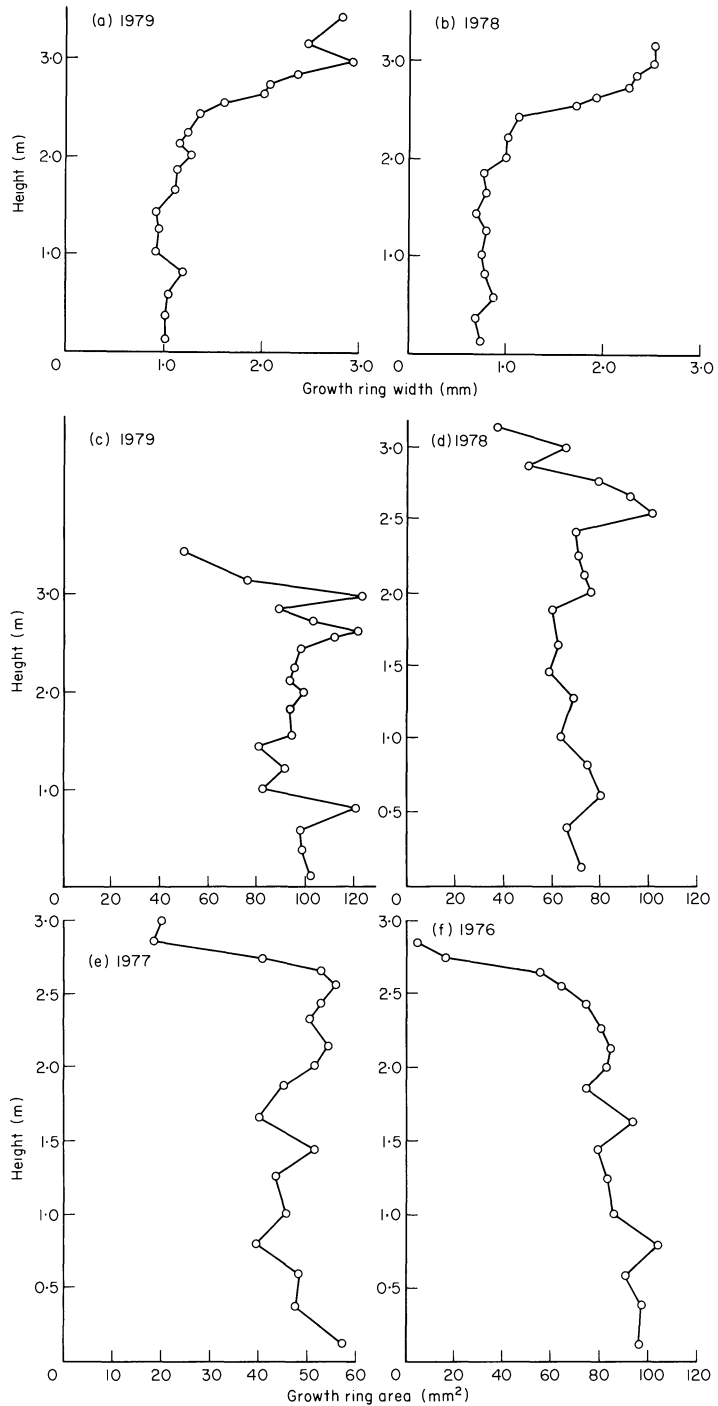


FIG. 2. Annual growth ring width in: (a), 1979; (b), 1978; and annual growth ring area in: (c), 1979; (d), 1978; (e), 1977; (f) 1976; of a *Pinus rigida* tree (number 31) in the New Jersey Pine Barrens as a function of height along the bole.

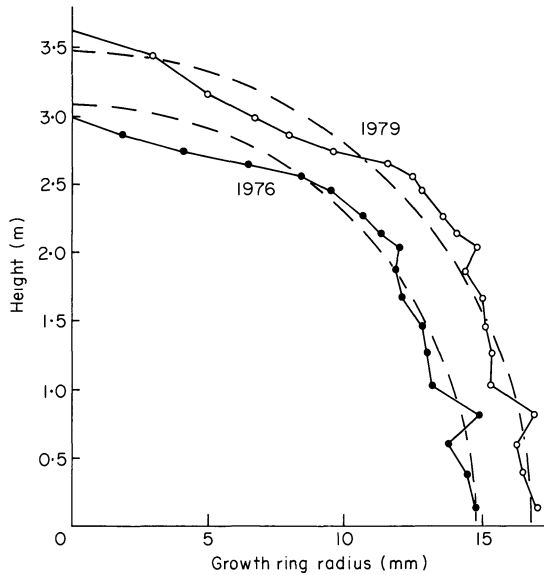


FIG. 3. Radii of outer edge of growth rings in *Pinus rigida* individuals as a function of height along the bole. (●—●), in 1976 and (○—○), in 1979. Results are consistent with the ellipsoid model, which is represented by dashed lines.

