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SIZE BIMODALITY IN PLANT POPULATIONS: AN ALTERNATIVE HYPOTHESIS[1]

Michael Huston[2]

Bimodal size distributions have recently been reported in even-aged populations of freshwater fish (Shelton et al. 1979, Timmons et al. 1980), coniferous and broad-leaved trees (Ford and Newbould 1970, Ford 1975, Mohler et al. 1978), a broad-leaved herb (Ford 1975, Ford and Diggle 1981), and a grass, Festuca paradoxa (Rabinowitz 1979). Such bimodality in monospecific plant populations has been thought to result from competition in which large plants preempt resources and suppress the growth of small plants (Ford 1975, Ford and Diggle 1981). This mechanism of dominance and suppression is expected to produce a pattern of increasing bimodality with increasing plant density. However, Rabinowitz (1979) found the opposite density response in Festuca paradoxa. I illustrate here an alternative mechanism for producing bimodality, which provides a plausible explanation for the unexpected pattern of increased bimodality at decreased planting density found by Rabinowitz (1979).

Bimodal size distributions can result from initially unimodal size distributions when there is discontinuous variation in exponential growth rates among individuals. Normally distributed variation in exponential growth rates will not produce bimodality. Sources of discontinuous variation may be genetic heterogeneity, environmental heterogeneity, or dominance-and-suppression competition. Such competition may be considered asymmetric because the resulting negative effects are experienced only by the smaller plants. The expected distribution of mass resulting from asymmetric competition becomes more bimodal as increasing plant density increases the number of suppressed plants. Symmetric competition, in which each individual has a negative effect on its competitors proportional to its size, can also produce bimodality, but only in spatially random populations, where variation in the number of neighbors produces variation in exponential growth rates.

In a spatially random scatter of points, the expected number of points within an area of some specified size A can be determined using the Poisson function with the parameter equal to the mean number of points in A. If the points represent plants and A is the area from which one plant draws resources (i.e., the zone of resource depletion), one can predict the number of neighbors within each plant's zone of resource depletion. If a plant's growth rate is inversely proportional to the number of its neighbors, the reduction in the plant's intrinsic growth rate caused by resource depletion can be calculated. Thus, it is possible to use the distribution of the number of neighbors to determine the distribution of reduction in growth rate expected in a randomly spaced plant population of known density (Table 1). The mean reduction in growth rate increases monotonically with increasing density, but the variance is greatest at intermediate densities. The primary difference between spatially random and spatially uni-

TABLE 1. Poisson frequency distributions of the number of neighbors within area A, for plants in spatially random populations with various mean densities, where A is the area of one plant's zone of resource depletion. Growth rate multipliers* based on these values are shown, for comparison with corresponding multipliers for spatially uniform populations.

Number of neighbors	Mean density (plants/A)							
	0.1	0.5	1.0	2.0	3.0	4.0	6.0	8.0
	Frequency							
0	0.90	0.61	0.37	0.14	0.05	0.02		
1	0.09	0.30	0.37	0.27	0.15	0.07	0.01	
2		0.08	0.18	0.27	0.22	0.15	0.04	0.01
3		0.01	0.06	0.18	0.22	0.20	0.09	0.03
4			0.02	0.09	0.17	0.20	0.13	0.06
5				0.04	0.10	0.16	0.16	0.09
6				0.01	0.05	0.10	0.16	0.12
7					0.02	0.06	0.14	0.14
8					0.01	0.03	0.10	0.14
9						0.01	0.07	0.12
10							0.04	0.10
11							0.02	0.07
12							0.01	0.05
13								0.03
14								0.02
15								0.01
	Growth rate multiplier							
Mean	0.95	0.82	0.65	0.40	0.31	0.24	0.17	0.12
Variance	0.026	0.068	0.084	0.053	0.036	0.014	0.012	0.003
	Growth rate multiplier for spatially uniform population							
Mean	1.0	1.0	1.0	0.50	0.33	0.25	0.17	0.12
Variance	0	0	0	0	0	0	0	0

* The growth rate multiplier is calculated as $1/(N + 1)$, where N is the number of neighbors. Actual growth rate is the product of this multiplier and the intrinsic growth rate.

form populations is in the variances of the growth rate reductions, rather than in the means. Since each individual in a spatially uniform population has the same number of neighbors, the variance is zero.

