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LOCAL DENSITY VARIATION MAY MIMIC EFFECTS OF ASYMMETRIC COMPETITION ON PLANT SIZE VARIABILITY

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Plants grown at higher densities are usually smaller (Harper 1977, Silvertown 1987) and show greater size variation (Weiner and Thomas 1986) than do plants grown at lower densities for the same period of time. The increase in size variability in populations grown at higher densities has been interpreted as strong support for the hypothesis that competition between plants is "asymmetric" or "one-sided," i.e., that larger plants are able to obtain a disproportionate share of resources (relative to their size differences) and suppress the growth of smaller individuals (Weiner and Thomas 1986, Weiner 1986). In this note we present the results of two models of plant competition which suggest an alternative explanation under some conditions: variation in local density due to non-uniform spatial pattern may result in increases in size variation at higher densities even if competition is "symmetric."

Model 1—Plant Size Proportional to "Available Area"

Methods. In this simple static model we assumed that plants were distributed randomly in two-dimensional space, and that they attained a certain maximum size (with a variance) if they had more area available than they could use. Available area was determined by Voronoi (or Thiessen) polygons (Mead 1966, Rhynsburger 1973, Liddle et al. 1982, Mithen et al. 1984) which define the total two-dimensional area which is closer to each plant than to any other. The maximum plant size in the absence of competition was set at 100 "mass units" with a coefficient of variation of 20%: plants achieved this size if they had 10 or more "area units" available. If an individual plant's polygon area was <10 area units, the plant's size was then reduced proportionally from what it would have been if the maximum useable area had been available. Plant sizes were analyzed for three densities: very low (0.038 plants/unit area; virtually no plants competing), low (0.105 plants/unit area; approximately 50% of the plants competing), and high (0.419 plants/unit area; all plants competing). Size variability was measured as the coefficient of variation (Weiner and Thomas 1986).

Results. When the density was very low and all plants inhabited polygons which were greater in area than the maximum area which a plant could utilize, the variation in sizes was determined by the model's inherent size variation (Fig. 1a). As the density was increased, some plants had polygons smaller than the maximum utilizable area, while individuals in larger polygons achieved their maximum potential size; this resulted in greater size variation than in the absence of competition (Fig. 1b). As density was increased further, all polygons were smaller than the maximum useable area, resulting in further increases in size inequality, as the distribution of plant sizes reflected the distribution of polygon sizes (Fig. 1c). Increases in density beyond this point resulted in no further changes

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in size variability, because density does not affect the relative distribution of polygon sizes generated from random points.

Model 2—A Computer Simulation of Plant Growth and Competition

Methods. A growth-simulation model was used to show how symmetric vs. asymmetric division of available resources can result in differential growth of plants and changes in size inequalities with time. In this model, plants were simulated as seedlings growing in two-dimensional space. The size of an individual (W) was proportional to the two-dimensional area it covered. The amount of resources (R) obtained at time t by each individual plant was used to determine the size in the next time period (W_{t+1}):

$$W_{t+1} = 1.70(R_t) - b(R_t)^2$$

where b was randomly assigned to each plant and normally distributed with a mean of 0.0035 and a standard deviation of 0.00013. The amount of resources obtained (R_t) was equal to the area occupied only by this individual (S_u) plus a proportion of the space shared with other individuals (S_c):

$$R_t = S_u + S_c$$

Noncompeting plants grew sigmoidally to an average maximum size of 200 units^2 with a coefficient of variation of 4.06%. The degree of competitive asymmetry reflected how resources in shared areas (from S_c) were divided between or among individuals. In asymmetric competition, the largest individual usurped all of the resources in an area of overlap. In symmetric competition, resources in an area of overlap were shared equally by all plants that co-occurred in that area. The term "symmetric competition" has also been used in several other studies to describe a situation in which contested resources are shared by individuals in proportion to their sizes (Weiner and Thomas 1986). Equal sharing irrespective of size, as in this model, is even more symmetric. Plants were initiated as seedlings with a mean size of 2.0 units^2 and a coefficient of variation of 8.5% and then grown for 15 discrete time-units. Plants could not decrease in size: if W_{t+1} was less than W_t, then W_{t+1} was set equal to W_t. This model is similar in structure to that of Firbank and Watkinson (1985; see also Yodzis 1978). The model was run for all combinations of (1) two spatial patterns: hexagonal (uniform) and random, (2) five densities (0.001, 0.01, 0.032, 0.10, and 0.16 individuals/unit^2), and (3) two competitive symmetries: symmetric and asymmetric. A population of 100 individuals was used for each of five replicate runs of the simulation, with the total area being varied to obtain the desired densities. To reduce possible edge effects, simulation runs included an additional border area 10 units wide in which plants were located and grown in a similar fashion, but not included in the analysis. Size variability was measured as the coefficient of variation.