#### *Analysis of neighbourhood interference*

There were significant correlations ( $P < 0.05$ ) between the mean plant growth rate for the 4 years and all measures of local interference examined except the angular dispersion of neighbours within a 2 m radius. These included: the number of neighbours; sum of neighbour heights; sum of neighbour (girth)<sup>2</sup> [proportional to basal area]; sum of neighbour height  $\times$  (girth)<sup>2</sup> [proportional to bole volume]; mean neighbour height  $\times$  (girth)<sup>2</sup>; and the sum of reciprocal neighbour distances (Fig. 4a-f; Table 1). These correlations were significant for each year's growth rate and for many measures of local interference, but only the mean growth rate for the 4 years and a selection of interference measures are presented here. While, as expected, there was a significant correlation between subject tree age and its size ( $P < 0.05$ ) there were no significant correlations between size or age and growth rate. This suggests that possible age- or size-dependent differences amongst these individuals are overshadowed by the effects of interference.

To test the general hyperbolic form of the model, linear and hyperbolic regressions of each of the simple measures of competition against the average growth rate for the 4 years were compared. A linear regression using the reciprocal of the average growth rate was used to test the hyperbolic formulation (Table 1). In most cases, the regression employing the reciprocal of the growth rate resulted in a higher coefficient of determination and, more importantly, a better distribution of residuals. The only two independent variables for which the reciprocal of the mean growth rate gave a poorer fit than the mean growth rate itself, were those which had the lowest coefficients of determination and the lowest significance—number of neighbours and sum of the reciprocal of neighbour distances.

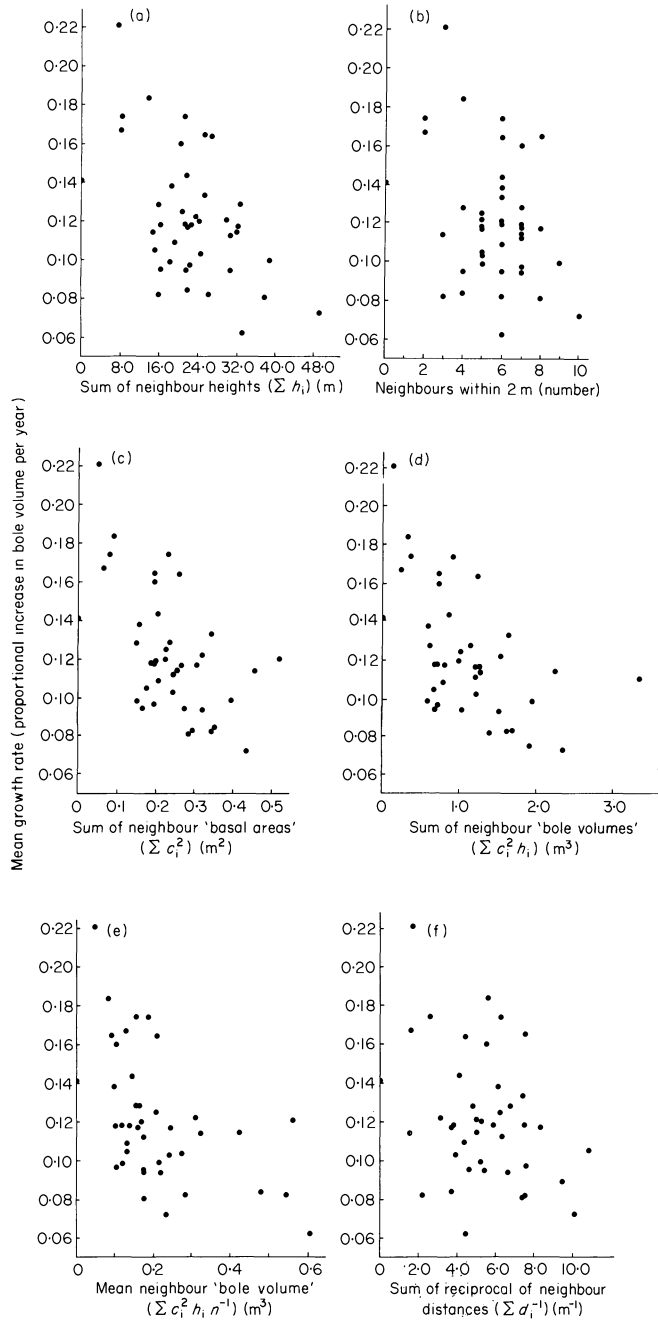
Neighbourhood interference in *Pinus rigida*