Symmetric competition among seedlings in a spatially random population was simulated using the exponential growth function $m_t = m_0 e^{rt}$, where m_0 = initial (i.e., seed) mass, r = exponential growth rate, and m_t = seedling mass at time t. This is a reasonable model for seedling growth (Fresco 1973). In these simulations, each plant was randomly assigned values for m_0, r, and germination time chosen from normal distributions (for m_0, mean = 0.64 mg, SD = 0.14 mg; for r, mean = 0.07 mg·mg^{-1}·d^{-1}, SD = 0.01 mg·mg^{-1}·d^{-1}; for germination time, mean = 12 d, SD = 1 d). Values for all parameters were based on data for *Festuca paradoxa* (Rabinowitz 1979, Turner and Rabinowitz 1983). Each individual was randomly assigned a number of neighbors based on the Poisson distribution for a given mean density. The growth rate reduction factor resulting from neighbors within each plant's zone of resource depletion was calculated as the inverse of the number of plants within the zone, including the central plant. This reduction factor was multiplied by the randomly assigned exponential growth rate to determine

the actual exponential growth rate (r) for each plant. Typical results for a simulation of 50 d of growth are presented in Fig. 1.

Bimodality produced by this model is a consequence of the discontinuous distribution of exponential growth rates resulting from a Poisson distribution of the number of neighbors. Incorporating a distance-weighting factor between interacting plants tends to make the distribution more continuous and slow the appearance of bimodality, but does not affect the qualitative conclusions; there will always be some isolated plants at an appropriately chosen density. While a very simple exponential growth model was used in these simulations, any growth model with a positive second derivative would produce the same qualitative results.

The density response of the Poisson-generated pattern of exponential growth rates is maximum bimodality of size distributions at intermediate densities (Fig. 1). At densities sufficiently low that most individuals have no neighbors (e.g., uniform distribution), there is no variance resulting from neighbor effects and no bimodality. At high densities, all individuals share resources with neighbors, and variance in growth rates is low enough to slow or prevent the appearance of bimodality. In contrast to bimodality resulting from
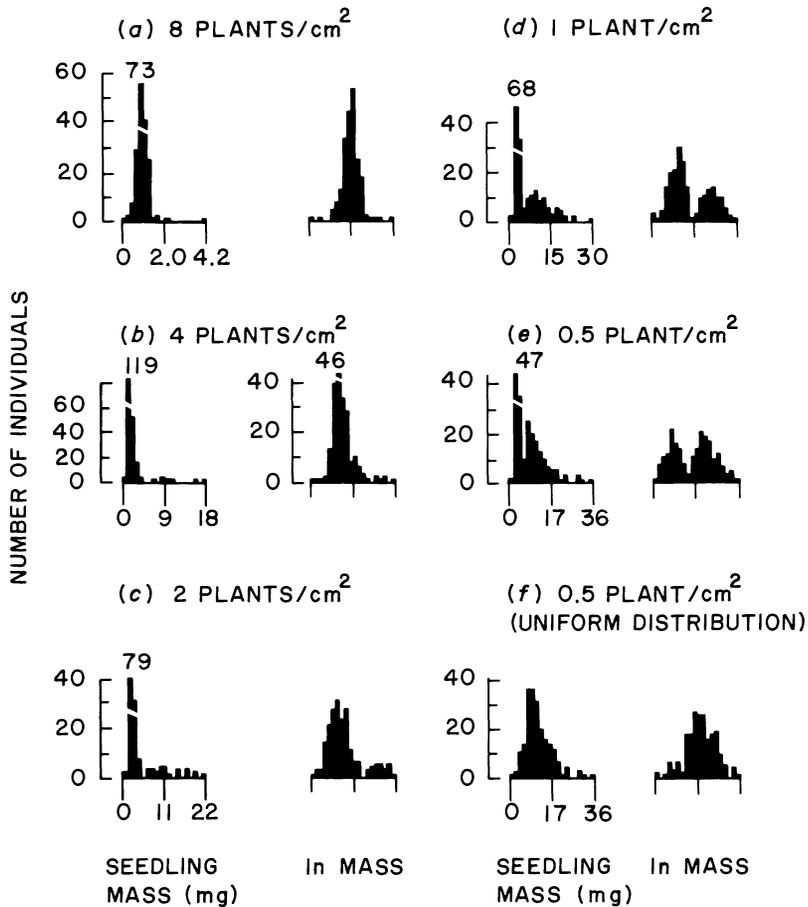
FIG. 1. Distributions of simulated seedling masses and ln-transformed masses for spatially random populations of 200 individuals at five densities, and for one spatially uniform population of 200 individuals, after 50 d of growth. Bimodality is more easily detected in ln-transformed data than in the untransformed data.

