

A null model for neighborhood models of plant competitive interactions

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Neighborhood (spatial) models of plant populations have *assumed* implicitly that competition between adjacent individuals is the primary determinant of observed dynamics. In contrast, non-spatial models now routinely *test* this assumption against the null hypothesis that individual differences in intrinsic growth rate alone can explain observed patterns. In a widely-used neighborhood model (Pacala and Silander 1990), competition is modelled as a direct effect of neighbors on target plant biomass, which in turn affects plant fecundity. We have developed a statistical null model for Pacala and Silander's (1990) neighborhood model for plant monocultures that explicitly incorporates variation in plant growth rate, and permits a test of the hypothesis that neighborhood competition controls plant ground area occupied (= rosette diameter) and biomass. An additional alternative hypothesis to our model is that neighbors can affect fecundity *independently* of their effects on plant diameter and biomass. We tested these three hypotheses – (1) no effect of competition (null); (2) neighborhood competition directly affecting plant diameter and biomass, and indirectly affecting fecundity (Pacala and Silander 1990); (3) neighborhood competition directly affecting plant diameter, biomass, and fecundity – by replicating, with appropriate controls, Silander and Pacala's (1985) experiments with the rosette-forming crucifer, *Arabidopsis thaliana*. Neighborhood competition in dense stands resulted in simultaneous changes in plant diameter, biomass, and fecundity relative to plants grown in the absence of competition. There also were apparent effects of neighbors on plant fecundity independent of their effects on plant size alone. The null model was not supported, but Pacala and Silander's model did not fit the data as well as the model that incorporated direct effects of neighbors on plant fecundity.

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Models and interpretations of population dynamics of plant monocultures and mixtures routinely assume that competition is the overriding determinant of observed patterns. Such models rarely consider alternative hypotheses, despite theoretical and experimental evidence that intrinsic variation in plant growth rate alone can give rise in plant populations to hierarchical distributions of biomass, height, or other metrics of plant size (Koyama and Kira 1956, Koch 1966, 1969, Turner and Rabinowitz,

1983, Uchmański 1985, Ellison 1987, Bonan 1988). To date, tests of the null hypothesis that growth rate variation alone generates size hierarchies have been performed only with respect to *non-spatial* models of plant competitive dynamics (Turner and Rabinowitz 1983, Ellison 1987). In non-spatial models, competitive effects are a function of overall average plant density and the specific location of each plant need not be known (e.g. Aikman and Watkinson 1980, Benjamin 1988).

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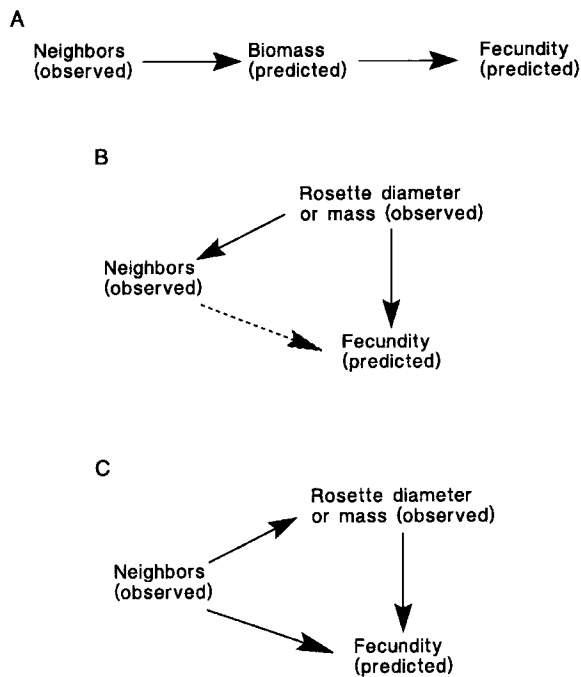


Fig. 1. Schematic diagram of the effects of neighbors on plant biomass and fecundity. (A) PS; (B) null model and (C) alternative model. The dotted line in B refers to a potentially spurious correlation that emerges between number of neighbors and plant fecundity due to the common dependence of both number of neighbors and plant fecundity on two correlated metrics of plant size (biomass and rosette diameter). See text for detailed explanations.

In contrast, spatial, or neighborhood, models of plant population dynamics incorporate competition implicitly. These models proceed from the assumption that plants, being sessile, are influenced directly only by near-neighbors; i.e. individual (target) plant performance is some composite function of the number of individuals and their distance from the target plant (e.g. Mack and Harper 1977, Weiner 1982, Watkinson et al. 1983, Pacala and Silander 1985, 1987, 1990, Silander and Pacala 1985, Pacala 1986a,b, 1987, Firbank and Watkinson 1987, Sutherland and Benjamin 1987, Bonan 1988; see Czárán and Bartha 1992, Ford and Sorrenson 1992, and Benjamin and Sutherland 1992 for recent reviews of spatial models of plant population dynamics). In these models, a *neighborhood* is defined simply as a finite area in which a number of plants compete with each other for resources. There has been a steady improvement in the predictive power of neighborhood models as modelling techniques have improved and more parameters have been incorporated (Czárán and Bartha 1992, Ford and Sorrenson 1992). Pacala and Silander (1990) have extended their neighborhood models, initially developed for plant monocultures, to multispecies systems, with encouraging results. However, the effects of growth-rate variation have not yet been incorporated explicitly into spatial

models of plant competition. In this paper, we formulate a spatial model for plant monocultures that permits explicit testing of the assumption that neighborhood competition determines plant diameter, biomass, and fecundity. This model yields three explicit, contrasting, testable hypotheses concerning the role of neighbors in determining target plant performance. We evaluated the model and tested among the hypotheses using monocultures of *Arabidopsis thaliana* (L.) Heyn. (Brassicaceae).

Our model is derived from the neighborhood model of Pacala and Silander (1990). Although there are many different models of neighborhood competition (reviewed by Benjamin and Sutherland 1992, Ford and Sorrenson 1992), Pacala and Silander's has the fewest assumptions and parameters that need to be estimated (Czárán and Bartha 1992). This model (referred to throughout as PS) also has been developed more extensively than most other neighborhood models, and has been found to be reasonably accurate in its predictions of dynamics of both monocultures and mixtures. We do not mean to imply that the PS model is the most complete, or most general of the published spatial models of plant population dynamics (Czárán and Bartha 1992). However, given its simplicity and applicability to a variety of situations (Pacala and Silander 1990), the PS model presents the most accessible starting point from which to investigate underlying assumptions common to all classes of spatial models of plant population dynamics.

Models of the effects of size and neighbors

A précis of the Pacala and Silander neighborhood model

In PS, each plant is modelled as having a circular neighborhood of fixed radius (r), with the target plant located at the center of the circle and occupying no real area. The biomass of any given plant is predicted from a hyperbolic function of the number of conspecific and heterospecific neighbors within the distance r of the target plant. PS is a two-species model:

$$\hat{w}_i = \frac{M_i}{(1 + c_{ij} n_i + c_{ji} n_j)} \quad (1a)$$

$$\hat{w}_j = \frac{M_j}{(1 + c_{ij} n_j + c_{ji} n_i)} \quad (1b)$$

where w_i is the adult aboveground biomass of an individual of species i , M_i is the biomass of species i with no neighbors, and c_{ij} is an interference coefficient that gives the effect of n_j individuals of species j , within a neighborhood of fixed radius r , on the species i target plant (Pacala and Silander 1990: 115). Then, fecundity S_i of plant i is predicted as a linear function of the biomass \hat{w}_i

predicted from Eqs 1a and 1b (Pacala and Silander 1987, 1990):

$$\hat{S}_i = a_i + b_i \hat{w}_i \quad (1c)$$

where a_i and b_i are estimated (linear regression) constants. Schematically, this model is represented in Fig. 1A: the number of neighbors determines individual plant biomass, and predicted biomass determines fecundity.