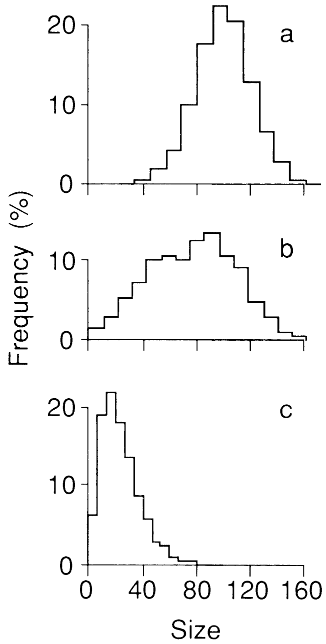

FIG. 1. Increase in size variability with increasing density in a "two-sided" model of plant interference based upon Voronoi polygons around randomly dispersed points (model 1). When all plants had polygons greater than the maximum area which could be utilized (a), there was no competition and sizes were distributed in a random normal fashion with a mean of 100 units and a coefficient of variation of 20%. As the density was increased (b), some individuals were still able to achieve their maximum potential size, whereas others had polygons smaller than the maximum useable area (CV = 41%). At higher densities (c), all plants had polygons smaller than the utilizable area (CV = 60%).

Results. Density-dependent behavior in the model appeared to be consistent with that commonly found in real plant populations. For all combinations of planting arrangement and competitive symmetry, total yield increased with density and appeared to be close to the maximum yield at the highest density investigated. Growth of individual plants followed a sigmoidal curve, reaching a smaller asymptote at higher densities.

When the spatial pattern of plants was hexagonal, there was a major increase in size variability when competition was asymmetric (Fig. 2a). The coefficient of variation increased from 4% at the lowest density to almost 150% at the highest density. However, when competing plants in a hexagonal pattern shared contested resources equally, there was no major effect of density on size variability.

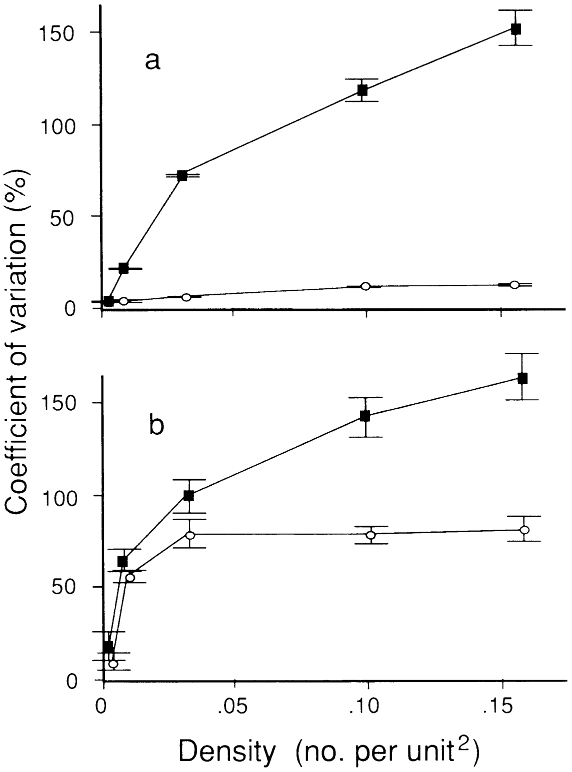

FIG. 2. Relationship between plant density and size inequality in the growth simulation model (model 2) for (a) hexagonal and (b) random planting arrangements. ■ = asymmetric competition; ○ = symmetric competition. Values shown are the means and ranges of five replicate runs of the model.

