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**Neighbor interactions among herbaceous plants in a perennial
grassland**

Holmes, Robert Duane, Ph.D.

The University of Arizona, 1988

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NEIGHBOR INTERACTIONS AMONG HERBACEOUS PLANTS
IN A PERENNIAL GRASSLAND

by

Robert Duane Holmes

A Dissertation Submitted to the Faculty of the
DEPARTMENT OF ECOLOGY AND EVOLUTIONARY BIOLOGY

In Partial Fulfillment of the Requirements
For the Degree of

DOCTOR OF PHILOSOPHY

In the Graduate College

THE UNIVERSITY OF ARIZONA

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As members of the Final Examination Committee, we certify that we have read
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ABSTRACT

Individual clumps of the perennial grass Bouteloua gracilis from which 25% or 75% of neighbors had been removed to a radius of 50 cm displayed significantly higher biomass production over one summer than did control plants. Neighbor removal also resulted in increased tiller production and flowering as compared to control plants. These results clearly demonstrate the importance of competition to B. gracilis in this system. In contrast, significant differences in predawn leaf water potential were found on only two of four sampling dates during the growing season. On the driest sampling date, increased variability in leaf water potential within treatments obscured the effect of treatment, even though the difference in mean leaf water potential between 75% removal and control treatments (0.35 MPa) was quite high. On the wettest sampling date, all plants appeared well-hydrated, and there was only negligible difference among treatments.

In a second study, I examined the effect of near neighbors on the fecundity of an annual herb,

Machaeranthera tanacetifolia (Asteraceae). Fecundity was negatively related to the number of neighbors within a biologically meaningful neighborhood radius for both conspecific neighbors and grass neighbors in 1984, and for grass neighbors in 1985. However, in no case did neighbors explain more than 6% of the variance in fecundity of M. tanacetifolia, and most plants produced few or no seeds regardless of the number of neighbors.

I present a simple graphical model in which competition from neighbors serves as a necessary but not sufficient condition for high fecundity; other factors must also be favorable if a plant is to be successful. Application of this model to my data revealed that the amount of area occupied by neighbors had an important effect on fecundity for the subset of the population for which other conditions were inferred to be most favorable. As other conditions became less favorable, neighbors became less relevant to fecundity. I then discuss these results in terms of a general model of the interacting effects of competition and other factors, and distinguish four possible classes of outcome.

CHAPTER 1: INTENSITY AND IMPORTANCE
OF COMPETITION FOR WATER IN BOUTELOUA GRACILIS

INTRODUCTION

Few ecologists doubt that competition is widespread in natural communities. Broad literature surveys by Connell (1983) and Schoener (1983), for example, found evidence of interspecific competition in the majority of studies surveyed. Fowler (1986) reviewed the evidence for competition among plants of arid and semiarid environments, and concluded that "the occurrence and potential importance of competition in these communities can now be taken as given" (p. 104). However, all three reviews cite cases in which competition was detected in some sites or some years of a study, but not in others. This suggests that the degree of competition varies both spatially and temporally, being sometimes above the threshold for statistical detection, and sometimes below it. Ecological research would thus more profitably be directed toward documenting and explaining the changing magnitude of competition,

rather than merely establishing its presence at some times and places (cf. Toft and Shea 1983, Fowler 1986).

Welden and Slauson (1986) provide a valuable framework for considering this variability. They point out the distinction between the intensity of competition (the magnitude of its physiological effect, and consequent reduction in fitness) and its importance (its effect relative to all other factors affecting fitness). Competition may be statistically detectable within a system only in some years or sites for one or both of two reasons: (1) the intensity of competition is variable, with competition exerting a strong effect only at some times and places; or (2) the variable contribution of other factors affecting fitness (such as predation or climate) leads to variation in the relative importance of competition independent of change in its intensity. Studies which trace the pattern of changes in both the intensity and the importance of competition will increase our understanding of its dynamics, and its changing role in determining community structure. One way to perform such a study is to manipulate the density of putative competitors, and observe the effect on an ecologically significant physiological variable and on more direct measures of fitness.

In the arid regions of southwestern North America, there is strong evidence that plant water status is closely related to fitness. Within-site correlations between plant productivity and annual precipitation (Cable 1975, McMahon and Schimpf 1980) and the results of experimental water additions (Lauenroth et al. 1978, Inouye et al. 1980) clearly show that water availability limits plant growth in these regions. Furthermore, several experimental studies (see below) coupled with the well-known correlation of plant size with distance from nearest neighbors (e.g. Yeaton and Cody 1976, Yeaton et al. 1977, Nobel 1981, Ehleringer 1984), suggest that both intra- and interspecific competition are widespread in arid and semi-arid regions (see review by Fowler 1986).

Few studies, however, have directly examined the effect of the experimental removal of neighbors on the water status of remaining individuals. Fonteyn and Mahall (1978, 1981) demonstrated that individuals of two desert shrub species (Larrea tridentata and Ambrosia deltoidea) had lower (more negative) water potentials -- indicating greater water stress -- in the presence of the other species than when all heterospecifics had been removed. Removal of all conspecific neighbors increased stomatal conductance in a desert shrub, Encelia farinosa (Ehleringer 1984), and a desert grass, Hilaria rigida (Robberecht et

al. 1983). The latter two studies also showed an effect of neighbor removals on the growth of the remaining plants.

In the study reported here, I examined the effects of experimental removal of 25% and 75% of neighbors on focal individuals of the perennial grass Bouteloua gracilis. I measured both long-term growth responses (tiller production, biomass accumulation) and short-term responses (predawn water potential). My results illustrate the changing intensity and importance of competition during the growing season, and reveal the long-term importance of even small changes in neighbor density.

MATERIALS AND METHODS

Study site and species:

This study was conducted at the Appleton-Whittell Research Sanctuary, an ungrazed preserve of 3160 ha at 1500 m elevation in semi-arid grassland 110 km southeast of Tucson, Arizona. Annual precipitation at the site averaged 436 mm (19-year average, unpublished records from the Research Ranch), with approximately half to two thirds falling during the summer monsoon season of late June-September. The study site had a total plant cover of about 50%, and was dominated by perennial grasses, with

Bouteloua gracilis (H.B.K.) Lag. the most abundant species.

Experimental design:

Ninety small clumps of Bouteloua gracilis (4-40 tillers) were selected for study. I attempted to choose clumps with comparable densities of neighboring plants, and the majority of neighboring individuals were B. gracilis in every case. The plants were grouped into 15 spatially discrete blocks of 6 plants each, and plants within a block were randomly assigned to one of three treatments, with 2 replicates per treatment per block: Control (no manipulation), 25% removal (25% of neighboring plants within 0.5 m removed), and 75% removal (75% of neighbor individuals removed). Plants were removed by clipping at ground level, and individuals to be removed were selected by a stratified random procedure to increase angular dispersion of removed plants. After clipping, removed plants were treated topically with glyphosate herbicide, and reclipped as necessary to prevent regrowth.

Leaf water potentials were initially measured before dawn on 17 June 1986. I then performed removals that day and the day following. Predawn water potentials were measured again for all plants on 19 June, 26 June, 12 August, and 17 October 1986. Water potentials were

measured using a pressure chamber (Scholander et al. 1965). I sampled the youngest fully expanded leaf from a single tiller on each plant at each sampling interval, and individual tillers were sampled no more than once during the course of the experiment. Plants were sampled in the same sequence on every sampling date, and all plants within each block were sampled within about 10 minutes of each other. Water potential was measured not more than 3-5 min after a leaf was removed from the plant, and all leaves were enclosed in aluminum foil sheaths from the moment of cutting until the completion of the measurement.

I counted the number of tillers on each focal plant on 26 June, prior to the initiation of summer growth. On 17 October, I harvested the entire aerial portion of all plants. After removal of attached roots and any dead material left from previous years, I measured the following growth parameters for each plant: total number of tillers, number of reproductive tillers, number of spicate inflorescences, and oven-dry weights (48 hr at 70 C).

Statistical analysis:

Most statistical analyses used two-way analysis of variance (ANOVA) or covariance (ANCOVA) models, with block and removal treatment as factors. For water potential data, pre-treatment water potential was used as the

covariate, in order to control for variability due to microspatial differences among individuals. For dry weights and final tiller counts, the initial number of tillers served as the covariate, to control for differences due to initial size. Mean dry weight per tiller and proportion flowering were analyzed as a two-way ANOVA without covariate. Because of the smaller sample size of plants with flowering tillers, one-way ANOVA was used to test for removal treatment effects on number of spikes per flowering tiller.

RESULTS

Growth:

Plants with fewer neighbors grew more during the course of the experiment and had a higher rate of tiller production than plants with more neighbors; all treatments were statistically distinguishable (Table 1). In addition, plants in the 75% removal treatment had heavier tillers and a higher proportion of tillers flowering than plants in the other two treatments. There was no effect of neighbor removal on the number of spikes per flowering tiller.

Table 1. Effect of competition and microsite on focal plant growth. (a) Proportion of total sum of squares explained by treatment, block, and pre-treatment tiller number (where applicable) from ANCOVA or ANOVA of growth data. ***, $p < .001$. N.A. = not applicable. (b) Means or adjusted means of growth variables for the three experimental treatments. Means within a row not followed by same letter are significantly different by lsd at $p = .05$.