In the absence of neighbors within the defined neighborhood ($n_i=0$), Eqs 1a or 1b reduce to $\hat{w}_i=M_i$, a constant that is defined as maximum possible plant biomass. In this formulation, there is no allowance made for *variance* in plant biomass resulting from, for example, genetic background, maternal effects, or environmental variation. Instead, all of these other sources of variation are considered part of the model's error structure and are ignored when predicting fecundity (Eq. 1c). That is, in the model described by Eqs 1 and 2, *all* variance in predicted plant biomass \hat{w}_i and predicted plant fecundity \hat{S}_i results from competitive effects of neighbors, despite extensive theoretical studies (e.g. Koch 1966, 1969, Uchmański 1985, Bonan 1988) and empirical data from non-spatial studies (e.g. Koyama and Kira 1956, Turner and Rabinowitz 1983, Ellison 1987) that maximum plant biomass can be extremely variable, and that such variation may overshadow inter- and intraspecific competitive effects. We contend that for spatial models of plant competition, as for non-spatial models, one must first exclude the possibility that individual variation in plant biomass or fecundity accounts for variation in plant performance. Only then can competition be invoked as a causal mechanism for observed patterns of plant size or reproduction among plants in dense stands.

A null model and an alternative to the PS model of plant neighborhood interactions

We use the term "null model" to describe our model for neighborhood plant competitive interactions, because it explicitly accounts for individual variance in plant performance independent of competition. We then contrast our null model with the alternative hypothesis, that neighboring plants affect significantly plant biomass and reproduction in dense monocultures. We here present models for plant monocultures, although they are easily generalizable to multispecies assemblages. These models will be presented three ways: 1) as generalized path diagrams, showing causal relationships among variables; 2) as quantitative models; and 3) as a formal mathematical model. The qualitative description of the model is presented in this section, the quantitative model in the next, and the formal mathematical model is outlined in Appendix 1.

Restricted to one species, PS can be represented by a generalized path diagram (Fig. 1A): fecundity is a function of biomass, which is a function of number of neigh-

ors. Arrows in these diagrams represent functional relationships, which may be non-linear. These are not standard path diagrams (e.g. Mitchell-Olds 1987), in which arrows represent linear relationships. Fig. 1A makes clear an assumption of the PS model: neighbors affect target plant fecundity only by their effect on target plant biomass.

An appropriate null model (cf. Turner and Rabinowitz 1983, Ellison 1987), with no causal linkage between neighbors and fecundity, is shown in Fig. 1B. In this model, both fecundity and the number of neighbors are simple functions of a single metric of plant size (e.g. aboveground biomass, area of ground occupied). The apparent correlation between neighbors and fecundity is due to their common dependence on a third variable, size. Fecundity is often biomass-dependent (e.g. Weiner 1988), but how can number of neighbors depend on biomass or ground area occupied?

Most spatial models of plant population dynamics, including PS, assume that plants are mathematical points occupying no area; however, most real plants occupy some area. A given plant mass can be distributed in space in many ways (Miyanishi et al. 1979), so it may be appropriate to use either a measure of ground area occupied or plant biomass as a metric of plant size. Ground area occupied can affect the ability of neighbors to obtain resources through asymmetric uptake of light or nutrients (e.g. Weiner and Thomas 1986). For rosette-forming plants like *Arabidopsis*, plants of larger diameter will have fewer neighbors when, as in PS, plants are considered as points lacking any area, and neighborhoods are defined by a fixed radius. For example, a 6-cm rosette will have 0 neighbors if the neighborhood is defined to be of radius 3 cm (as in Silander and Pacala 1985). Neighborhoods of smaller radii have no biological meaning for a plant of this size, while if the neighborhood were larger the plant could have some neighbors. While in practice one would not expect a chosen neighborhood size to be smaller than the radius of the largest plant in the population, choosing neighborhood sizes by minimizing residual sums of squares (as done by Silander and Pacala 1985) can in fact result in neighborhoods smaller than the largest plant (see Results and discussion, below). Consequently, in spatial models where neighborhood radii are defined based on distances between plant centers, the relationship between actual ground area occupied and plant biomass ought to be considered (cf. Simberloff 1979). In such models, the number of *possible* neighbors an individual can have within a given distance of its center, like the number of seeds it can produce, could be dependent on plant diameter, which may show variation *independent* of competitive interactions.

PS is the simplest alternative to the proposed null model. However, other alternatives exist. For example, relaxing the assumption in PS that neighbors affect target plants only through their effects on plant biomass results in the model illustrated in Fig. 1C, in which biomass is a function of neighbors and fecundity is a function of both

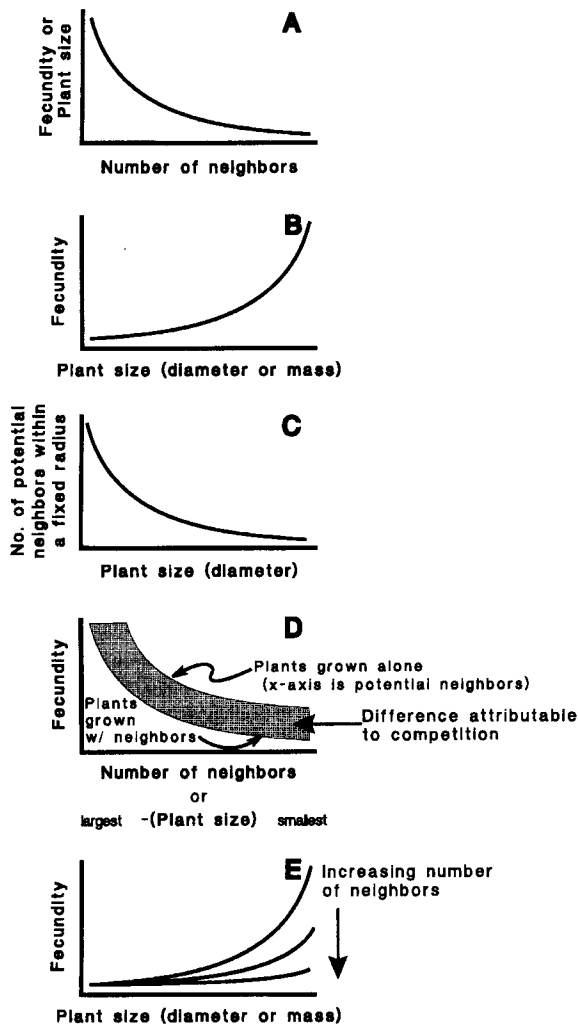


Fig. 2. Effects, alone and in concert, of number of neighbors and plant size on plant fecundity. See text for detailed explanation.

biomass and the number of neighbors. One possible mechanism for an additional effect of neighbors on fecundity is a shift in morphology in response to crowding (Gibson et al. 1992).

These three models conceptually form a nested hierarchy: the null model (Fig. 1B) posits no effect of neighbors on biomass, rosette diameter or fecundity; PS (Fig. 1A) posits a direct effect of neighbors only on biomass (and/or rosette diameter); the second alternative (Fig. 1C) posits direct effects of neighbors on both biomass (and/or rosette diameter) and fecundity.

