

still provides sound justification for calling attention to the importance of these kinds of interactions.

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HOW COMPETITION FOR LIGHT AND NUTRIENTS AFFECTS SIZE VARIABILITY IN *IPOMOEA TRICOLOR* POPULATIONS¹

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Because of the correlation between fitness (i.e., survivorship and fecundity) and size within plant populations, the determinants of size differences are of great interest. One of the ecological factors that affects size variability is competition, also termed interference. A recent review found that plants grown at higher densities showed greater size variability than plants grown at lower densities in 14 out of 16 published experiments (Weiner and Thomas 1986). Little is known about the mechanisms by which competition increases size variability. I advanced the hypotheses that competition for light is “asymmetric” and will increase the variability in plant size over that of noncompetitive situations, whereas competition for nutrients is “two-sided” and will reduce size variability (Weiner 1985). To test these

hypotheses I performed an experiment with the annual vine *Ipomoea tricolor* in which root and shoot competition were separated.

In “asymmetric” (Begon 1984) or “one-sided” competition large individuals are able to obtain more resources than their share (based on relative size) and to suppress the growth of smaller individuals. If plant competition is one-sided, plants grown with competition should show greater size inequality than plants grown without competition in the absence of density-dependent mortality. In two-sided competition, resources are shared equally or in proportion to size. If plant competition is two-sided, competing plants should show the same or lower size variability than noncompeting plants (Weiner and Thomas 1986). Thus, symmetry or asymmetry is a characteristic of among-individual competition that can be observed at the population level.

Materials and Methods

Populations of *Ipomoea tricolor* Cav. var. “Pearly Gates” were grown under four competitive regimes. These were (1) no competition: one individual per container, with one stake, which it climbed; (2) shoot competition only: eight individuals, each in its own container, placed in a closed circle around one stake, which all eight plants climbed; (3) root competition only: eight

TABLE 1. The effect of shoot and root competition on size inequality in 57-d-old experimental populations of *Ipomoea tricolor*. Means and medians are significantly different ($P < .01$) except for those connected by a common underline. Significant differences in the Coefficient of Variation (cv) and Gini Coefficient (G) are denoted by arrows with * ($P < .05$) or ** ($P < .01$).

	Treatment			
	Individually grown	Shoot competition	Root competition	Shoot + root competition
No. plants	21	24	21	29
Dry mass of aboveground plant tissue (g)				
Mean	6.34	4.84	1.42	1.26
Median	6.28	5.05	1.37	1.26
cv (%)	14.0	24.5	19.4	25.1
G	0.081	0.139	0.112	0.143

individuals per container, each climbing one of eight different stakes, which were placed around the periphery of the container in a circle with a radius of 0.4 m; (4) root and shoot competition: eight individuals per container, all of which climbed the same single stake. Sample size was 21 for treatment 1; there were three replicates for treatments 2 and 3 and four replicates for treatment 4. Plants were grown in a soil medium of 50% sterilized loam and 50% Pro-mix in 1-L, 14.4 cm deep containers in a glasshouse at the United States Department of Agriculture Research Center in Beltsville, Maryland, USA. Seeds were sown at twice the desired densities on 28 February 1985, and seedlings were thinned to the appropriate densities immediately after germination. Pots were kept well watered and, when they were large enough, the plants were placed so that they were touching the stakes. Six plants died from disease within the first few weeks and these were excluded from the analyses. On 26 April each plant was cut at soil level and placed in a paper bag. Plants were dried in an oven for 2 d at 70°C and then weighed. Size variability is best evaluated in terms of measures of inequality (Weiner and Thomas 1986); these include the Coefficient of Variation ($CV = SD/\bar{x}$, where SD is the standard deviation and \bar{x} is the mean; Sen 1973) and the Gini Coefficient ($G = \frac{\sum_{i=1}^n \sum_{j=1}^n |x_i - x_j|}{[2 \bar{x} n(n-1)]}$), where n is the number of individuals and x_i and x_j are the sizes of individuals i and j , respectively; Weiner

and Solbrig 1984). Confidence intervals for CV and G were obtained using the "bootstrap" method (Efron 1982, Diaconis and Efron 1983). In this technique, the statistic is calculated for each of 1000 artificial samples of the same size as the original sample, which are taken from the original sample with replacement. Confidence intervals for the statistic are determined from the distribution of the bootstrapped estimates of the statistic, using a bias correction (Efron 1982).