Variable	E F F E C T S			
	Pre-treat. Tiller No. (1 df)	Block (14 df)	Treatment (2 df)	Other (72 df)
Dry Wt. Current Yr's Growth	.148 ***	.070	.433 ***	.349
# of Tillers at End of Exp't	.456 ***	.034	.380 ***	.129
Mean Dry Wt Per Tiller	N.A.	.192	.182 ***	.626
Proportion of Tillers Flowering	N.A.	.197	.177 ***	.625
# of Spikes per Flowering Tiller	N.A.	N.A.	.033	.967

(b)	Control	25% Removal	75% Removal
Dry Wt. Current Yr's Growth (g)	1.27 a	1.58 b	2.96 c
# of Tillers at End of Exp't	18.2 a	26.0 b	33.9 c
Mean Dry Wt Per Tiller (g)	.069 a	.060 a	.091 b
Proportion of Tillers Flowering	.022 a	.036 a	.084 b

Water Potentials:

Water potentials of all plants were low at the beginning of the experiment, and continued to decline during the relatively dry first week of the experiment. Later in the summer rainy season, water potentials were considerably higher (Figure 1).

Table 2 summarizes the results of analyses of covariance for the water potential samples. There was a significant Treatments X Blocks X Covariate interaction in the ANCOVA for 19 June only, indicating that treatment affected the water potentials of only a subset of the plants. Since the experimental removals were performed on 17 and 18 June, some plants had had less than 24 hours' exposure to the experimental treatments at the time water potentials were measured. Closer inspection of the data (Figure 2) reveals that plants that received manipulations on 17 June and early on 18 June showed a consistently smaller drop in water potential from 17-19 June in the removal treatments than in the controls. In contrast, plants that received manipulations late on 18 June did not show this treatment effect, presumably because too little time had elapsed between application of the treatment and the 19 June sampling. If these plants (the last 5 blocks) are omitted from the ANCOVA for 19 June, the Treatments X Blocks X Covariate interaction becomes statistically

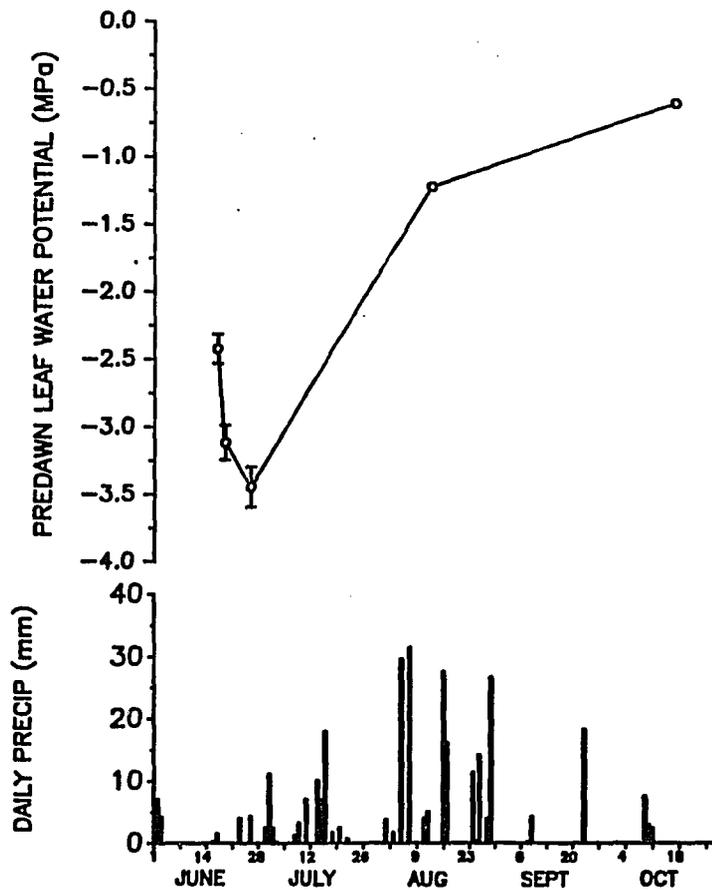


Figure 1. Daily precipitation and predawn leaf water potential of *Bouteloua gracilis* over the course of the 1986 growing season. Top: Mean leaf water potential (uncorrected for covariate) of all plants ($n = 90$) for five sampling dates. Bottom: Daily precipitation record from Research Ranch headquarters, approximately 3 km from study site. Water potentials were low in June, which followed the spring dry season and preceded the summer rains; water potentials were much higher in August, at the height of the rains, and in October, at the end of the growing season.

Table 2. Effect of competition and microsite on focal plant water potential on four sampling dates during the growing season. (a) Sum of squares explained by treatment, block, and pre-treatment water potential, from ANCOVAs of predawn water potentials (proportion of total sum of squares for that date in parentheses). All interaction terms involving treatment were nonsignificant at $p = .05$. Note that data for 19 June exclude 5 of the 15 blocks (see text for details). *, $p < .05$; **, $p < .01$; ***, $p < .001$. (b) Adjusted mean water potentials (MPa) for the three treatments. Means for a single date not followed by same letter are significantly different by lsd at $p = .05$.

(a)

DATE	E F F E C T			
DATE	Treatment (2 df)	Block (14df)	Pre-treatment Water Pot. (1 df)	Other N.S. Terms&Error (72 df)
19 Jun	500(.18)**	555(.20)	547(.20)***	1120(.42)
26 Jun	172(.02)	3398(.35)**	386(.04)*	5806(.60)
12 Aug	282(.27)***	520(.49)***	110(.10)***	144(.14)
17 Oct	12(.02)	237(.32)*	4(.01)	493(.66)

9 df for 19 June
47 df for 19 June

(b)

	Control	25% Removal	75% Removal
19 June	-3.31 a	-2.90 b	-2.58 b
26 June	-3.62 a	-3.45 a	-3.27 a
12 August	-1.38 a	-1.34 a	-0.98 b
17 October	-0.65 a	-0.60 a	-0.56 a

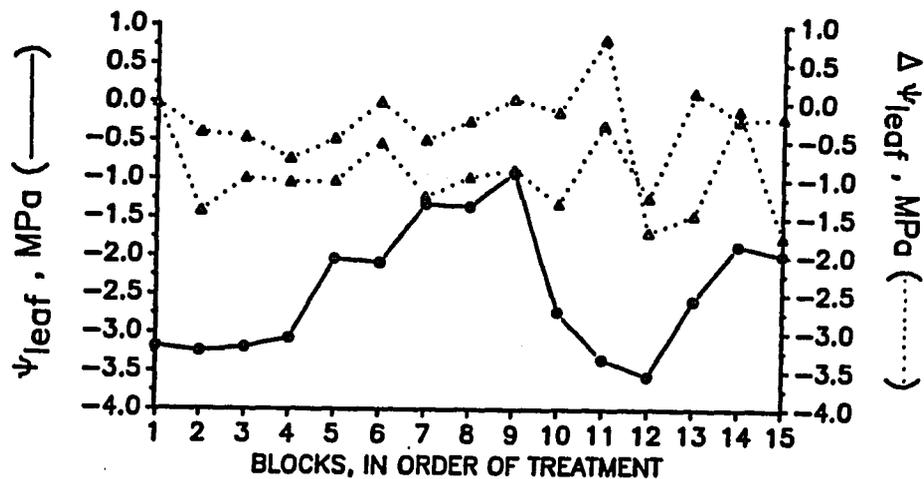


Figure 2. Block means of pre-treatment water potential on 17 June (solid line; mean of 6 plants per block) and change in water potential from 17 June to first experimental sampling on 19 June (Δ Δ , control plants; \blacktriangle \blacktriangle , 75% removals; mean of 2 plants per treatment per block). Plants in the 75% removal treatment consistently dried out less from 17-19 June in blocks receiving manipulations on 17 June (Blocks 1-6), and early on 18 June (Blocks 7-10). Those blocks receiving manipulations latest on 18 June (Blocks 11-15) showed no consistent treatment effect.

insignificant. Therefore, the analysis reported in Table 2 for 19 June uses this reduced data set.

Removal of neighbors significantly increased the water potential of focal plants on 19 June and 12 August, but not on 26 June or 17 October (Table 2). On 17 October, all plants were well hydrated, and water potential differed little among treatments. On 26 June, on the other hand, the magnitude of the treatment effect was relatively large (a difference of 0.35 MPa between 75% removal and control, approximately the same as the .40 MPa difference on 12 August, when treatment showed a statistically significant effect). However, other sources of variation in water potential were more pronounced on 26 June (the driest sampling date); this additional variation, which fell under the error term in our ANCOVAs, led to a non-significant treatment effect on that date.

DISCUSSION

Measures of growth and shoot production integrate many factors important to an individual's fitness over the full growing season, and thus provide a meaningful index of the long-term importance of those factors to Bouteloua gracilis. Removal of competitors was the single most

important factor affecting biomass production in my experiment (Table 1). The same is true for tiller production, except for the obvious effect of initial tiller number (plants that were larger at the beginning of the experiment were also larger at the end). Competitor removal also explains a large and statistically significant proportion of the variance in tiller size and flowering. The long-term importance of competition is unequivocal.