T. Hara (pers. comm.) has pointed out that because none of these three models incorporates either size of neighbors or their distances from the target plant (e.g. Weiner 1982), they are appropriate to situations where competitive interactions between plants are predominantly symmetric. Yokozawa and Hara (1992) present a

general model for the interaction between canopy photosynthesis and competition in monocultures. Their model illustrates that symmetric competition will dominate the population dynamics of plants that grow primarily in diameter – e.g. rosettes like *Arabidopsis thaliana* (used by Silander and Pacala 1985, and in the experiments reported here), while asymmetric competition should be more important for trees and other plants with more vertical growth forms. In situations where competition is known to be asymmetric (i.e. dominance and suppression, sensu Turner and Rabinowitz 1983), models analogous to those of Weiner (1982), Hara (1992), and Yokozawa and Hara (1992) should prove to be more useful. However, the apparent predictive power of PS in both monocultures and mixtures (Pacala and Silander 1990) raises the possibility that their simple model may be adequate in many herbaceous plant assemblages.

Quantitative distinctions between the models

Tests to compare the three models in Fig. 1 can be developed by making the relationships among the variables more precise. The competitive effect of neighbors on plant biomass is commonly hyperbolic (Fig. 2A). For monocultures, Pacala and Silander's biomass predictor (Eqs 1a and 1b) reduces to:

$$\hat{w} = w_{\max} / (1 + c n_r) \quad (2)$$

where \hat{w} is predicted plant biomass, w_{\max} is biomass in the absence of neighbors, and c is a decay constant giving the effect of n neighbors within a fixed radius r on biomass. Similar hyperbolic equations have been used to model the effect of neighbors on fecundity (Fig. 2A):

$$\hat{S} = S_{\max} / (1 + c_s n_r) \quad (3)$$

where S is the predicted number of seeds produced per plant, S_{\max} is the maximum number of seeds produced by a plant with no neighbors (in a neighborhood of radius r), c_s is a decay constant, and n_r is the number of neighbors in a neighborhood of radius r (Silander and Pacala 1985).

The relationship between plant biomass and fecundity may be linear or exponential (Fig. 2B) (Samson and Werk 1986, Weiner 1988, Thompson et al. 1991). In populations of *Arabidopsis thaliana*, not only the shape, but also the slope and intercept of the biomass-fecundity relationship has been shown to depend on plant genotype (Aarssen and Clauss 1992, Clauss and Aarssen 1992). The PS fecundity predictor is a linear relationship between biomass and number of seeds:

$$\hat{S} = a + b \hat{w} \quad (4)$$

where \hat{S} and \hat{w} are the predicted fecundity and predicted biomass, respectively, while a and b are estimated coefficients. Substituting Eq. 2 into Eq. 4, and equating it to Eq. 3 provides the model for the path diagram in Fig. 1A:

$$\hat{S} = a + b w_{\max} / (1 + c n_r) = S_{\max} / (1 + c_s n_r) \quad (5)$$

To quantify the null model (Fig. 1B), we need to specify how plant biomass, or another correlated measure of plant size influences the potential number of neighbors in the absence of density-dependent mortality (Fig. 2C). If a plant were considered to be a circle with radius ρ in a neighborhood of radius r (cf. Simberloff et al. 1978, Simberloff 1979, Cox 1987, Wu et al. 1987), then the area that could be occupied by neighbors is $\pi(r^2 - \rho^2)$. The potential number of neighbors is then $d\pi(r^2 - \rho^2)$, where d is the average plant density (Upton and Fingleton 1985). The reproductive output of a plant growing alone with n potential neighbors should then be compared with the reproductive output of a plant of similar biomass growing in competition with n actual neighbors (Fig. 2D). Any observed reduction in reproductive effort of plants with neighbors relative to similar-sized plants growing alone can then be attributed to neighborhood competitive effects (Fig. 2D, shaded region). If the two curves in Fig. 2D are statistically indistinguishable, then one cannot reject the null hypothesis that plant size effects or growth rates alone are responsible for observed declines in reproductive output with plant biomass. If the two curves are distinctly different, the null hypothesis would be rejected, the difference being attributable to neighborhood competition.

If plant biomass and fecundity are both functions of the number of neighbors (e.g. the path diagram in Fig. 1C), then the coefficients a and b in Eq. 4 must be expressed as functions of the number of neighbors, not as constants. In this case, the relationship between biomass and fecundity is one of a family of curves, depending on the number of neighbors (Fig. 2E). A model for the relationship in Fig. 1C is:

$$\hat{S} = a_n + b_n \hat{w} \quad (6)$$

where a_n and b_n depend in some fashion on n , the number of neighbors. Differences between the fits of Eqs 4 and 6 to empirical data can be assessed graphically or statistically (see Statistical analyses, below).

Hypotheses

Our model yields three testable, contrasting hypotheses concerning the relationship between neighbors, target plant size (expressed as ground area occupied or individual biomass), and target plant fecundity. Like the model, each hypothesis can be described in terms of the path diagrams (Fig. 1), the quantitative models (Eqs 2–6 and Fig. 2), or the formal model (Appendix 1).

Null hypothesis. The observed relationship between number of neighbors and fecundity is an epiphenomenon of the true relationship between intrinsic growth rate and

plant fecundity. In other words, the relationship between neighbors and fecundity for competing plants is the same as the relationship between potential neighbors and fecundity for plants grown alone (Fig. 1B). Statistically, this null hypothesis would be supported if the two lines illustrated in Fig. 2D were indistinguishable.

General alternative. The observed relationship between number of neighbors and fecundity is due to a direct causal relationship over and above effects of growth-rate variation. To support this alternative hypothesis, we must be able to show that the two lines illustrated in Fig. 2D are somehow different. Such a difference may arise in one of two ways:

Alternative hypothesis I. The number of neighbors influences fecundity only through its effect on plant size (as in PS). This is the path diagram in Fig. 1A. In terms of the quantitative models, this hypothesis is given by Figs 2A and 2B. In terms of Eqs 4 and 6, this hypothesis would be supported if $a_n = a$ and $b_n = b$ (i.e. a and b are constants, not functions of number of neighbors).

Alternative hypothesis II. There is an additional direct effect of neighbors on target plant fecundity independent of their effect on plant size. This is the contrast between Figs 2B and 2E. Statistically, the coefficients a and b in Eqs 4 and 6 will not both be constants (as in Alternative hypothesis I), but rather both a and b will vary with the number of neighbors.

These hypotheses can be tested by comparing size and fecundity of plants grown alone (i.e. no inter-plant competition) and in dense, competitive stands (cf. Turner and Rabinowitz 1983, Ellison 1987). We can then compare the variance in size and fecundity of plants grown in the absence of neighbors to plants of similar size with neighbors (comparison of the null hypothesis with the general alternative). To allow for valid statistical comparisons, the size range of the individually grown plants should be the same as, or exceed, the size range of plants growing in dense stands. Previous experimental investigations of neighborhood competition models have not included plants growing alone as controls (e.g. Mack and Harper 1977, Waller 1981, Fowler 1984, 1988, Mithen et al. 1984, Weiner 1984, Goldberg 1987, Thomas and Weiner 1989). Alternative hypotheses I and II can be distinguished statistically using only the plants grown in dense stands (see Statistical analyses, below).

Methods

Mouse-eared cress, *Arabidopsis thaliana*, a widespread, temperate old-field annual, is particularly well-suited for monoculture studies in general and neighborhood studies in particular. It grows as a nearly circular, flat rosette, the

area occupied by each rosette can be easily measured, and fecundity can be estimated by counting siliques. Numerous morphological and physiological mutants have been identified and isogenic lines are available. Seed viability is high, germination is nearly synchronous, and time to flowering and fruiting are determined by day length, not plant size (Karlsson et al. 1993). Finally, using *Arabidopsis thaliana* allowed us to replicate the study of neighborhood competition that led to the development of the neighborhood models under discussion here (Silander and Pacala 1985).