FIG. 4. Mean bole growth rate (proportional increase in bole volume) of *Pinus rigida* individuals in the new Jersey Pine Barrens during 1976–79 in relation to selected simple measures of local interference: (a), number of neighbours within 2 m; (b), sum of neighbour heights; (c), sum of the square of neighbour girth [sum of 'basal areas']; (d), sum of neighbour height  $\times$  (girth)<sup>2</sup> [sum of 'bole volumes']; (e), mean neighbour height  $\times$  (girth)<sup>2</sup> [mean bole volume<sup>3</sup>]; (f), sum of reciprocals of neighbour distance.



TABLE 1. Comparison of linear and hyperbolic models of several measures of local interference for *Pinus rigida* individuals in the New Jersey Pine Barrens.

Measure	Linear model		Hyperbolic model	
	$r^2$	$P$	$r^2$	$P$
Sum of neighbour heights	0.27	<0.001	0.28	<0.001
Sum of neighbour (girth) <sup>2</sup>	0.37	<0.001	0.40	<0.001
Sum of neighbour (girth) <sup>2</sup> × height	0.33	<0.001	0.41	<0.001
Mean neighbour (girth) <sup>2</sup> × height	0.24	<0.001	0.31	<0.001
Number of neighbours	0.12	<0.05	0.10	<0.05
Sum of reciprocals of neighbour distances	0.10	<0.05	0.08	<0.05
Angular dispersion of neighbours		NS		NS

Regression analyses to test the more complete version of the model were performed. The measure of competition,  $W$ , defined in eqn (2) becomes

$$W = \sum_{i=1}^n h_i c_i^2 d_i^{-2} \tag{3}$$

where:  $n$  is the number of neighbours;  $h_i$  is the height of the  $i$ th neighbour;  $c_i$  is the circumference of the  $i$ th neighbour; and  $d_i$  is the distance to the  $i$ th neighbour. The measure of competition,  $W$ , was the independent variable and the reciprocal of the growth rate was the dependent variable. The results are displayed for the mean growth for the 4 years (Fig. 5a) and for each year separately (Fig. 5b–e). All the regression coefficients were highly significant. Again, given the formulation of the measure of interference, it is clear that the hyperbolic model provides a better fit to the data than the linear model, in terms of both the amount of variation explained and the distribution of the residuals. In addition, regression analyses were performed using several modified versions of the measure of interference. Of these, only a version in which the effect of an individual decreases with the distance, rather than the square of the distance,

$$W = \sum_{i=1}^n h_i c_i^2 d_i^{-1}, \tag{4}$$

resulted in an equally good or improved fit (Table 2). The results of this modified version of the model are displayed in Fig. 6.

TABLE 2. Comparison of two measures of neighbourhood interference in hyperbolic model for *Pinus rigida* individuals in the New Jersey Pine Barrens.

Dependent variable reciprocal of growth rate (year)	Independent variable	
	$\sum c_i^2 h_i / d_i^2$ $r^2$	$\sum c_i^2 h_i / d_i$ $r^2$
1979	0.48	0.52
1978	0.27	0.29
1977	0.25	0.26
1976	0.21	0.25
Mean 1976–79	0.46	0.53

