Plant ecology

Spatial dynamics of self-thinning

Gareth Hughes

FIELD data suggest that density-dependent mortality (self-thinning) in even-aged, single-species plant populations is accompanied by changes in spatial pattern, towards a more regular distribution of surviving plants. A substantial body of such data relates to natural populations of forest trees, where practical difficulties deter study of the development of spatial pattern over time. Instead, changes in spatial pattern are inferred from comparisons of the patterns of otherwise similar populations of different ages¹ or, as in a new study² by Kenkel, from comparisons of the patterns of live and dead members of a single population.

Kenkel used various spatial statistics to analyse pattern in a 65-year-old jack pine (*Pinus banksiana*) population growing in a relatively homogeneous physical environment. The pattern of the initial (live plus dead) population shows no departure from randomness, but when both the dead and the live trees are considered separately, they show non-random patterns. The dead trees are more aggregated than can be accounted for by random mortality, whereas the survivors tend to have a regular pattern.

Spatial inter-relationships between live and dead trees indicate that the development of a regular pattern of live trees cannot be wholly explained by differential mortality in higher density patches in the initial population. Kenkel suggests that these results are consistent with a two-phase model of intraspecific competition: first, competition for soil resources leads to thinning of relatively high-density patches in the population; and second, competition for light leads to a regular pattern of dominant, surviving trees.

The development of a regular pattern among surviving members of a plant population is highly suggestive of the action of intraspecific competition. As Ford pointed out³, however, it is difficult to prove a causal link between variations in plant growth and resource use when it is the assumed outcome of competition that is being studied. Two types of investigation can help to draw this link: simulation experiments with model systems; and field experiments in which some measure of resource use is obtained while spatial pattern is artificially manipulated.

Leps and Kindlmann described⁴ models of the development of spatial pattern over

time in even-aged plant populations. They used their simulation model to investigate the development of pattern over time in two situations: individual plant survival dependent on the competitive influence of neighbouring plants; and random mortality. They found that when survival depends on the influence of neighbours, spatial pattern becomes more regular over time whether the initial pattern is aggre-

Root-system sketches of *Haplopappus* (left) and *Chrysothamnus* (right) plants (drawn by C. Weber-Johnson). Late in the dry season, soil moisture changes most dramatically at 25 cm. This depth corresponds to a separation point for root biomass of the two species: *Haplopappus* lateral roots are concentrated in the upper, driest soil; *Chrysothamnus* laterals in the wetter soil. The thick taproots of *Chrysothamnus* can reach below 600 cm. (From ref. 5.)

gated or random. But when survival is independent of the influence of neighbours, spatial pattern approaches randomness from both aggregated and regular initial patterns. These results thus support the idea that intraspecific competition is the driving force for the development of a regular spatial pattern, but do not provide much insight on the nature of the competitive processes involved.

Desert shrub communities provide rather better opportunities for plant removal experiments than forest tree populations. Manning and Barbour have now investigated⁵ relationships between plant spatial pattern and resource use in two coexisting desert shrubs, *Haplopappus cooperi* and *Chrysothamnus teretifolius*. *Haplopappus* plants have a random pattern, *Chrysothamnus* plants an aggregated pattern, and individuals of the two populations are randomly distributed with respect to each other. For *Haplopappus*, removal of neighbouring plants of either or both species results in an increase in predawn xylem pressure potential (XPP), suggesting that competition for water has been relaxed. For *Chrysothamnus*, predawn XPP is not influenced by the removal of neighbours of either or

both species, suggesting that competition for water has not been affected by the experimental treatments. In this case, the above-ground spatial patterns reveal little about intra- or interspecific competition. The explanation for the competitive interactions within and between these two species seems to lie instead in their respective root morphologies (see figure).

In terms of Kenkel's model², the first phase of competition, for water, depends on the distribution of below-ground biomass. If the second phase, competition for light, is relatively unimportant, as seems likely in the desert-shrub community, and above-ground spatial pattern is determined by seed-dispersal mechanisms or the action of herbivores, Manning and Barbour's results⁵ are not necessarily at odds with studies¹⁻⁴ associating intraspecific competition with the development of a regular pattern of surviving plants.

Plant populations experiencing intense intraspecific competition for resources exhibit a characteristic increase in mean biomass per plant (w) as the population density of surviving plants (d) declines. The 'self-thinning rule' is the empirical observation that in even-aged, single-species populations of genetically distinct plants, density-dependent mortality leads to the relationship $w = kd^{-3/2}$, where k is a constant. Although one of the earliest descriptions⁶ of the self-thinning rule provided an heuristic expla-

nation based on distance to nearest neighbour as a measure of pattern, few attempts to account for the rule have embraced the spatial dynamics of self-thinning.

More recently, a re-evaluation⁷ of data on which the self-thinning rule is based suggests that self-thinning does not obey a single quantitative rule. Deviations from the proposed value of $-3/2$ for the exponent of the biomass-density relationship have been related⁸ to differences in the relative weights and dimensions of plant parts. It would be interesting to see how such variation is associated with changes in plant spatial pattern under self-thinning of the type identified by Kenkel. But, as Manning and Barbour's work reminds us, there is often more to plant spatial pattern than meets the eye. □

1. Veblen, T.T. in *The Ecology of Natural Disturbance and Patch Dynamics* (eds Pickett, S.T.A. & White, P.S.) 35-51 (Academic, Orlando, 1985).

2. Kenkel, N.C. *Ecology* **69**, 1017-1024 (1988).

3. Ford, E.D. *J. Ecol.* **63**, 311-333 (1975).

4. Leps, J. & Kindlmann, P. *Ecol. Mod.* **39**, 45-57 (1987).

5. Manning, S.J. & Barbour, M.G. *Am. J. Bot.* **75**, 885 (1988).

6. White, J. & Harper, J.L. *J. Ecol.* **58**, 467-485 (1970).

7. Weller, D.E. *Ecol. Monogr.* **57**, 23-43 (1987).

8. Weller, D.E. *Ecology* **68**, 813-821 (1987).

Gareth Hughes is at the Edinburgh School of Agriculture, University of Edinburgh, West Mains Road, Edinburgh EH9 3JG, UK.