Our experimental protocol and design replicated Silander and Pacala's (1985) with the addition of solitary control plants. Isogenic seeds of wild-type *Arabidopsis* were obtained from Gyorgy Redei of the Univ. of Missouri. Plants were grown in 26 × 52 cm plastic flats filled with sterilized Cornell Mix, an artificial potting medium (Boodley and Sheldrake 1977). Flats were placed in controlled environment chambers, maintained at 22°C and 70% relative humidity, and flats were rotated weekly among chambers to minimize chamber effects. Each flat was sprayed daily with 400 ml deionized water, and fertilized twice weekly with 1/4 strength Hoagland's solution.

Plants were grown in two different planting regimes: as individual plants (non-competing 'controls'), and in dense, competitive monocultures. Each of the two control flats was divided into 72 individual isolated cells by a plastic insert, and a single seed was placed in the center of each cell. Cells were sufficiently large to insure that these non-competing plants were not root-bound throughout the experiment. One flat was grown under long-day (14 h light) and one was grown under short-day (10 h light) conditions. Time to flowering in *Arabidopsis* is dependent on day length, not genetic background (Karlsson et al. 1993); long-day plants fruited after 4–6 wk, while short-day plants of identical genotypes did not fruit until 10–11 wk after germination. Because of their extended growth period, short-day plants were heavier, had more leaves, had longer leaves, and produced more seeds than did long-day plants. We took advantage of this variation to ensure that the size range of individually grown plants exceeded the size range seen in the high density plants. Of all individually grown plants, 70% of the seeds germinated, and 63% of the germinants survived to flowering (26 short-day and 36 long-day plants).

In the three high density flats, seeds were broadcast haphazardly across the flats to provide a range of densities and number of neighbors (as in Silander and Pacala 1985). The overall planting density was designed to yield the equivalent of 10³ or 10⁴ seedlings m⁻². Working from the assumption of 70% germination, we planted two flats with 200 seeds each (to yield ≈ 10³ m⁻²) and one flat with 2000 seeds (to yield ≈ 10⁴ m⁻²). These three flats were grown under long-day conditions. The location of each plant in the high density flats was marked on acetate sheets overlaid on the flats. Each week, the total (circular) area occupied by each plant was marked on the overlay.

Above-ground plant material was harvested before plant senescence (6 wk for long-day plants and 11 wk for short-day plants). We measured the length (± 1 mm) of the longest leaf (= rosette radius, used in an estimator for area occupied), removed the siliques, and then dried (70°C, 48 h) and weighed (± 0.001 g) the shoot. Throughout, we report fecundity as S' , the number of siliques per plant. The number of seeds in each silique was counted for all of the low density plants. Plants with more siliques produce slightly fewer seeds per silique. The relationship between number of siliques/plant (S') and number of seeds/plant (S) was found to be: $S = 34.71 \cdot (1 - 0.71 \cdot \exp(-0.07 \cdot S'))$ ($r^2 = 0.57$; $n = 62$; all fitted parameters significantly different from 0; SAS PROC NLIN). This relationship can be used to estimate total seed production from silique counts of plants in the high density flats. When the high density plants were harvested, the position of each plant in the flat (x , y coordinates of the plant's center) was recorded, length of longest leaf measured, siliques counted and removed, and the shoot dried and weighed. We also recorded the number of neighbors whose centers fell within concentric circular neighborhoods N_r : $r \in \{1, 2, 3, 4, 5, 6 \text{ cm}\}$ measured from each plant's center. To avoid edge effects in the high density flats, plants whose centers fell within 6 cm of the flat edge were excluded from all analyses.

Statistical analyses

Comparisons between the null and general alternative hypotheses, and between the two alternative hypotheses were examined using statistical models. Differences between statistical models were tested by comparing residual sums-of-squares (RSS). For example, we tested between the two alternative hypotheses by contrasting RSS of the two models given by Eqs 4 and 6. Eq. 4 is a special case of Eq. 6, because the former can be generated from the latter by reducing the number of parameters. If the reduced model (e.g. Eq. 4) was appropriate (as assumed by PS), then the difference in RSS between the full and reduced models should have been small. The hypothesis that the two models fit equally well was tested using the statistic:

$$F = \frac{(RSS_{\text{model } r} - RSS_{\text{model } f}) / (p_f - p_r)}{RSS_{\text{model } f} / (n - p_f)}$$

where $RSS_{\text{model } r}$ and $RSS_{\text{model } f}$ were the residual sums-of-squares from the reduced and full models, respectively, p_r and p_f were the number of parameters in the two models, and n was the sample size. If the reduced model was true, the statistic F approximates an F-distribution, with $(p_f - p_r)$, $(n - p_f)$ degrees of freedom (Draper and Smith 1981). Calculations were done using SAS version 6.03

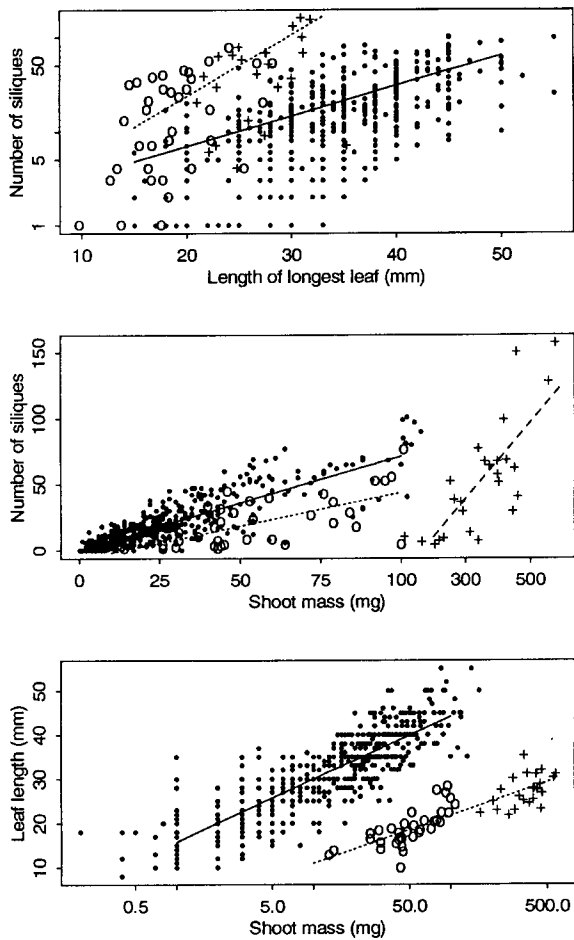


Fig. 3. Relationships between plant radius and fecundity (top); plant biomass and fecundity (middle); and allometric changes between plant radius and plant biomass (bottom) as a function of density. ● plants grown at high density (14 h day); ○ plants grown individually (14 h day); + plants grown individually (10 h day).

(SAS Institute, Cary, NC) and S-Plus (Becker et al. 1988, Statistical Sciences Inc. 1990) on a Sun microcomputer.

Preliminary analyses showed that the error variance could not be assumed to be constant, and transformations did not eliminate heteroscedasticity. Responses from larger individuals were more variable; the trend in variance could be modelled as a linear function of maximum leaf length. Consequently we report distribution-free (non-parametric) summary statistics throughout the text. We also used weighted non-linear regression, with weights of $1/\text{leaf length}$, to fit each model, because we could use weighted regression to fit easily many different types of models. We fitted a few models using gamma regression models (cf. Pacala and Silander 1990). The results of the gamma regression models were essentially the same as those obtained using weighted regression.