Results and Discussion

Competitive regime had a highly significant effect on dry mass distribution ($P < .001$, Kruskal-Wallis test). With one exception (comparison of treatments 3 and 4), the dry mass distribution for each treatment was significantly different from that of every other treatment ($P < .001$, Wilcoxon two-sample tests). Root competition was far more severe than shoot competition in its effect on plant size, but it did not have a significant effect on size variability as measured by the Gini Coefficient or the Coefficient of Variation (Table 1, Fig. 1). Visible effects of root interference were observed soon after germination, whereas competition for light began only after plants were large enough to shade one another. While shoot competition did not reduce mean plant size as much as root competition did, it did result in a significant increase in size variability

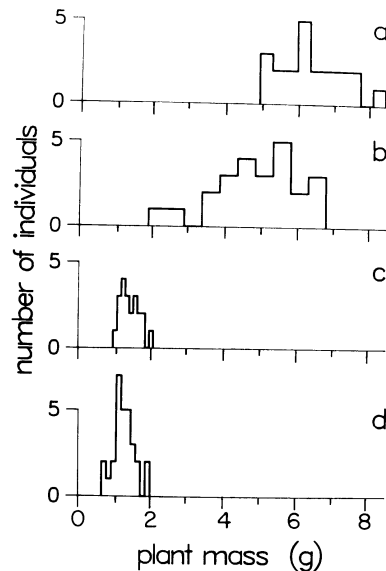


FIG. 1. Dry mass distributions for experimental populations of *Ipomoea tricolor* grown (a) without competition, (b) with shoots competing, (c) with roots competing, (d) with both shoots and roots competing. Each population is divided into 10 equal size classes, from the minimum to the maximum value.

over plants grown without competition ($P < .05$). Plants suffering from both root and shoot competition were not significantly smaller than those suffering from root competition only, but they showed the greatest size variability. In plants competing both above and below ground, root competition accounted for the reduction in mean plant size, but shoot competition accounted for the increase in size inequality. The results support the hypothesis that competition for light is "asymmetric" and that the observed increases in plant size variability with increasing density may have been primarily due to competition for light.

There may be situations in which competition for nutrients is also asymmetric, i.e., situations in which nutrients can be preempted by individuals with larger roots. Because a leaf is shaded only by leaves above it, competition for light appears to be inherently asymmetric.

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ELASTICITY: THE RELATIVE CONTRIBUTION OF DEMOGRAPHIC PARAMETERS TO POPULATION GROWTH RATE¹

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In their study of the population dynamics of three closely related species of *Ranunculus*, using stage-classified matrix projection models, Sarukhan and Gadgil (1974) tried to measure the relative importance of sexual and vegetative reproduction. To do so they multiplied the matrix coefficients corresponding to each mode of reproduction by a certain factor, and compared the resulting shifts in population growth rate (λ). To make the results comparable for different species, the growth rates were normalized to unity. In effect,

they calculated the proportional change in λ resulting from a proportional change in each of the reproductive pathways. Similar numerical perturbation experiments have been reported by Hartshorn (1975), Enright and Ogden (1979), Bierzychudek (1982), and others.

A more analytical approach (Caswell 1978) is to calculate directly the sensitivity of λ to changes in elements of the population projection matrix:

$$s_{ij} = v_i w_j / \langle v, w \rangle = \partial \lambda / \partial a_{ij} \quad (1)$$

where s_{ij} is the sensitivity, a_{ij} is the (i, j) element of the matrix A , and v and w are the dominant left and right eigenvectors, respectively. This sensitivity measures the impact on the growth rate λ of an infinitesimal change in the transition a_{ij} , relative to the impact of equal absolute changes in other elements. It is related to models of selection (Lande 1982), and can thus be used to evaluate the hypothetical pressure of natural selection on the various life history traits. Applied in a number of studies (e.g., Caswell and Werner 1978, Tuljapurkar 1982, Caswell 1983, Schmidt and Lawlor 1983, Pinero et al. 1984, Ebert 1985), the sensitivity index has proved important in the theory of life history.