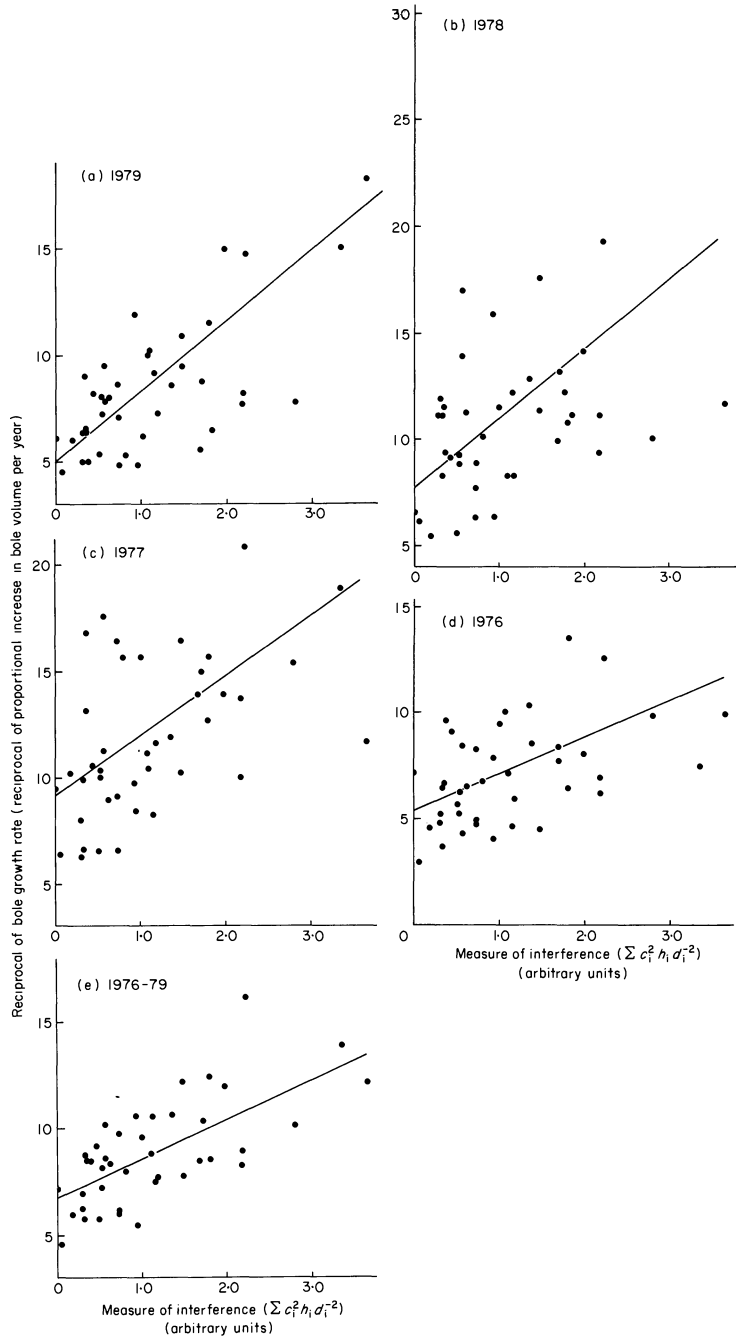
Neighbourhood interference in *Pinus rigida*

FIG. 5. Reciprocal of the bole growth rate (proportional increase in volume) of *Pinus rigida* individuals in the New Jersey Pine Barrens during 1976–79 for: (a), 1979; (b) 1978; (c), 1977; (d), 1976; (e), mean for 1976–79; in relation to the measure of local interference defined by equation (3). All the regression lines have slopes which are significantly different from zero ( $P < 0.001$ ).