Results and discussion

Observed relationships between density, size, and fecundity

High density (competing) plants had significantly longer leaves (median = 3.0 cm, $n=651$) than plants grown in the absence of competition (median = 2.16 cm, $n=62$) ($P=0.0001$, 2-tailed Mann-Whitney test), but produced fewer siliques for any given leaf length (Fig. 3). In contrast, high density plants were significantly lighter (median mass = 0.012 g) than individually-grown ones (median mass = 0.085 g) ($P<0.0001$, 2-tailed Mann-Whitney test), but produced more siliques for any given mass (Fig. 3). We observed some changes in leaf orientation between dense and solitary plants. Solitary plants formed flat rosettes, while leaves of dense plants were at an approximately 30° angle relative to horizontal. Change in leaf angle in rosette plants can affect light interception (Niklas and Owens 1989); these allometric changes with density (Fig. 3) were not anticipated and they suggested that fecundity may be influenced by variation in plant size and shape as well as by competition.

The relationship between fecundity and maximum leaf length (L) appeared to be exponential (Fig. 3). The statistical model

$$S' = \exp(a + bL) \quad (7)$$

was fitted to data from all solitary plants (both short- and long-day) to obtain the parameter estimates $\hat{a}=0.16$ (SE = 0.61) and $\hat{b}=0.15$ (SE=0.021). We also fitted this exponential function separately to the short- and long-day solitary plants, and found no significant difference between the slopes of the best-fit lines for the two light treatments considered separately ($F=2.11$; $df=2, 58$; $p=0.13$). For subsequent analyses, we therefore considered the short-day plants as equivalent to very large long-day plants; the former effectively increased the length of the tails of the fecundity and size distributions of the latter.

We similarly fitted Eq. 7 to data from all densely-grown plants, irrespective of the number of neighbors per plant. The estimated parameters were $\hat{a}=0.46$ (SE = 0.19) and $\hat{b}=0.074$ (SE=0.0039). The intercept (\hat{a}) did not differ significantly between solitary and dense plants, but the slope (\hat{b}) for high density plants was significantly smaller than for solitary ones. This result substantiated the qualitative observation that for a given maximum leaf length L , solitary plants produced more siliques than dense ones (Fig. 3). This result also indicated that for plants of a given leaf length, there was an apparent effect of competition on fecundity over and above the effects of rosette diameter alone. The observation that leaves of high-density plants were not flat, but were inclined $\leq 30^\circ$ from the horizontal does not affect these results. For leaves at maximum observed inclination (30°), their horizontal projection would be $L\cos(30^\circ)=0.87L$. If all of the

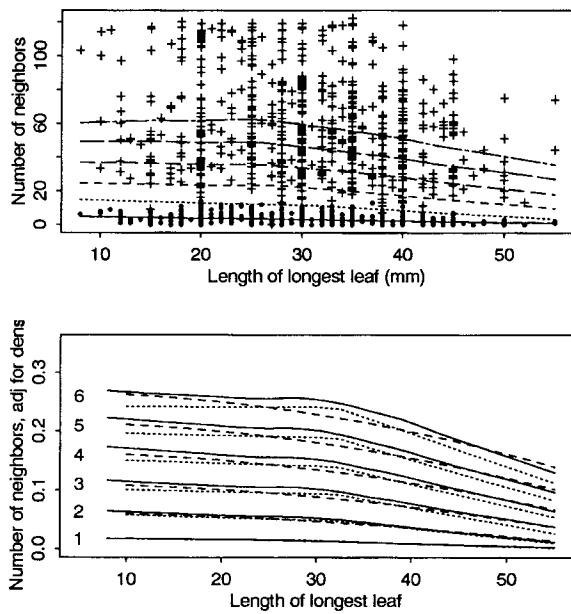


Fig. 4. Relationship between plant radius and number of neighbors for different neighborhood sizes. Top: data from a single high density (10^4 m^{-2}) flat, with lines fitted by loess smoothing. Points shown are number of neighbors within a 1-cm neighborhood (\bullet) and a 6-cm neighborhood (+). Points for neighborhoods of intermediate radii are not shown. Each line represents the loess smooth for a different neighborhood radius: 1 cm (—); 2 cm (.....); 3 cm (-----); 4 cm (---); 5 cm (-.-.-); 6 cm (---). Bottom: comparisons between three methods for fitting the relationship between n_r and L . Three lines are shown for each of the six neighborhood radii (1, 2, ..., 6 cm), indicated to the left of each set of three lines. The loess smooth (—) and the step-wise regression (.....) models consider individual plants to be points that fill no area, while the third model (-----) considers plants to occupy finite circular areas ($>0 \text{ cm}^2$) and estimates number of neighbors as a density function. See text for details.

longest leaves in the high-density population were oriented at 30° , \hat{b} (Eq. 7) would change to $\hat{b}/0.87 = 0.085$, which is still much smaller than the slope estimated for the solitary plants (0.15). As leaf angle $\rightarrow 0^\circ$, $\hat{b} \rightarrow 0.074$.

In the preceding analyses, we used length of longest leaf as a metric for plant size, since it directly measures rosette diameter ($= 2L$) (see below – Separating out the effects of plant size alone from neighborhood effects). Although the relationship between S' and L (Fig. 3) accorded well with how we expected competition to affect plant size and reproduction, the amount of residual variation in the model using L alone was large. We therefore examined the behavior of the model with the addition of biomass in the size term. This procedure also facilitated direct comparisons with PS.

The relationship between biomass and fecundity appeared to be linear (Fig 3), so Eq. 4 was fitted using SAS PROC REG. Parameter estimates for solitary plants were $\hat{a} = 7.6$ (SE = 4.5), and $\hat{b} = 156$ (SE = 19), while estimates for high density plants were $\hat{a} = 0.29$ (SE = 0.43), and

$\hat{b} = 710$ (SE = 14). Surprisingly, high density plants produced significantly more siliques than did individually-grown plants of similar masses (Fig. 3). The residual sums-of-squares for the biomass model (Eq. 4, RSS = 1137.4) was smaller than that for the leaf-length model (Eq. 7, RSS = 3139.8). A model combining both leaf length and biomass is

$$S' = \exp(a + bL) + d w \quad (8)$$

This model (RSS = 1137.4) fitted equally as well as the biomass only model (Eq. 4). Unlike our results using L as a measure of plant size, the results using biomass as a measure of plant size did not illustrate a negative effect of competition on plant fecundity, in contrast to the assumptions of PS. Therefore, we continued to use L as a measure of plant size in our attempt to differentiate between effects of plant size and effects of neighbors on fecundity.

Separating out the effects of plant size alone from neighborhood effects

The contrast between the null hypothesis and the general alternative hypothesis – that the relationship between neighbors and fecundity was not a spurious correlation – was tested in two different but complementary ways: (a) by estimating the relationship between plant size and number of neighbors (see Fig. 2D); and (b) by comparing the fecundity of plants grown individually to the fecundity of plants in the dense flats that lack neighbors in a fixed radius. We report results of analyses done using the number of neighbors at the end of the experiment. Mortality was $< 5\%$ in all dense flats, and analyses using number of neighbors immediately following germination yielded similar results.