asymmetric competition, bimodality from symmetric competition is produced without any competitive interaction between large and small plants. Small plants compete with other small plants in clusters by depleting resources in the local area but do not interact with faster-growing isolated individuals.

The pattern produced by these simulations is very similar to the increase in bimodality with decreased densities that was found in experiments with *Festuca paradoxa* (Rabinowitz 1979) (Fig. 2). The reduced size of the mode of smaller plants in comparison with the simulated distributions (Fig. 1) may result from reduced viability of smaller seeds, since the density of seedlings was approximately half the planting density. This pattern of increased bimodality with decreasing plant density is the opposite of the pattern that would be produced by dominance and suppression alone. While there is no reason that asymmetric competition

(dominance and suppression) and symmetric competition (resource depletion) cannot occur simultaneously, the low growth rates resulting from extreme resource depletion may slow or prevent the expression of dominance and suppression (e.g., Turner and Rabinowitz 1983).

Asymmetric competition probably occurs most often for light, when tall plants shade smaller individuals but are not shaded themselves (Ford and Diggle 1981). Asymmetric competition might also occur where large individuals preempt resources, such as water in deserts. Symmetric competition seems more likely to occur among plants of smaller size, for soil nutrients or moisture; these resources may be depleted by many plants without any individual obtaining a monopoly.

During the growth of a plant population or community, there is likely to be a shift from symmetric competition to asymmetric competition as plant cover
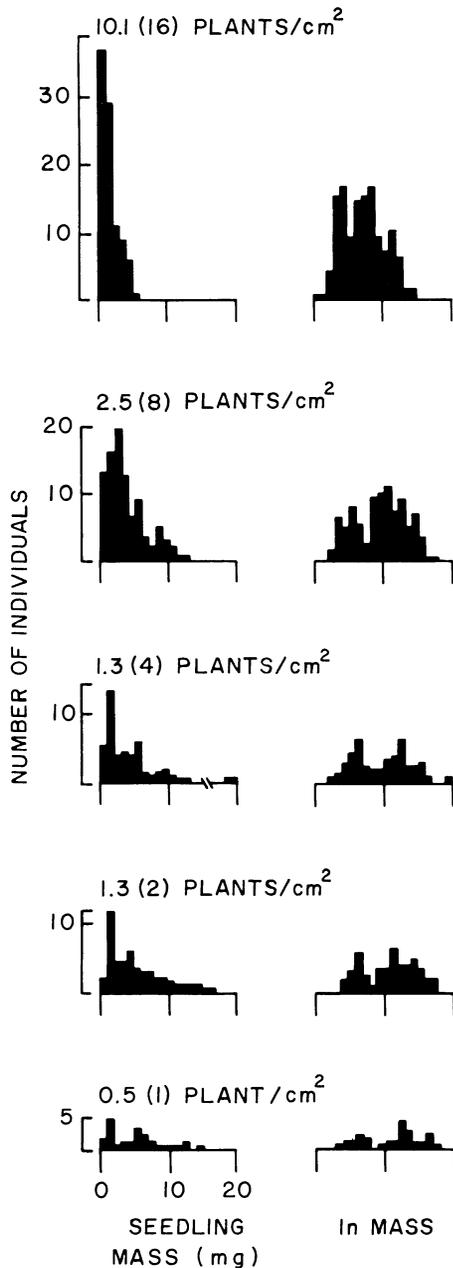
FIG. 2. Actual distributions of seedling mass and ln-transformed masses from experimental plantings at five densities of hand-broadcast seed for *Festuca paradoxa*, after ≈45 d of growth. Final densities (plants/cm²) are given and initial seed densities are in parentheses. For 16 seeds/cm², one of three replicates is presented; the other four histograms are combinations of three replicates each. Calculated from data in Rabinowitz (1979); the logarithmic plots are redrawn from fig. 1 of that paper.