My results are similar to those of Fonteyn and Mahall (1978, 1981), Robberecht et al. (1983), and Ehleringer (1984), in demonstrating an effect of neighbor removal on the water status of remaining individuals, and ultimately on their growth. However, whereas the three previous studies dealt with responses to the removal of all neighboring individuals (or all neighbors of a particular species) within a given radius of the focal plant, my study involved less drastic neighbor manipulations. The 25% removal treatment, in particular, was roughly equivalent to removing a single large neighbor individual. Thus, my results reveal that even small changes in a plant's neighborhood can affect fitness substantially over the course of an entire growing season; that is, the presence or absence of a single individual has significant long-term ecological consequences for its neighbors.

My experiment also documents the changing intensity and importance (sensu Welden and Slauson 1986) of competition for water over the course of the summer growing season. The intensity of competition -- its absolute magnitude -- is measured by the change in water potential that results from experimental neighbor removal. The importance of competition at any point during the growing season can be estimated by the proportion of total variation in water potential that is explained by treatment (e.g. Welden and Slauson 1986: 36). I feel justified in my use of predawn water potential as a measure of the intensity and short-term importance of competition, since water potential differences in B. gracilis translate into differences in photosynthetic rate or other parameters closely tied to fitness. Predawn water potential is correlated with midday stomatal conductance in B. gracilis (Sala et al. 1981), and is closely related to soil water potential (Ritchie 1981, Sala et al. 1981), which Detling et al. (1978) found to be an important predictor of net photosynthesis in this species. Much evidence linking plant water potential with various components of fitness exists from other species as well (e.g. Hsiao and Acevedo 1974, Cutler and Rains 1977).

It is likely that the plants in my study competed for soil nutrients, particularly nitrogen, as well as water (Lauenroth et al. 1978). Thus, the effect of my

experimental treatments on growth may depict competition for more than water alone. Nevertheless, my water potential measurements are of interest because they track the changing importance and intensity of competition for one limiting resource throughout the growing season.

The importance of competition for water was relatively high on two of the four sampling dates, 19 June and 12 August, but was minimal on the other two dates, 26 June and 17 October (Table 2). Closer examination suggests competition was unimportant in determining water potential for different reasons on 26 June and 17 October. On 26 June, the intensity of competition -- a difference of 0.35 MPa in adjusted mean water potentials between 75% removals and controls -- was roughly the same as on the two dates with important competitive effects. However, competition was less important on 26 June, because of the greater amount of variation in other factors, as indicated by the greater error sum of squares (Table 2). Falling just at the beginning of the summer rainy season, 26 June was the driest of the four sampling dates (Figure 1). Sala et al. (1981) report increased variability of leaf water potential in Bouteloua gracilis as drought stress increases, and data from our pilot experiments in 1985 also corroborate this (Young and Holmes, unpublished data). It seems likely that as soil moisture decreases, microsite differences in soil

water availability and water holding capacity become increasingly important.

In contrast, the importance of competition was low on 17 October because its intensity was also low (a difference in adjusted mean water potentials of only 0.09 MPa between 75% removals and controls, expected by chance alone in 45% of samples). On this sampling date, active tillers on all plants appeared to be well hydrated regardless of the presence of neighbors. That is, water was not a limiting resource at that time.

These results suggest that competition is most significant at intermediate levels of water availability during the growing season, when water is scarce enough to limit growth, yet abundant enough that the effect of competition is not overpowered by microsite variability. A similar pattern may hold between years as well, with competition for water being more important in years of intermediate precipitation than in unusually wet or dry years. There is some evidence that plants in water-limited environments experience less competition during dry periods (e.g. Friedman and Orshan 1974). A reduction of competition in wet years is perhaps less likely, since excess water over a period of weeks is likely to result in increased growth of the plants until the excess is consumed.

Welden and Slauson (1986) assert on logical grounds that the importance and intensity of competition need not be correlated, and they discuss some of the implications of this. My results provide empirical support for their claim. In a relatively harsh and unpredictable environment such as the semi-arid grassland I studied, it is unlikely that an effect of low intensity will prove to be important in the short term; however, my results provide examples of the other three possible permutations of high and low intensity and short-term importance: high intensity, high importance (19 June and 12 August); high intensity, low importance (26 June); low intensity, low importance (17 October).

CHAPTER 2: WITHIN-POPULATION VARIATION
IN COMPETITIVE RESPONSE IN AN ANNUAL FORB,
MACHAERANTHERA TANACETIFOLIA

INTRODUCTION

Since plants are sessile, the fitness of individuals within a population can be measured fairly easily. It is also relatively straightforward to measure at the individual level many of the ecological factors that determine fitness. Studies have documented variation in fitness as a result of individual differences in seed size (refs), germination time or order (Ross and Harper 1972), genotype (Turkington and Harper 1979, Aarssen and Turkington 1985), and microsite (Fowler and Antonovics 1981).

Because each plant interacts primarily with only a few near neighbors, biotic interactions can also profitably be studied at the individual level. The number, size, and distribution of nearby competitors significantly affect focal plant performance in natural populations (Hickman

1979, Waller 1981, Weiner 1982, 1984, Lorimer 1983, Matlack and Harper 1986, Goldberg 1987), in cultivated fields (Liddle et al. 1982, Firbank and Watkinson 1987), and in greenhouse flats (Mack and Harper 1977, Weiner 1982, Mithuen et al. 1984, Silander and Pacala 1985, Pacala and Silander 1987). Pacala and Silander (1985, Silander and Pacala 1985, Pacala 1986a,b, 1987) are laying a promising theoretical foundation for the study of competition at the neighborhood level.

In a number of the empirical studies, however, neighbors were found to be extremely poor predictors of focal plant performance despite their statistical significance. This is especially true of Waller (1981), Liddle et al. (1982), Firbank and Watkinson (1987), and Goldberg (1987), in which neighbors typically explained less than 25% of the variance in focal plant fecundity. It is uncertain whether these "failures" result from limitations of the neighborhood approach, or from the true unimportance of competition in the systems studied.

In this paper, I present the results of a neighborhood analysis of intra- and interspecific competition in an annual forb, Machaeranthera tanacetifolia (Asteraceae). Neighbors explained very little of the variance in fecundity in the population I studied; indeed, they appeared to set only an upper limit to fecundity. In the

second part of the paper, I present a simple graphical model to separate the effect of neighbors from that of all other factors affecting fecundity, and apply this model to a reanalysis of my data. The model reveals a number of new insights into the pattern of competitive effects within this population, and the way in which other factors can limit the expression of competition.

MATERIALS AND METHODS

Study site and species:

This study was conducted at the Appleton-Whittell Research Sanctuary, a 3160 ha ungrazed preserve at 1500 m elevation in semi-arid grassland 110 km southeast of Tucson, Arizona. Annual precipitation at the Sanctuary averages 436 mm (unpublished records), with approximately half to two thirds falling during the summer monsoon season of late June-September. The study site was an upland mesa with fairly uniform topography and few shrubs. Total plant cover was about 50% and consisted mostly of perennial grasses, especially Bouteloua gracilis, with lesser amounts of B. chondrosioides, Aristida spp., and Hilaria belangeri.

The focal species for this study was Machaeranthera tanacetifolia (Asteraceae), the most common annual species on the site in both years of the study. M. tanacetifolia germinates in winter or early spring, but grows primarily during the summer rainy season and flowers in late September and October. As is typical of arid-zone annuals, it shows large year-to-year variability in abundance, size, and fecundity. In the two years of my study, M. tanacetifolia individuals tended to be small (usually 4-10 cm in height) and relatively unbranched, with an average of only 3-5 flower heads, although a few individuals grew much larger.

Procedure:

This study employed 99 permanent quadrats measuring 0.5 m X 0.5 m, which were established in 1983 as part of another study. Most of these quadrats had been subjected to experimental removal of one or more grass or forb species in 1983, and these removals were maintained by repeated clipping during 1984 and 1985, the years of the study reported here. Because these removal treatments persisted throughout the course of this study, I assume they affected only the frequency with which M. tanacetifolia encountered various potential neighbor species, and not its response to those neighbors actually

present. Quadrats were mapped at the end of each year's growing season (in October 1984 and November 1985) by tracing the canopy outline of each individual of every species on a sheet of clear acetate held over the plot. A system of superimposed cross-hairs was used to minimize parallax in mapping. The number of flower heads was counted for each M. tanacetifolia individual, and this was also recorded on the maps.

Data Analysis:

For these analyses, I define the neighborhood of an individual as being a circle of specified radius, centered on the middle of that individual's canopy. Any plant whose canopy intersects that neighborhood is a neighbor of the focal plant, and its impact is assumed to be proportional to the area of intersection (the "neighbor area"). The effect of neighbors can thus be described by regressing focal plant fecundity (number of flower heads) against total neighbor area. Using digitized maps of each plot, I computed the neighbor area for each M. tanacetifolia individual for neighborhoods of 1, 2, 4, 6, 8, and 12 cm radius. These neighborhoods spanned a range of sizes from somewhat less than an average individual's canopy size to larger than the largest individual's canopy. The digitized

data were also used to compute the canopy area of each M. tanacetifolia individual.