Because real plants occupy space in proportion to their size, we expected that larger plants would have fewer neighbors for predefined neighborhoods of fixed radii. The relationship (a) between plant size and number of neighbors was estimated in three different ways. First, non-parametric regression (loess smoothing; Cleveland 1981, Efron and Tibshirani 1991) was used to examine the form of the relationship between leaf length, L , and the number of neighbors within a given radius, n_r (Fig. 4). Non-parametric regression estimates the predictive relationship between two variables, without requiring an a priori specification of the form of that relationship (e.g. linear or quadratic). There was no apparent relationship for $r = 1$ cm (Fig 4). At other neighborhood radii, the relationship appeared to change at leaf lengths around 30 mm. At leaf lengths < 30 mm, the regression line is nearly flat (slope ≈ 0); at larger leaf lengths, the slope of the regression line was < 0 . To test whether the slope changed at some break point, we fitted the following break-point regression model:

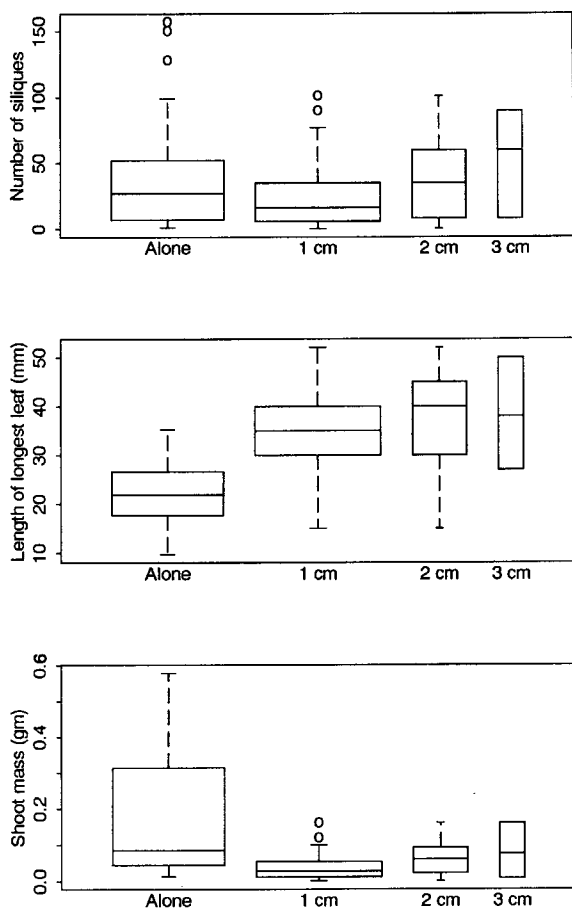


Fig. 5. Distributions of silique production (top); L (middle); and w (bottom) for plants grown alone, and for densely-grown plants with no neighbors within 1, 2, or 3 cm. Box-and-whisker plots show the median (center horizontal line), upper and lower quartiles (box), 1.5 Hspreads (whiskers), and extreme values (circles) (Tukey 1977). The width of each box is proportional to the square root of the sample size. Sample sizes are $n=62$ plants grown alone; $n=76$ dense plants with $n_r=0$; $n=14$ dense plants with $n_2=0$; and $n=3$ dense plants with $n_3=0$.

$$n_r = \begin{cases} y + b_1(L - x) & \text{if } L < x \\ y + b_2(L - x) & \text{if } L \geq x \end{cases} \quad (9)$$

This procedure estimated the break-point (x) at which the slope changes, the height of this break point (y), the slope

of the regression line for $L < x$, and the slope for $L > x$. The results of this non-linear regression were in close agreement with the loess smoothing, indicating a break-point near $r=30$ mm and a y that increased significantly with r (Fig. 4).

Finally, if a plant were considered to occupy a fraction p of a circle with radius ρ in a neighborhood of radius r then the area that could be occupied by neighbors is $\pi(r^2 - p\rho^2)$. The expected number of neighbors in a similar area in the high flats was then given by $d\pi(r^2 - p\rho^2)$, where d was the average plant density in these high density flats (Ripley 1981, Upton and Fingleton 1985). The parameters d and p were estimated by a non-linear regression of the observed number of neighbors within each of the 6 radii on leaf length. The predicted lines from this model (Fig. 4) were in close agreement with both the non-parametric and the breakpoint models.

All three regression models – loess, break-point, and non-linear – yielded predicted values of n_r with little variance over a large range of L (Fig. 4). This result was in marked contrast to the large amount of variance in n_r actually observed (Fig. 4), and illustrated that there was little difference, at least for *Arabidopsis*, in considering plants as points or plants as actual space-fillers in this neighborhood analysis.

To illustrate further the contrast between the null hypothesis and the general alternative hypothesis (contrast b, above), we compared the fecundity of plants grown individually with the fecundity of densely-grown plants lacking neighbors within a fixed radius. Our null hypothesis states that the relationship between the number of neighbors and plant fecundity in dense stands should be the same as the relationship between the number of potential neighbors and fecundity for plants grown alone. Statistically, we tested this hypothesis by determining if the distribution of silique production of plants grown alone was identical to the distribution of silique production of densely-grown plants where $n_r=0$. These distributions are illustrated in Fig. 5. Contrasts could only be performed for $r = \{1, 2, 3 \text{ cm}\}$, as there were no plants in the dense flats which had $n_r=0$ for $r \geq 4$ cm. These distributions were not significantly different (Table 1) for any of the neighborhood sizes, and we could not reject this null hypothesis. We note that because of small sample sizes for $r=2$ cm ($n=14$) and $r=3$ cm ($n=3$), that the statistical power was low for these tests.

Curiously, similar results were not obtained for either

Table 1. Results of Kolmogorov-Smirnov goodness-of-fit tests for distributions shown in Fig. 5.

Contrast	S'		L		w	
	D	P	D	P	D	P
Solitary vs dense ($n_1=0$)	0.18	0.24	0.68	0.0001	0.53	0.001
Solitary vs dense ($n_2=0$)	0.22	0.47	0.71	0.0001	0.38	0.07
Solitary vs dense ($n_3=0$)	0.49	0.51	0.78	0.06	0.38	0.80

Table 2. Estimates of constants c and c_s in Eqs 2 and 3 for densely-grown plants^a.

r (cm)	Biomass		Fecundity	
	c (SE) ^b	RSS	c_s (SE) ^b	RSS
1	0.366 (0.067)	7922	0.317 (0.071)	5421
2	0.232 (0.039)	7619	0.174 (0.039)	5377
3	0.131 (0.027)	7879	0.089 (0.025)	5511
4	0.092 (0.024)	8060	0.057 (0.019)	5591
5	0.049 (0.015)	8387	0.031 (0.012)	5802
6	0.025 (0.009)	8640	0.014 (0.006)	5801

^a $n = 651$ plants pooled over 3 flats.

^bestimate of c and $c_s \neq 0$ ($P < 0.05$) for all r .

distributions of L or w (Fig 5, Table 1). These results indicated that, for a given plant diameter or biomass, plants with no neighbors within neighborhoods of 1 and 2 cm in a dense population had leaf length distributions that differed from similarly sized plants grown alone (Fig. 5). The median L of plants with no neighbors in each of these two neighborhoods was greater than the median L of plants grown alone (Table 1). Conversely, the median w of dense plants with no neighbors within 1 cm was significantly less than the median w of plants grown alone (Fig. 5, Table 1).

Biologically, these results indicated that there were some effects of neighbors up to 2 cm distant on plant shape and mass, but these neighbors appeared to have had no detectable effects on target plant fecundity. In light of our analyses of the effects of neighbors on rosette diameter, and its effects on target plant fecundity (see Observed relationships between density, size, and fecundity, above), our results show that leaf length as a predictor of plant fecundity under-represented the magnitude of neighborhood competitive effects and consequently over-estimated plant fecundity. On the other hand, biomass as a predictor over-represented the magnitude of neighborhood competitive effects and underestimated plant fecundity. This result appears to be a consequence of interactive changes in the relationships between plant size, plant fecundity, and number of neighbors.

The results of the analyses illustrated in Figs 3 and 4 indicated that an increase in number of neighbors reduced fecundity of target plants in dense stands. These results also indicated that in comparing the performance of plants in dense stands with plants grown alone, the overwhelming difference – attributable to neighborhood interactions – was a change in biomass and leaf length (Fig. 5, Table 1). Unfortunately, the very low variance in predicted n_s (Fig. 4) precluded quantification of the magnitude of competitive effects on fecundity over and above their effects on plant size (the shaded region of Fig. 2D). When applied to similarly-sized plants grown alone, this predictor for n_s produced virtually no variation in the distribution of predicted S' that could be compared with observed values for plants grown alone. We could, however, investigate further the effects of neighbors on plant

size and fecundity in dense stands (comparisons between the two alternative hypotheses).