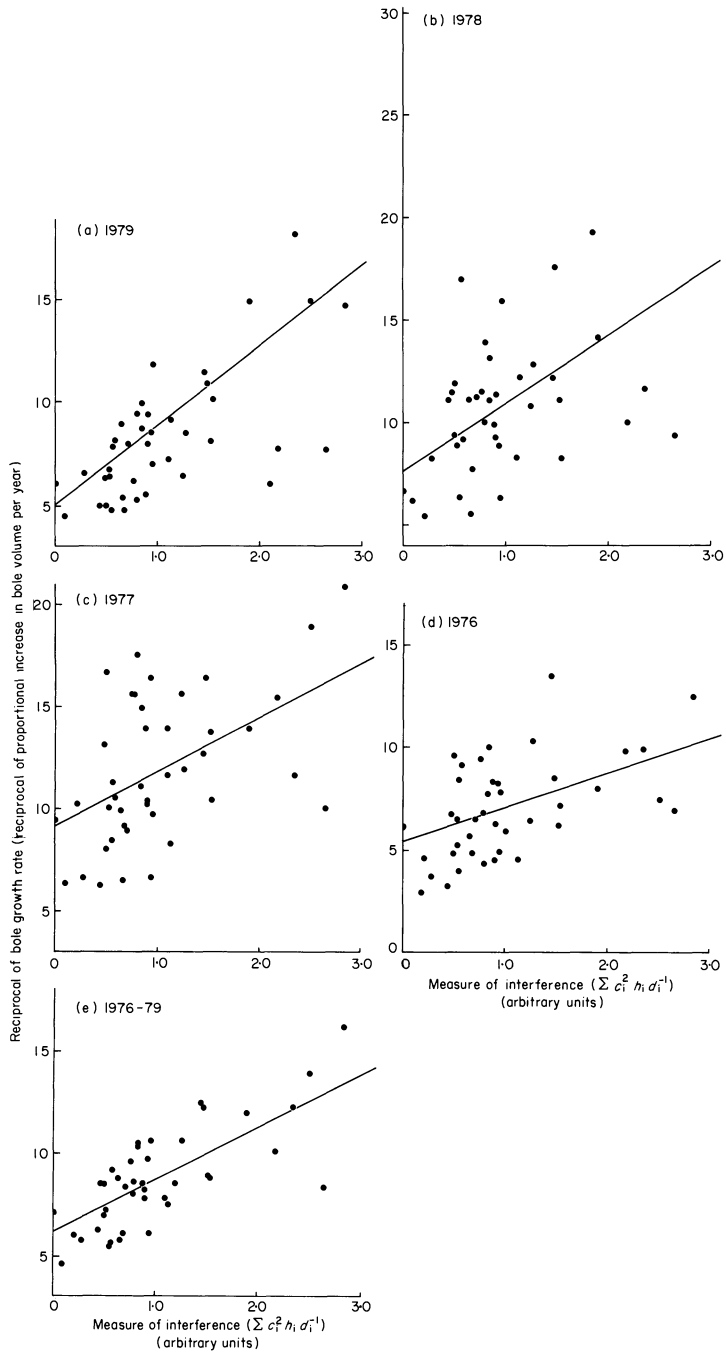


FIG. 6. Reciprocal of the bole growth rate (proportional increase in volume) of *Pinus rigida* individuals in the New Jersey Pine Barrens during 1976-79 for: (a), 1979; (b), 1978; (c), 1977; (d), 1976; (e), mean for 1976-79; in relation to the modified measure of local interference defined by equation (4). All the regression lines have slopes which are significantly different from zero ( $P < 0.001$ ).

## DISCUSSION

In this study, the total size of the neighbours within 2 m of a subject tree was clearly the most important factor in determining the differences in individual growth rates. It accounted for most of the variation explained by the more complete model. The distance of neighbours was also important.

It is surprising that the angular dispersion of neighbours,

$$= 1 - \sqrt{(\sum \sin a_i)^2 + (\sum \cos a_i)^2/n} \quad (5)$$

(Zar 1974)\* within 2 m was not negatively correlated with the growth rate and never made a significant contribution to the variation in growth rates. This is surprising because the angular dispersion of neighbours is thought to be an important determinant of neighbour effects and has been significant in other studies (Mack & Harper 1977; Waller 1981). I can only speculate as to the reasons for its lack of relevance in the present study. In a natural stand of trees with intense competition the arbitrary limit of 2 m may result in a false impression of neighbour angular dispersion. In fact, all individuals have neighbours in all directions, although the distances and sizes may vary greatly. While the 2-m limit may bias variables other than angular dispersion, it may have less of an effect on them. For example, since the effect of a neighbour decreases with its distance, it follows that those beyond a certain distance can be disregarded. Mack & Harper (1977) and Waller (1981) calculated the angular dispersion of neighbours separately for different neighbour distance intervals, but there seems to be no theoretical justification for this, especially if there is large variation in angular dispersion values for the range of distances studied, as was the case in the present study.

While these data provide support for the model advanced (eqns (1) and (3)), a modified version (eqns (1) and (4)) in which neighbour effects decrease with the distance (as opposed to the square of the distance) resulted consistently in a slightly better fit to the data (Fig. 7a-e; Table 2). While *ex post facto* curve fitting is different from the testing of a previously developed model, this result suggests that the modified model is more appropriate in this case. There are three aspects of this study which could be related to the improved fit of the modified model: (i) competition was presumably for light in the *Pinus rigida* population whereas in the *Polygonum spp.* study, where the effect of a neighbour seemed to decrease with the square of its distance, competition was for nutrients and water in very shallow soil; (ii) unlike other studies, fractional increase in size, rather than total size, is the dependent variable; and (iii) trees may be viewed best as shells of living tissue surrounding a non-living body of xylem and interacting only at their peripheries (J. L. Harper, personal communication). While it is clear that a neighbour's effect decreases with its distance, the type of data presented here may not permit us to determine with confidence which is the best formulation. Because of the constraints imposed by field data, experimental manipulation may be required to decide between alternative formulations. Also the effect of neighbour distance, or of any neighbour variable, may vary from one community to another depending upon the mechanism of interference. How general neighbourhood models of interference can be is unknown, and will not be known until models are built and tested in a range of different communities.

\* Note the error in Waller's (1981) correction of an error in Mack & Harper (1977).

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