Most recent analyses of competition at the neighborhood level (e.g. Weiner 1982, Silander and Pacala 1985, Pacala and Silander 1985, 1987, Pacala 1986a,b, Goldberg 1987) have used a hyperbolic form of this regression:

$$F = A/(1 + CN), \quad (1)$$

where F = fecundity of focal plant, N = number (or area) of neighbors), and A and C are empirically fitted parameters. This equation accommodates the non-linearity found in most data sets and also has an intuitively appealing interpretation, in which some fixed amount of resource (A) is divided among the focal plant and its neighbors (N , scaled by C , their resource-gathering ability relative to the focal plant). However, I found that the parameters fitted by this equation, and the proportion of the variance in fecundity explained by the regression, were highly sensitive to the precise location of just a few data points. Therefore, I employed a linear regression using log-transformed variables for my analyses:

$$\ln (F + 1) = a + b * \ln (N + 1), \quad (2)$$

where F = fecundity (measured as number of flower heads), and N = neighbor area. This equation gave generally

similar results to the hyperbolic equation, but proved to be more robust to small changes in the data.

I performed separate analyses for M. tanacetifolia neighbors and perennial grass neighbors, to distinguish between the effects of intra- and inter-specific competition. (Heterospecific neighbors other than grasses were rare.) Results from 1984 and 1985 were analyzed separately, to allow for the detection of year-to-year variability. In each case, my data analysis followed the protocol outlined below (c.f. Silander and Pacala 1985):

1. The most appropriate neighborhood size was chosen by regressing fecundity against neighbor area for each of the five neighborhood radii for which neighbor areas were calculated (1, 2, 4, 6, 8, and 12 cm). The "best" neighborhood size was that for which the regression explained the greatest proportion of the variance in fecundity.

2. The distance between individual plants may affect the intensity with which they compete. To see whether this was important within the best-sized neighborhood, I separated each neighborhood into concentric annuli, based on the radii for which I had measured neighbor areas (e.g. for an 8 cm neighborhood, annuli of 0-1, 1-2, 2-4, 4-6, and 6-8 cm). The neighbor area within each annulus was weighted by dividing by the median distance from the focal

plant to all points in that annulus or the square of that distance, and focal plant fecundity was regressed against this distance-corrected neighbor area measure as before. The amount of additional variation in fecundity that is explained by the inclusion of distance correction is a measure of the importance of distance to neighbors within the neighborhood.

3. Neighbors that are evenly distributed around the focal plant may exert a greater effect than neighbors that are clumped at one side (e.g. Mack and Harper 1977, Weiner 1982, Silander and Pacala 1985). I tested for the importance of angular dispersion of M. tanacetifolia neighbors using the formula given by Silander and Pacala (1935), except that the contribution of each neighbor to the index of angular dispersion was weighted by that neighbor's area.

4. Focal plants less than 8 cm from a plot boundary were excluded from all the preceding analyses, since at least some portion of their neighborhood was unknown. The only exception to this is that plants less than 12 cm from a boundary were excluded from comparisons of 8 and 12 cm neighborhoods. Once a best neighborhood size and any necessary corrections for neighbor distance and angular dispersion had been determined, I repeated the regression using all plants whose best-sized neighborhoods did not

intersect a plot boundary. Except when the best neighborhood radius was 8 cm, this resulted in the inclusion of more plants in the analysis.

RESULTS

The results of the neighborhood analyses for M. tanacetifolia neighbors and grass neighbors in the two years are shown in Figure 3. There was a statistically significant negative relationship between focal plant fecundity and the area of grass neighbors in both years, and of M. tanacetifolia neighbors in 1984 only. (Note that I selected the best of five regressions at different neighborhood radii; the critical probability value which gives an overall Type I error rate of .05 is $1 - (1 - .05)^{1/5}$, or .0102.) Best-fitting neighborhood radii were 2 cm for M. tanacetifolia neighbors and 8 cm for grass neighbors in 1984, and 4 cm for grass neighbors in 1985. For M. tanacetifolia neighbors in 1985, no neighborhood size gave a fit significantly different from random. In every case, corrections for distance to neighbors and for angular dispersion of neighbors failed to improve the fit of the regression.

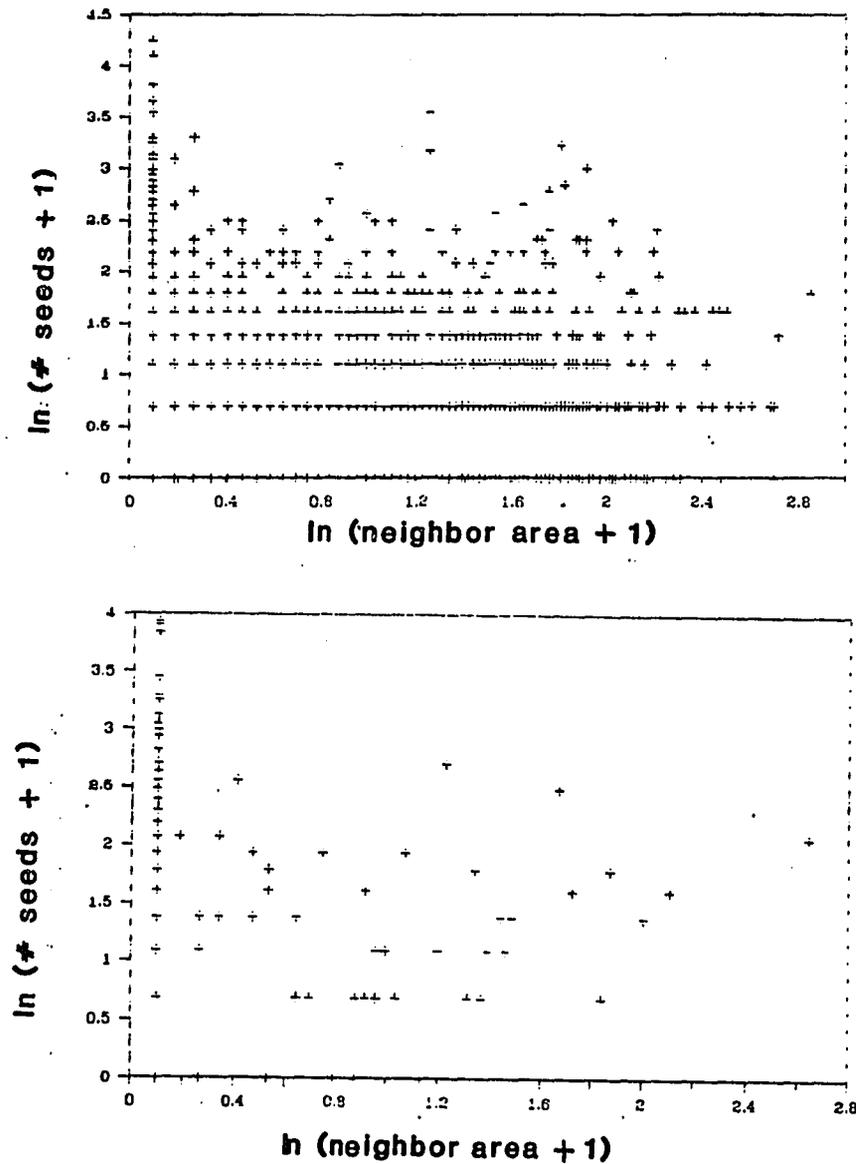
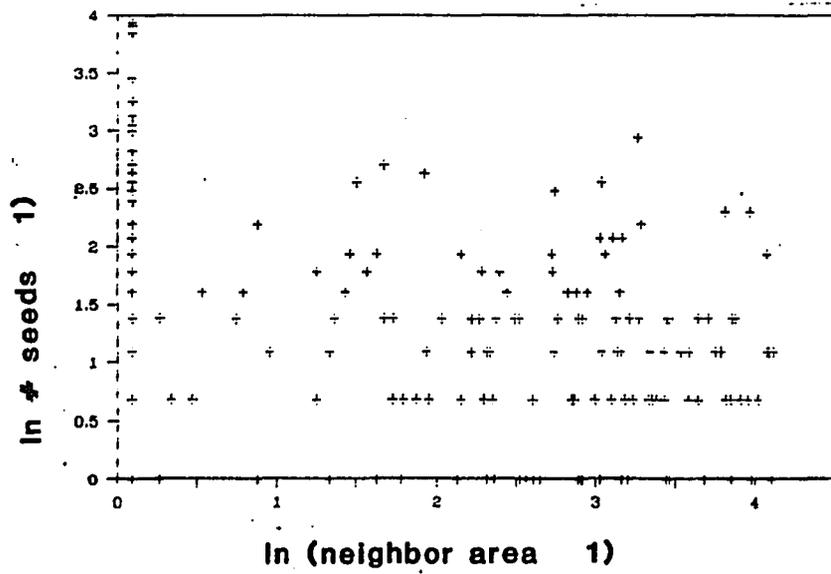
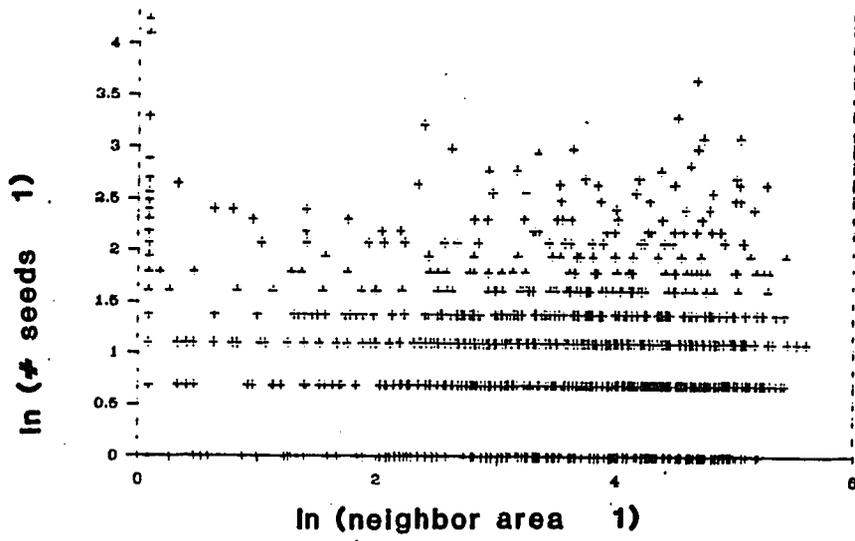


Figure 3. Fecundity of focal *M. tanacetifolia* individuals plotted against area of neighbors; both axes are log-transformed. Note that neighbors appear to set only an upper limit to fecundity. (a) Conspecific neighbors, 1984, 2 cm neighborhood radius ($r^2 = .0199$, $n = 2278$, $p < .0001$); (b) Conspecific neighbors, 1985, 2 cm neighborhood radius ($r^2 = .0006$, $n = 242$, $p = .7103$); (c) Grass neighbors, 1984, 8 cm neighborhood radius ($r^2 = .0090$, $n = 1184$, $p = .0010$); (d) Grass neighbors, 1985, 4 cm neighborhood radius ($r^2 = .0613$, $n = 214$, $p = .0002$).