Neighborhood effects on size and fecundity

Plants with many neighbors were small, but plants with few neighbors were either small or large (cf. Goldberg 1987). The variability in the relationship between n_s and w was much larger than that found by Silander and Pacala (1985) for the same species grown under similar conditions. If a hyperbolic model (Eq. 2) was fitted to the biomass data, significant effects of neighbors were observed at all radii (Table 2), although the estimate of the competitive effect (c) declined with increasing radius (Table 2). The number of neighbors similarly reduced significantly fecundity at all neighborhood sizes (Table 2), and there was considerable variation in fecundity among plants with the same number of neighbors (Fig. 6).

Some of the variation in fecundity among plants with the same number of neighbors can be explained by plant rosette diameter (Fig. 6). The joint relationship among plant diameter, number of neighbors, and fecundity can be portrayed graphically by grouping plants into quintiles of leaf length (L). The smallest plants (quintile 1) had few

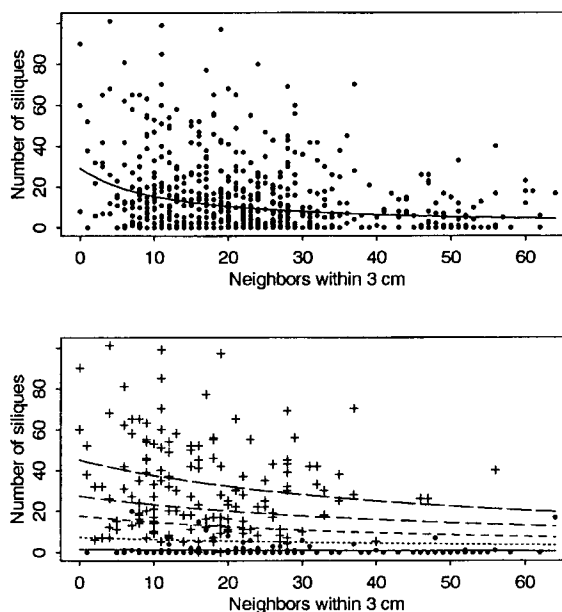


Fig. 6. (Top) Relationship between the number of neighbors within 3 cm and fecundity. The line indicates a fitted hyperbolic regression (Eq. 3) through all points. (Bottom) Relationship between number of neighbors within 3 cm and fecundity, illustrating the change in this relationship with changes in plant diameter. Lines indicate fitted hyperbolic regressions (Eq. 3) for each quintile of leaf length: 8–21 mm (—); 22–28 mm (.....); 29–33 mm (- - -); 34–38 mm (- - -); 39–55 mm (—). ● plants with leaves < 21 mm (smallest quintile); + plants with leaves > 38 mm (largest quintile). Points for other quintiles (intermediate in position and variance) not shown.

Table 3. Weighted^a residual sums of squares for fecundity models.

Equation no. ^b	$f(L)^c$	$g(L)$	df	Neighborhood radius r (cm)					
				1	2	3	4	5	6
3	fitted constant	$1 + cn$	2	5421.5	5377.2	5511.6	5591.5	5697.0	5801.2
7	$\exp(a + bL)$	1	2	3139.8	3139.8	3139.8	3139.8	3139.8	3139.8
10 ^d	$\exp(a + bL)$	$1 + cn$	3	3055.2	3058.4	3087.3	3107.1	3120.1	3138.8
12 ^d	$\exp(a + bL)$	grouped ^e ($1 + c_L n$)	7	2936.9	2919.0	2927.4	2945.2	2965.2	2992.0

^a Variance weights are always $1/L$. 648 high density plants used in the analysis.

^b Refers to equation numbers in text.

^c In the exponential model, fitted parameters were $\hat{a} = 0.46$, $\hat{b} = 0.0738$.

^d All reductions in RSS of model 12 relative to model 10 are statistically significant ($P < 0.05$).

^e Estimators based on groupings according to quintiles of L . See text for details.

to many neighbors and produced almost no siliques (Fig. 6). As L increased, the relationship between n_r and S' became more negative (Fig. 6). For other values of r between 1 and 6 cm, the pattern was qualitatively similar.

We modelled the dependence of fecundity on both rosette diameter and number of neighbors in each of the following three ways:

$$S' = [\exp(a + bL)] / (1 + cn_r) \quad (10)$$

$$S' = aL / (1 + c_L n_r) \quad (11)$$

$$S' = [\exp(a + bL)] / (1 + c_L n_r) \quad (12)$$

These models differ in whether rosette diameter affected the fecundity of plants with no neighbors (Eqs 10 and 12) and whether rosette diameter affected the response to neighbors (Eqs 11 and 12). Eq. 10 describes the case where fecundity depends on rosette diameter, but the coefficient c , which measures the effects of neighbors, is constant. The coefficient c_L in Eqs 11 and 12 allow the effects of neighbors to depend on plant size. All three models are special cases of the general model (modified from Eq. A2 [Appendix 1]):

$$S' = f(L) / g(L) \quad (13)$$

where $g(L) \neq 1$. The differences in fit among the models

can be tested by comparing residual sums-of-squares for nested models.

PS assumed that the relationship between number of neighbors and fecundity was a linear function of plant biomass. In other words, the function $g(L)$, which scales the effects of neighbors on fecundity, was a constant (i.e. either Eq. 7 or 10 would provide an adequate fit). This hypothesis was tested by dividing plants into groups based on plant size and testing whether the effect of neighbors (the c_L coefficient) was the same in each group. We defined five groups based on leaf length. To equalize the number of individuals in each size group, we used quintiles of leaf length to assign individuals to a group: (quintile 1: leaf length from 5 to 21 mm ($\bar{x} = 17.5$); quintile 2: 22–28 mm ($\bar{x} = 25.7$); quintile 3: 29–33 mm ($\bar{x} = 31$); quintile 4: 34–38 cm ($\bar{x} = 35.9$); quintile 5: 39–55 mm ($\bar{x} = 42.9$).

Eq. 3, which in the notation of Eq. 13, has a constant numerator term (S_{max}) and constant denominator crowding coefficient c , has the largest RSS at all neighbor radii (Table 3). When $f(L)$ was set as the exponential function (Eq. 10), there was a significant improvement in the fit of the model at all r (Table 3). The fit was further improved by allowing the crowding coefficient c in the denominator $g(L)$ to vary according to leaf length quintile (Eqs 11, 13; Table 3). These analyses were repeated using a linear function of biomass to express plant size effects on fecun-

Table 4. Weighted^a residual sums of squares for fecundity predictors based on w .

Equation no. ^b	$S' =$	df	Neighborhood size (cm)					
			1	2	3	4	5	6
4	$a + bw$	2	1137.4	1137.4	1137.4	1137.4	1137.4	1137.4
2	$w / (1 + cn_r)$	2	5421.0	5377.0	5511.0	5591.0	5697.0	5801.0
5 ^c	$(a + bw) / (1 + cn_r)$	3	1108.4	1098.2	1082.5	1094.0	1104.6	1100.6
5 ^{c,d}	$(a + bw) / (1 + c_L n_r)$	7	1100.2	1086.4	1075.8	1081.2	1088.4	1083.5

^a Variance weights are always $1/L$. 648 high density plants used in the analysis.

^b Refers to equation numbers in text.

^c All reductions in RSS of model with c estimated for separate quintiles of L (last model above) relative to model with c estimated from all plants pooled are statistically significant ($P < 0.05$).

^d Modification of eq. 5 to include estimators based on groupings according to quintiles of L . See text for details.