When the spatial pattern was random and competition was asymmetric, size variation always increased with density (Fig. 2b). With a random spatial pattern and symmetric competition, size variation also increased at low densities, but leveled off at a relatively constant variation at higher densities. Inequality in size was always higher for asymmetric than for symmetric competition.

Discussion

Both models suggest that variation in local density can generate size variability even if competition is symmetric. In the polygon model (model 1), in which competition is symmetric, size variability increases as the number of plants experiencing competition increases. At densities greater than that at which all plants are experiencing competition (i.e., densities resulting in "constant final yield"), there is no further increase in size variability with increasing density. Thus, the results at higher, but not lower, densities are consistent with the predictions of Weiner and Thomas (1986). If the spatial pattern were uniform, such that all polygon sizes were equal, density would have no effect on size variability in this model.

The simulation model of plant growth and interference (model 2) also demonstrates that, at lower densities and with random spatial patterns, size variation can increase with density if interactions are either symmetric *or* asymmetric. However, where the spatial pattern is regular, only asymmetric competition can lead to increases in size variation with density. Similar results were obtained from an exponential model of plant growth with symmetric competition and a Poisson distribution of local density (Huston 1986). At higher densities (above 0.032 individuals/unit^2) our second model shows increases in size variation only when competition is asymmetric.

Thus these models suggest that the conclusions of Weiner and Thomas (1986) may need to be qualified. According to our models, an observed increase in size variability at higher densities provides strong support for the hypothesis that competition is asymmetric only if (1) the increase in variation occurs over relatively high densities or (2) if the spatial pattern is uniform.

Unfortunately, many previous studies do not provide sufficient information on the density–yield responses or on the spatial arrangements used. In 3 of the 16 studies reviewed by Weiner and Thomas (1986), a regular planting pattern is specified (Edmeades and Daynard 1979, Hedley et al. 1983, van Andel et al. 1984). These studies did show increased size variability at higher densities, thus strengthening the conclusion that competition was asymmetric in these cases. In several of the other studies cited, densities were high enough to provide the maximum final yield, supporting the conclusion that competition is asymmetric in these cases as well. However, there may be natural and agricultural populations in which the spatial pattern is not uniform and densities are below those achieving the maximum yield. In such cases, increases in size inequality at higher densities should not be considered conclusive evidence that competition is asymmetric, because the result is also consistent with our spatial pattern hypothesis. It is unclear how important this phenomenon is in nature. Natural populations are rarely uniform in spatial pattern, and density–yield trajectories have not been determined for many natural populations.

If spatial pattern is an important factor in generating size variation in the field, we would expect to see greater size variation in experimental populations grown in a random pattern than in populations grown in a regular pattern. Although few data are available, Weiner (1985) found no significant effect of random vs. uniform pattern on size variability in experimental populations of *Lolium multiflorum* and *Trifolium incarnatum*. Similarly, Brewster and Salter (1980) found no effect of within-row spacing pattern on size uniformity in bulb onions. However, in greenhouse populations of *Prunella vulgaris,* the coefficient of variation is significantly grater in random than in hexagonal arrays (T. E. Miller, *personal observation*).

Analyses of the effects of local neighborhood on target plant performance suggests that variation in the number and arrangement of neighboring plants leads to size variation within a population (e.g., Mack and Harper 1977, Weiner 1984, Pacala and Silander 1985, Silander and Pacala 1985). However, while some neighborhood studies have succeeded in accounting for much variation in plant size, in most cases a relatively small fraction of plant size variation can be attributed to individual differences in neighbor conditions (e.g., Waller 1981, Goldberg 1987).

Eventually the results of experiments which have varied the planting arrangement and those which utilized neighborhood analysis need to be reconciled. Explanations may involve the densities at which these experiments are performed or differences in the degree of competitive asymmetry (S. C. Thomas and J. Weiner, *unpublished manuscript*). We agree with Firbank and Watkinson (1987) that the development of a successful general model of competition and individual plant size depends upon a better understanding of the interactions between the factors which influence plant size, such as spatial pattern and competitive asymmetry.

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