THE MODEL

Motivation:

Competition from neighboring individuals clearly reduced the fecundity of M. tanacetifolia individuals at least some of the time (Fig. 3). However, neighbors explained only a small proportion of the variation in fecundity within the population I studied, despite the care taken to find the best neighborhood descriptor; values of r^2 range from .0090 to .0613 for the three cases where significant competitive effects were demonstrated. Is competition truly unimportant in this system, or does closer examination of the data show it to be more important than it appears at first glance?

In the three analyses in which I found a competitive effect of neighbors, competition appeared to constrain only the upper limit of fecundity. Most plants had few flower heads, regardless of the number of neighbors present, but plants with many flower heads were only found where there were few neighbors. That is, a lack of competition was a necessary but not a sufficient condition for high fecundity in this population; other biotic or abiotic factors must also have been involved in regulating fecundity. This pattern -- in which competition sets only an upper boundary to fitness -- appears to be quite prevalent in both natural

and experimental field populations (e.g. Waller 1981, Liddle et al. 1982, Goldberg 1987, Firbank and Watkinson 1987). The authors of the last three of these papers all suggest that this pattern results when factors other than competition also have important effects on an individual's performance; my interpretation agrees.

In the following section, I formalize this concept in a simple graphical model in which focal plant fitness is determined by the interaction between competition and a composite variable representing all other factors influencing fitness. The model provides a straightforward explanation for the "upper boundary" effect of competition, and makes interesting predictions about the role of competition in plant populations. After presenting the model, I apply it to my data and examine intrapopulation variation in the importance of competition.

The Model:

I model focal plant fitness as a function of two variables (Fig. 4): the number (or area) of competing neighbors, and "other factors" -- that is, a single-dimensional summary comprising microsite quality, seed size, germination order, genotype, amount of herbivory, and any other factor that might affect fitness. When other factors are favorable (Fig. 4, upper arrow), the

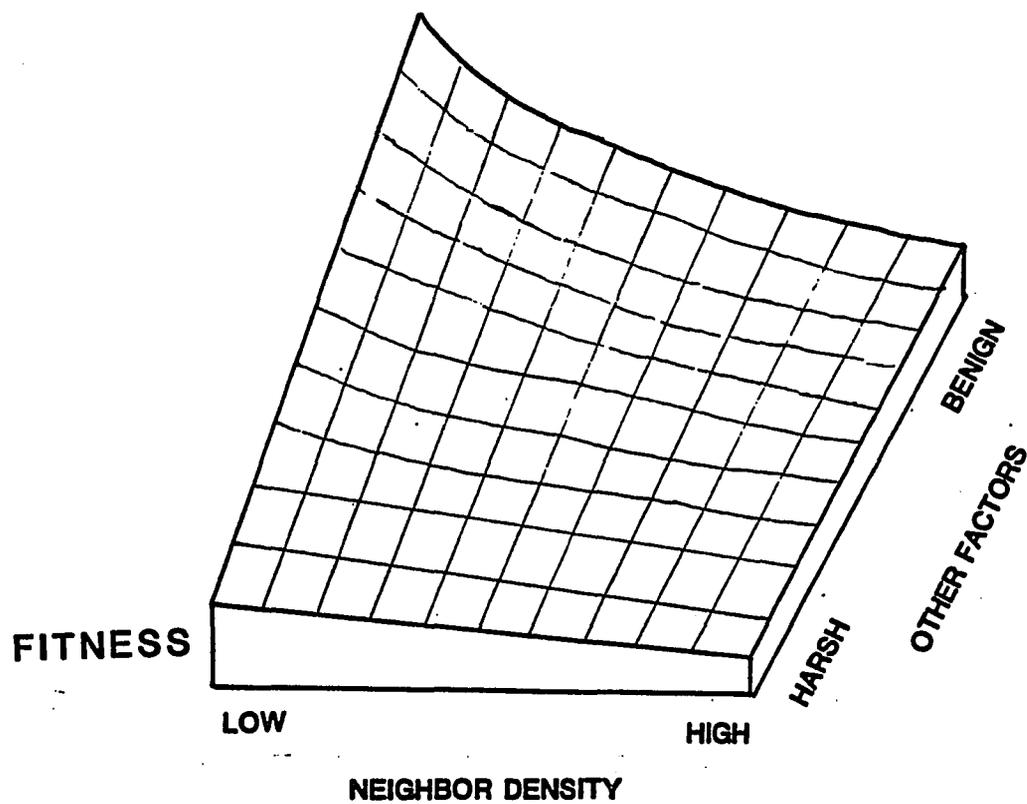


Figure 4. A graphical model of the interaction of competition and other factors in determining plant fitness. See text for explanation.

potential fitness of plants is high. As a result, increasing neighbor abundance can depress fitness substantially; competition is important here. On the other hand, when other factors are unfavorable (Fig. 4, lower arrow), all plants have low fitness, and neighbors therefore can have little effect. Studies which fail to consider variation in the harshness of other factors collapse the fitness surface shown in Fig. 4 into two dimensions (fitness vs. neighbors). This two-dimensional projection (cf. Fig. 3) would have the upper-boundary pattern and low r^2 values typical of neighborhood studies of competition.

Application to data:

It is difficult or impossible even to specify, let alone measure, all the factors that determine fitness in a natural population, and I did not attempt to do so in the population of M. tanacetifolia that I studied. Instead, I used an indirect approach to assign each plant a value for the harshness of "other factors", based on the assumption that differences in size among plants with the same amount of neighbors resulted from differences in the harshness of other factors. This assumption appears justified, since plants with few or no neighbors showed as much or more variation in size than plants with many neighbors; thus,

something other than competitive size hierarchies must have caused this variation. To perform the analysis, I first arrayed all focal plants in order of increasing neighbor area, and divided this array into intervals of twenty plants each. This procedure held the number of neighbors as constant as possible within each interval. The largest plant in each interval was, by assumption, the one for which other conditions were most favorable, and it was assigned a score of 1 for "other factors". Similarly, the second-largest plant within each interval received a score of 2, and so on down to the smallest of each 20-plant interval, which received a score of 20, indicating that other factors were at their harshest. Plants with the same other-factor score represent a subset of the population for which factors other than competition are held relatively constant; therefore, a regression of fecundity against neighbor area for each such subset measures the effect of competition at that particular level of harshness of other factors.

I performed this analysis for each of the two classes of neighbor (M. tanacetifolia and grasses) in each of the two years of my study. For 1984, I recognized 20 levels of harshness of other factors as described above; for 1985, because of much smaller sample sizes, I used only 6 levels for M. tanacetifolia neighbors, and 10 for grass neighbors.

I then regressed fecundity against neighbor area (using log-transformations as before) for each other-factor score separately.

Results:

The results of these analyses are shown in Figs. 5-8. In general, neighbors depress fecundity by a decreasing fraction as other factors become harsher -- that is, the slope of the relationship between neighbors and fecundity becomes less negative. This pattern is statistically significant for conspecific neighbors in 1984 (correlation between other-factor score and slope: $r = .684$, $n = 20$, $p < .0001$), and for grass neighbors in both years (1984: $r = .754$, $n = 20$, $p < .0001$; 1985: $r = .874$, $n = 10$, $p < .0001$). For conspecific neighbors in 1985, there is a strong trend in this direction, but it fails to reach statistical significance ($r = .775$, $n = 6$, $p = .070$).