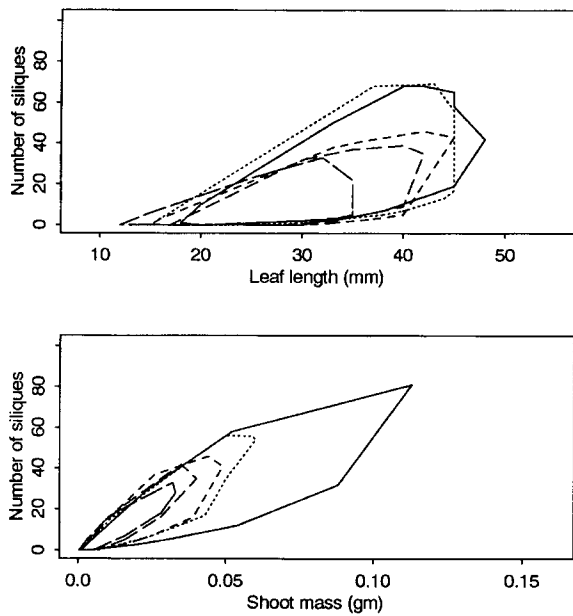


Fig. 7. Peeled (depth = 3) convex hulls (Becker et al. 1988) surrounding the joint distributions of plant size and fecundity for quintiles of number of neighbors. Top: relationship between S' and L . Bottom: relationship between S' and w . Quintiles of n_3 : 0–11 (—); 12–19 (.....); 20–24 (---); 25–31 (-.-.); 32–64 (—).

dity (Table 4). The results were qualitatively the same: the competitive effect of neighboring plants depended on the size of the target plant. In other words, the path diagram of Fig. 1C fitted the data significantly better than did PS, which assumes no effect of target plant size. Note that because the number of potential neighbors is related to both rosette diameter and biomass (Figs 1B, 1C, 2C), it might seem at first glance that removing their effects also would remove the effects of potential neighbors. However, this is true only when the relationship between biomass or diameter and neighbors is linear, while we found that for *Arabidopsis* this relationship is nonlinear (Fig. 4).

Covariance of number of neighbors, plant size, and plant fecundity

Fig. 7 illustrates the covariance between plant size, silique production, and the number of neighbors within 3 cm (n_3). The relationship between plant size and fecundity for each of five quintiles of n_3 (quintiles: 0–11; 12–19; 20–24; 25–31; 32–64 neighbors within 3 cm) is portrayed graphically by superimposed peeled convex hulls (Barnett 1976). The convex hull of a set of points defines the boundary of those points; peeling a convex hull reduces its sensitivity to bivariate outliers. To peel a convex hull, a convex hull is computed, then the points that lie on the hull are deleted and a new hull is com-

puted. The resulting peeled hull better describes the orientation and variability of the bulk of the data (Barnett 1976). Ellison (1993) provides additional details on construction and interpretation of convex hulls.

Fig. 7 illustrates thrice-peeled convex hulls that describe the ranges of observed S' and L for plants with varying n_3 . This figure illustrates that there was added variance in S' and L associated with decreases in n_3 , but the hulls were not nested. In other words, although the joint variance in S' and L changed with the magnitude of n_3 , this change in variance was not one-to-one. This is a graphical illustration of the additional effects of number of neighbors on fecundity over and above their effects on plant size alone.

Statistical contrasts were performed as described above for regression models using length of longest leaf as the size metric and testing whether regression coefficients were the same for all plants regardless of number of neighbors, or whether the regression coefficients varied with n_3 . Since the relationship between L and S' was exponential, a non-linear generalized ANCOVA was used to test whether coefficients of the regression line predicting fecundity from length of longest leaf were the same for all groups (quintiles) of neighbors. Two regression models were fitted to these data, using SAS PROC NLIN with the Marquardt direction-finding algorithm:

$$S'_{ij} = \exp(a + b L_{ij}) + \epsilon_{ij} \quad (14)$$

$$S'_{ij} = \exp(a_i + b_i L_{ij}) + \tau_{ij} \quad (15)$$

where S'_{ij} is the fecundity of plant j in the i 'th group, L_{ij} is the length of that plant's longest leaf, a and a_i are intercepts, b and b_i are slopes, and ϵ and τ are error terms. Eq. 14 fits a common slope and intercept to all groups, while Eq. 15 fits separate intercepts and slopes to each group. Eq. 15 fitted the data significantly better than Eq. 14 (RSS for Eq. 14 = 3139.8; RSS for Eq. 15 = 2936.9, $F = 3.72$, $P = 0.0003$).

Fig. 7 illustrates the same results for biomass (w). The results presented for 3 cm neighborhoods are qualitatively similar for all other neighborhood radii ≤ 5 cm; predictions of fecundity (or fecundity predictors) using predicted plant mass \hat{w} (RSS = 1137.4) were less precise than fecundity predictors derived from observed plant mass w (RSS = 1100.2) ($F = 4.82$, $P < 0.0001$). The model using biomass in the fecundity predictor also provided a significantly better fit than the model using leaf length.

Concluding remarks

In sum, our results indicate that neighborhood competition significantly affects plant population dynamics in monocultures. The effects of neighbors on target plants were apparent in plant biomass and diameter changes, as well as changes in plant fecundity relative to plants grown in the absence of competition. Previous models of

neighborhood competition in plant populations have either assumed that neighbors affect fecundity only through their effects on plant biomass, or have subsumed the effects of neighbors on plant biomass within their effects on plant fecundity. We have illustrated that neighbors affect plant shape, biomass, and fecundity simultaneously and that there are effects of neighbors on plant fecundity independent of their effects on plant shape and biomass alone. Further investigations into allometric changes in plant size and shape as a function of neighbors (cf. Gibson et al. 1992), and independent effects of neighbors on plant fecundity are necessary in order to accurately model neighborhood dynamics in plant populations.

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Appendix 1 – Formal definition of the model

This model for neighborhood competition models can be expressed formally as follows:

Let S' denote plant fecundity; M denote plant size (e.g. mass, amount of space occupied, etc.); p_i denote an individual plant within a set of interacting (competing) plants $\{\mathbf{P}\}$; n_r denote the number of neighbors within N_r , a neighborhood of fixed radius r around p_i .

For arbitrary functions f and g and h , and arbitrary operators \oplus and \otimes :

$$S' = f(M) \quad (\text{for plants grown individually}) \quad (\text{A1})$$

$$S' = f(M) \oplus g(f(M), n_r) \otimes h(n_r) \quad (\text{for plants grown in dense stands}) \quad (\text{A2})$$

where $f(M)$ expresses the effect of plant size alone on seed production; $g(f(M), n_r)$ expresses effects of n_r neighbors on fecundity resulting from their effects on plant size; and $h(n_r)$ expresses any additional direct effects of n_r neighbors on seed production, *independent* of their effects on plant size. In Silander and Pacala's (1985) neighborhood model the functions f and g of Eq. A2 were not explicitly included; their effects were subsumed within h . In contrast, in the most recent formulation of this model (Pacala and Silander 1990), the function $h \equiv$ identity function (i.e. has no effect).

In terms of this formal model, the null hypothesis suggested would be supported if $\forall N_r: r \in \{\mathbf{R}\}$ (the set of neighborhood radii), $g(f(M), n_r) \equiv$ the identity function. The null hypothesis would be rejected if $\exists N_r: r \in \{\mathbf{R}\}$, $g(f(M), n_r) \neq$ the identity function. The first alternative hypothesis would be supported if $\forall N_r: r \in \{\mathbf{R}\}$, $g(f(M), n_r)$ is a non-zero function that increases with n_r , but $h(n_r) \equiv$ the identity function (e.g. 0 if \otimes is additive; 1 if \otimes is multiplicative). The second alternative hypothesis would be supported if $h(n_r)$ was not an identity function.