The proportion of the total variation in fecundity that is explained by neighbor area also tends to decline as other factors become harsher, at least for conspecific neighbors in 1984 (correlation of other-factor score and regression r^2 : $r = -.547$, $n = 20$, $p = .0126$) and grass neighbors in 1985 ($r = -.810$, $n = 10$, $p = .0045$). For conspecific neighbors in 1985, a similar pattern appears to exist, except that there is a relatively high positive

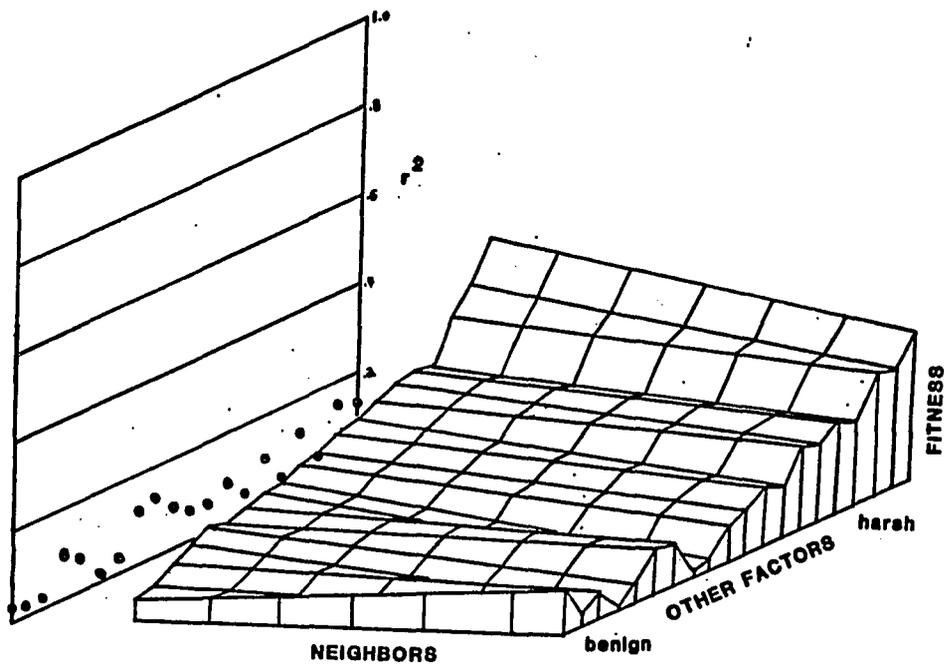


Figure 5. Fitness surface for effect of conspecific neighbors in 1984 (2 cm radius), showing the decline in fitness as neighbor area increases and as other factors become more harsh. The effect of neighbors diminishes as other factors become harsher. The figure shows the best linear fit to a regression of $\ln(\text{\# flower heads} + 1)$ vs $\ln(\text{neighbor area (cm)} + 1)$ for each value of "other factors". On left is a plot of r^2 for each regression.

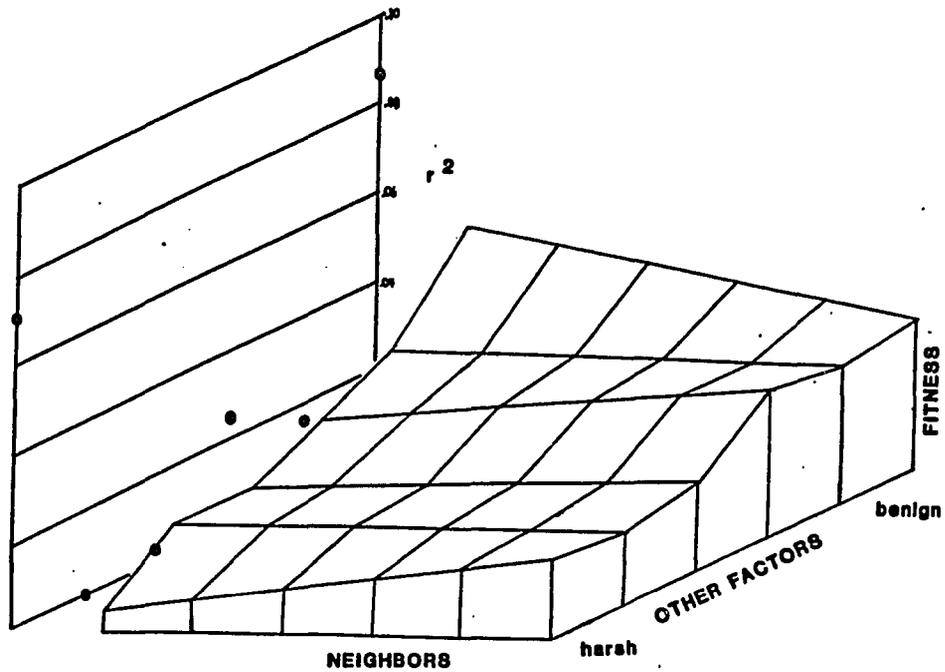


Figure 6. Fitness surface for effect of conspecific neighbors in 1985 (2 cm radius). See Figure 5 for details. Even though no significant effect was present for the population as a whole, a strong effect of neighbors appears to exist when other factors are most benign.

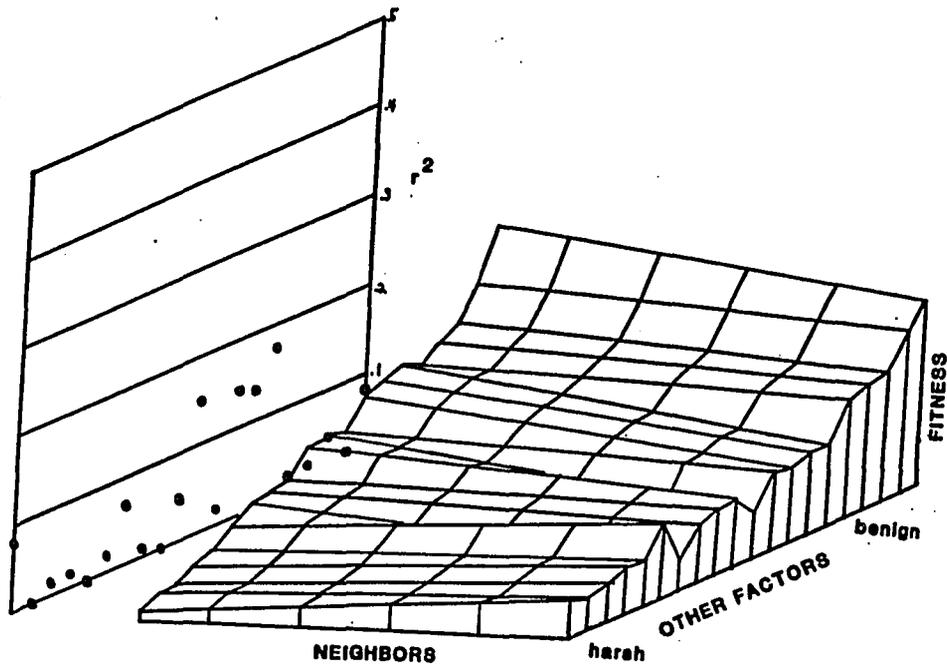


Figure 7. Fitness surface and plot of r^2 values for effect of grass neighbors in 1984 (8 cm radius).

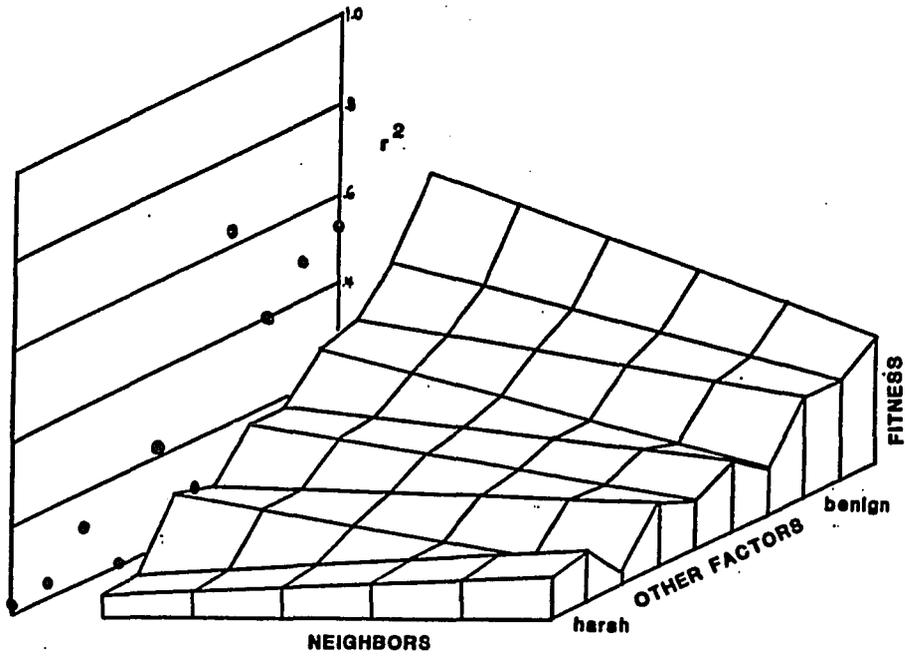


Figure 8. Fitness surface and plot of r^2 values for effect of grass neighbors in 1985 (4 cm radius).

correlation between fecundity and neighbor area when other factors are harshest. For grass neighbors in 1984, on the other hand, neighbor area explains the highest proportion of variance in fecundity for plants where other factors are intermediate in harshness.

DISCUSSION

Individual plants within this population of Machaeranthera tanacetifolia differed in their sensitivity to competition from neighboring conspecific and heterospecific plants. The effect of neighbors was most strongly felt when other factors were relatively favorable; as these other factors became harsher and themselves began to reduce the fitness of individuals, the role of competition declined. For the three cases in which there was clear evidence of competition (conspecific neighbors in 1984, and grass neighbors in both 1984 and 1985), a given quantity of neighbors had less effect on focal plant fecundity (i.e., the slope of a log-log regression of fecundity vs. neighbor area became less negative) as other factors became harsher (Figs. 5,7,8). For M. tanacetifolia neighbors in 1984 and grass neighbors in 1985, there was also a significant tendency for neighbors to explain less

of the variance in fecundity (regression r^2 declined) as other factors became harsher (Figs. 5,8). In the terminology of Welden and Slauson (1986), these represent decreases in the intensity and the importance of competition, respectively.

There is some suggestion of these patterns for conspecific neighbors in 1985 as well. A pronounced negative effect of neighbors was apparent for those plants for which other factors were most favorable, but appeared to be absent for all other plants; regression r^2 was also highest for the former group of plants. Thus, it seems likely that a subset of the population experienced significant intraspecific competition in 1985, even though little effect was apparent when examining the population as a whole (Fig. 6).

In every analysis, there was a tendency for neighbors to be positively related to fecundity when other factors were least favorable. There are three possible causes for this. First, under extremely harsh conditions, neighbors may have had a mutualistic effect on M. tanacetifolia, through shading the soil surface and preventing desiccation, for example. Such an effect, however, might be expected to be strongest at intermediate neighbor densities rather than at the highest densities as observed here; thus, this explanation appears improbable. Second,

plants with many neighbors may have died more often under harsh conditions, thus biasing upward the regression of fecundity (of surviving plants) on neighbor area. Neighborhood-level analyses of survivorship would address this question. Third, at this extreme of harshness, the presence of more neighbors might imply that the neighborhood was of slightly higher quality than if few or no neighbors were present. The positive relationship between neighbors and fecundity might then be due to a confounding of site quality and number of neighbors. This confounding might be expected to be most significant when site quality is extremely limiting to fitness and tends to overshadow any competitive effect.

In my analyses, I used an indirect method to estimate the fitness reduction due to competition: I assumed that variation in size among plants with similar neighbor areas resulted from variation in the harshness of these other factors. The presence of substantial variation in size even among plants without neighbors indicates that this variation is not merely the result of competitively-produced size hierarchies, but must be due in large part to other factors. Clearly, for a complete understanding of the way competition interacts with other factors affecting fitness, it is essential to single out particular factors (such as microsite, genotype, emergence time, etc.) and

measure their favorability directly. On the other hand, much can be learned, especially at the early stages of investigation, from the use of an indirect measure of favorability such as plant size. Such a measure integrates the effects of all factors influencing fitness, even if the identity of these factors and their possibly complex interactions cannot be fully specified.

However, since plant size is closely correlated with reproductive output ($r^2 = .915$ in 1985), its use as an index of the harshness of other factors introduces some artifacts into the analyses shown in Figs. 5-8. Giving plants other-factor scores based on size almost directly reduces variation in fecundity: for a given quantity of neighbors, the largest (and therefore usually the most fecund) plants are assigned a score of 1, the next largest and most fecund a score of 2, and so forth. Thus, neighbors inevitably explain a higher proportion of the variance in fecundity within other-factor levels than in the population taken as a whole. In contrast, the patterns of decreasing negative regression slope and decreasing r^2 with increasing harshness of other factors do not follow necessarily from the analytic methods employed. Instead, these results represent real patterns, valid descriptions of the manner in which competitive effects are expressed across individuals within a population.

Since this study used naturally-occurring individuals whose density was not manipulated during the study, some confounding of the effects of neighbor density and site quality was inevitable (e.g. Mitchell-Olds 1987). Plants with few and/or small neighbors were likely to be occupying relatively poorer sites on average than plants with many and/or large neighbors, leading to an underestimation of the effect of neighbors. However, this bias is unlikely to affect the general pattern of neighbors setting only an upper bound to fecundity, or my interpretation of that pattern. Indeed, Goldberg (1987) found a similar upper-limiting effect of neighbors for Solidago canadensis, even though she controlled for this confounding by using only high-density plots and thinning to produce a range of neighbor densities.

The effect of competition diminished -- in both absolute and relative terms -- as other factors became more restrictive in the population of M. tanacetifolia that I studied. If this is true of other systems as well, it suggests a general explanation for the wide variety of outcomes observed in studies of neighborhood competition. Individuals of a plant species are able to inhabit microsites spanning a range of soil moisture availability, nutrients, soil depth, insolation, etc.; likewise, individuals differ in seed size, germination time, degree

of herbivory, and access to mutualists. As these and other factors affecting fitness vary, they can affect the potential for competition to be expressed. Four broad classes of outcome can be distinguished (Fig. 9).

1) If conditions are harsh enough that the fitness of almost all individuals is limited by some factor other than the number of neighbors, no pattern will be evident in regressions of fitness against neighbors (Fig. 9, inset 1). For example, Mitchell-Olds (1987) found that over 50% of the variance in biomass of greenhouse-grown Impatiens capensis after 3 months of growth was explained by their biomass early in growth -- that is, by some combination of seed size, germination time, and intrinsic growth rate; site quality (pot effects) explained only 15% of variation in final biomass, and competition (size of potmate) explained a statistically insignificant 2.5%. Note, however, that in cases where no effect of competition is apparent for the population as a whole, further analysis using the model presented here may reveal that neighbors affect a small subset of the population, as was seen for M. tanacetifolia neighbors in 1985 (Fig. 6).

2) If the conditions experienced by individuals in a population span a wide range from favorable to harsh, then neighbors should appear to set only an upper bound to fitness (Fig. 9, inset 2). This is the pattern seen in M.

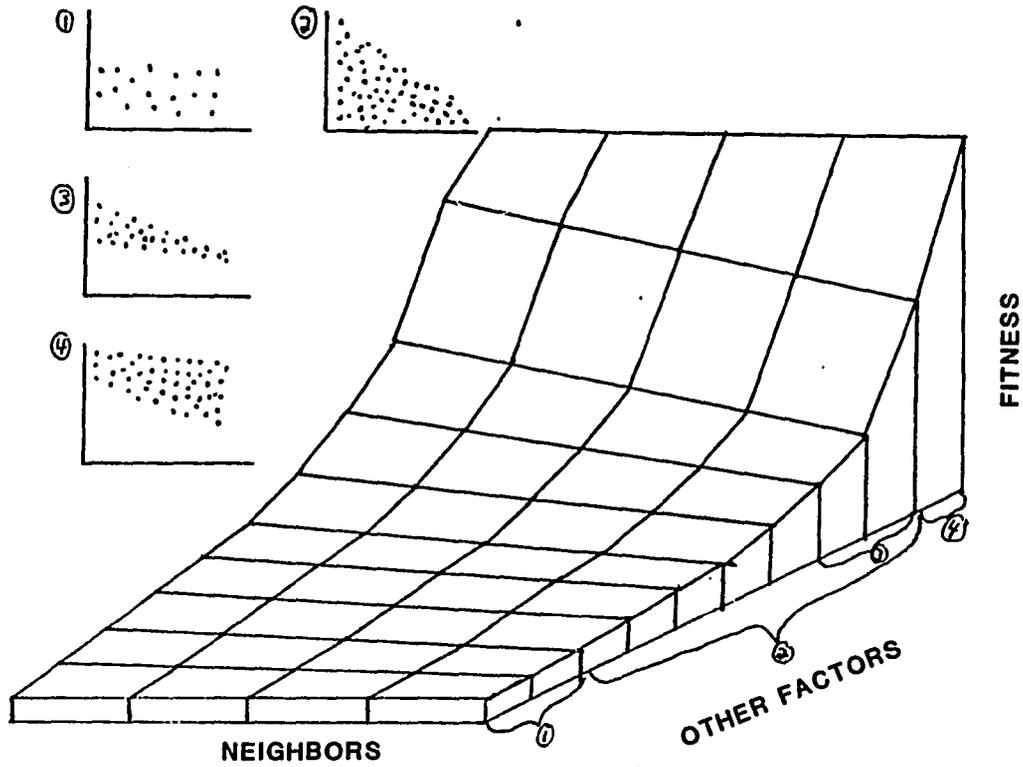


Figure 9. General model for the interaction between neighbors and other factors in determining plant fitness. The four numbered insets show the two-dimensional pattern that results when fecundity (vertical axis) is plotted against neighbor area (horizontal axis) for populations spanning different ranges of harshness of other factors.

tanacetifolia (Fig. 3). A survey of published neighborhood analyses of competition supports this hypothesis: All of the studies reporting an upper-limiting effect of neighbors (Waller 1981, Liddle et al. 1982, Goldberg 1987, Firbank and Watkinson 1987, and the present study) involved either natural populations or cultivated fields, where plants are likely to experience more variable conditions than in the greenhouse.

3) If the individuals in a population experience a relatively narrow range of conditions, there will be correspondingly little variation in fitness along this dimension. Any effect of competition in such a population should be readily apparent, and a regression of fitness against the quantity of neighbors should account for a high proportion of the variation in fitness (Fig. 9, inset 3). This may explain the high r^2 values often obtained in neighborhood studies of competition in the greenhouse (e.g. Mack and Harper 1977, Weiner 1982, Mithuen et al. 1984, Silander and Pacala 1985, Pacala and Silander 1987). Some natural populations may also experience relatively little variability of conditions among individuals, which would lead to similar outcomes (e.g. Hickman 1979, Weiner 1982; note that Weiner's analyses included only individuals with exclusively conspecific neighbors, and from a single patch, thus restricting microsite variability further). The

growth of forest trees is also often well explained by neighbors (Lorimer 1983, Weiner 1984). Since trees experience their environment at a relatively large spatial and temporal scale, they may average out much of the microspatial and short-term temporal differences which affect the annual herbs used in most other neighborhood studies.

4) If conditions are so favorable that some plants are unaffected by competition across the entire range of neighbor densities encountered, neighbors might affect the fitness of only those plants for which conditions are least favorable. In this case, neighbors would appear to set a lower limit to fitness (Fig. 9, inset 4). This case is the least likely to be encountered in nature, however, and I know of no studies reporting this pattern.

I have argued thus far that harshness of other factors may limit the possibility for competition to be expressed within the population. However, this argument can equally well be made in reverse -- the presence of severe competition limits the fitness effect of variability of other factors. This suggests that the various factors affecting reproductive success in this population (and others with similar behavior) might best be thought of as a series of sieves. To attain high reproductive success, a

plant must pass through all sieves successfully: have few conspecific and heterospecific neighbors, find a good microsite, avoid herbivory, have a good match of genotype to environment, etc. If a plant fails to pass any one of these sieves, it is doomed to relatively low fitness, regardless of its performance on the others. A selective regime such as this would place severe constraints on the tradeoffs a species can make in adapting to particular features of its environment.

This model of plant competition draws attention to variation in competitive effects within populations, and the way in which variation in other factors important to fitness can mask the effect of competition over the population as a whole. The model provides a general conceptual framework for integrating the effects of competition and other factors, and emphasizes the need to understand the variation in environmental harshness experienced by individuals within a population, and how these affect the expression of a single factor. It remains to be learned how general the model is, and whether there are other patterns of change in competitive effect as the harshness of other factors increases.

LITERATURE CITED

- Aarssen, L.W., and R. Turkington. 1985. Biotic specialization between neighboring genotypes in Lolium perenne and Trifolium repens from a permanent pasture. *J. Ecol.* 73: 605-614.
- Cable, D.R. 1975. Influence of precipitation on perennial grass production in the semidesert Southwest. *Ecology* 56: 981-986.
- Connell, J.H. 1983. On the prevalence and relative importance of interspecific competition: Evidence from field experiments. *Amer. Natur.* 122: 661-696.
- Cutler, J.M., and D.W. Rains. 1977. Effect of irrigation history on responses of cotton to subsequent water stress. *Crop Sci.* 17: 329-335.
- Detling, J.K., W.J. Parton, and H.W. Hunt. 1978. An empirical model for estimating CO₂ exchange of Bouteloua gracilis (H.B.K.) Lag. in the shortgrass prairie. *Oecologia* 33: 137-147.
- Ehleringer, J.R. 1984. Intraspecific competitive effects on water relations, growth, and reproduction in Encelia farinosa. *Oecologia* 63: 153-158.
-

- Firbank, L.G., and A.R. Watkinson. 1987. On the analysis of competition at the level of the individual plant. *Oecologia* 71: 308-317.
- Fonteyn, P.J., and B.E. Mahall. 1978. Competition among desert perennials. *Nature* 275: 544-545.
- Fonteyn, P.J., and B.E. Mahall. 1981. An experimental analysis of structure in a desert plant community. *J. Ecol.* 69: 883-896.
- Fowler, N. 1986. The role of competition in plant communities in arid and semiarid regions. *Ann. Rev. Ecol. Syst.* 17: 81-110.
- Fowler, N.L. and J. Antonovics. 1981. Small-scale variability in the demography of transplants of two herbaceous species. *Ecology* 62: 1450-1457.
- Friedman, J., and G. Orshan. 1974. Allopatric distribution of two varieties of Medicago laciniata (L.) Mill. in the Negev desert. *J. Ecol.* 62: 107-114.
- Goldberg, D.E. 1987. Neighborhood competition in an old-field plant community. *Ecology* 68: 1211-1223.
- Hickman, J.C. 1979. The basic biology of plant numbers. Pp. 232-263 in O.T. Solbrig, S.K. Jain, G.B. Johnson, and P.H. Raven (eds.), *Topics in plant population biology*. Columbia University Press, New York.

- Hsiao, T.C., and E. Acevedo. 1974. Plant responses to water deficits, water-use efficiency, and drought resistance. *Agric. Meteorol.* 14: 59-84.
- Inouye, R.S., G.S. Byers, and J.H. Brown. 1980. Effects of predation and competition on survivorship, fecundity, and community structure of desert annuals. *Ecology* 61: 1344-1351.
- Lauenroth, W.K., J.L. Dodd, and P.L. Sims. 1978. The effects of water- and nitrogen-induced stresses on plant community structure in a semi-arid grassland. *Oecologia* 36: 211-222.
- Liddle, M.J., C.S.J. Budd, and M.J. Hutchings. 1982. Population dynamics and neighborhood effects in establishing swards of Festuca rubra. *Oikos* 38: 52-59.
- Lorimer, C.G. 1983. Tests of age-independent competition indices for individual trees in natural hardwood stands. *Forest Ecol. and Management* 6: 343-360.
- Mack, R.N., and J.L. Harper. 1977. Interference in dune annuals: spatial pattern and neighborhood effects. *J. Ecol.* 65: 345-363.
- Matlack, G.R., and J.L. Harper. 1986. Spatial distribution and the performance of individual plants in a natural population of Silene dioica. *Oecologia* 70: 121-127.
-

- McMahon, J.A., and D.J. Schimpf. 1980. Water as a factor in the biology of North American desert plants. Pp. 114-171 in D. Evans and J. Thames (eds.), Water in desert ecosystems. Dowden, Hutchinson, and Ross, Stroudsburg, Pennsylvania.
- Mitchell-Olds, T. 1987. Analysis of local variation in plant size. *Ecology* 68: 82-87.
- Mithuen, R., J.L. Harper, and J. Weiner. 1984. Growth and mortality of individual plants as a function of "available area". *Oecologia* 62: 57-60.
- Nobel, P.S. 1981. Spacing and transpiration of various sized clumps of a desert grass, Hilaria rigida. *J. Ecol.* 69: 735-742.
- Pacala, S.W. 1986a. Neighborhood models of plant population dynamics. 2. Multispecies models of annuals. *Theor. Pop. Biol.* 29: 262-292.
- Pacala, S.W. 1986b. Neighborhood models of plant population dynamics. 4. Single-species and multispecies models of annuals with dormant seeds. *Amer. Nat.* 128: 859-878.
- Pacala, S.W. 1987. Neighborhood models of plant population dynamics. 3. Models with spatial heterogeneity in the physical environment. *Theor. Pop. Biol.* 31:359-

- Pacala, S.W., and J.A. Silander, Jr. 1985. Neighborhood models of plant population dynamics. 1. Single-species models of annuals. *Amer. Nat.* 125: 385-411.
- Pacala, S.W., and J.A. Silander, Jr. 1987. Neighborhood interference among velvet leaf, *Abutilon theophrasti*, and pigweed, *Amaranthus retroflexus*. *Oikos* 48: 217-224.
- Ritchie, J.T. 1981. Water dynamics in the soil-plant-atmosphere system. Pp. 81-96 in J. Monteith and C. Webb (eds.), *Soil water and nitrogen*. Dr. W. Junk, The Hague.
- Robberecht, R., B.E. Mahall, and P.S. Nobel. 1983. Experimental removal of intraspecific competitors -- effects on water relations and productivity of a desert bunchgrass, *Hilaria rigida*. *Oecologia* 60: 21-24.
- Ross, M.A., and J.L. Harper. 1972. Occupation of biological space during seedling establishment. *J. Ecol.* 60: 77-88.
- Sala, O.E., W.K. Lauenroth, W.J. Parton, and M.J. Trlica. 1981. Water status of soil and vegetation in a shortgrass steppe. *Oecologia* 48: 327-331.
- Schoener, T.W. 1983. Field experiments on interspecific competition. *Amer. Nat.* 122: 240-285.

- Scholander, P.F., H.T. Hammel, E.D. Bradstreet, and E.A. Hemmingsen. 1965. Sap pressure in vascular plants. *Science* 148: 339-346.
- Silander, J.A., Jr., and S.W. Pacala. 1985. Neighborhood predictors of plant performance. *Oecologia* 66: 256-263.
- Toft, C.A., and P.J. Shea. 1983. Detecting community-wide patterns: Estimating power strengthens statistical inference. *Am. Natur.* 122: 618-625.
- Turkington, R., and J.L. Harper. 1979. The growth, distribution and neighbor relationships of Trifolium repens in a permanent pasture. IV. Fine-scale biotic differentiation. *J. Ecol.* 67: 245-254.
- Waller, D.M. 1981. Neighborhood competition in several violet populations. *Oecologia* 51: 116-122.
- Weiner, J. 1982. A neighborhood model of annual plant interference. *Ecology* 63: 1237-1241.
- Weiner, J. 1984. Neighbourhood interference amongst Pinus rigida individuals. *J. Ecol.* 72: 183-195.
- Welden, C.W., and W.L. Slauson. 1986. The intensity of competition versus its importance: an overlooked distinction and some implications. *Quart. Rev. Biol.* 61: 23-44.

Yeaton, R.I., and M.L. Cody. 1976. Competition and spacing
in plant communities: the northern Mojave Desert. J.
Ecol. 64: 689-696.

Yeaton, R.I., J. Travis, and E. Gilinsky. 1977.
Competition and spacing in plant communities: the
Arizona upland association. J. Ecol. 65: 587-595.