increases and light becomes limiting. Differences in plant architecture that affect the intensity of light competition (such as narrow-leaved grasses vs. broad-leaved forbs) should also affect the relative importance of each type of competition (e.g., Turner and Rabinowitz 1983).

Regular, rather than random, distributions of adult plants are often found in natural plant populations (Harper 1977). Such regular distributions can be derived from initially random distributions of seeds if slowly growing individuals in dense clusters die or are overgrown by fast-growing (initially isolated) plants. Symmetric competition in a randomly distributed population can produce the variation in plant size necessary as an initial condition for asymmetric, "one-sided" competition to occur (Ford and Diggle 1981).

This simple model based on symmetric competition in a spatially random population provides an alternative mechanism for the appearance of bimodality. The model may explain why increasing plant density in experiments with regularly spaced plants (Ford 1975, Ford and Diggle 1981) produces results that conflict with patterns found in experiments with a random spatial pattern (Rabinowitz 1979).

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DYNAMICS OF SOIL SEED POOLS IN BURNED AND UNBURNED SAGEBRUSH SEMI-DESERTS[1]

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Description of soil seed pools in stable and seral vegetation have frequently been based on one sample in time and space (Cook 1980, Roberts 1981). Soil seed pools are thus rarely monitored in different seasons at the same site. Such patterns might be important in explaining successional processes such as the recovery of sagebrush semi-desert (West 1983) after fire.

All previous studies of soil seed pools in sagebrush-grass vegetation (Young and Evans 1975, 1977, Young et al. 1976) have taken place on sites that were seriously depleted of their perennial grass component by excessive livestock grazing. Our study site had a modicum of the introduced annual grass *Bromus tectorum* and much native perennial bunchgrass prior to fire (West and Hassan 1985). This area had not been burned for at least the past 100 yr, as indicated by the size and form of the fire-susceptible, nonsprouting and long-lived *Artemisia tridentata* ssp. *wyomingensis* and the few scattered *Juniperus osteosperma*.

We measured the importance of soil seed pools in the regeneration of vegetation after a mid-summer (26 July 1981) wildfire near Mills in Juab County, Utah. Details on the location and environment of the study site, the wildfire, and recovery of the vegetation have been published by West and Hassan (1985). Here we describe the soil seed pools on burned and unburned plots over the first 15 mo following the fire.

Methods

Vegetation was sampled (West and Hassan 1985) 5–10 d before the fire. Eight remaining patches of unburned vegetation were paired with the nearest burned areas on the same site in terms of elevation, slope, exposure, and soil profiles. Similarity of preburn total plant cover between plots was checked on a 1:8000 scale enlargement of a color-infrared aerial photograph taken by the Apollo lunar mission of 1 July 1975. The scattered *Juniperus* had unique spatial positions that could be used to interpret locations on the preburn aerial photos and on the ground after the burn (snags were left standing). Three pairs of burned and unburned plots that represented the greatest similarity in terms of total vegetation cover (as seen in the aerial photo enlargement), elevation, slope, and soil textural Series were chosen from the eight possible pairs.

Ground surface and vascular plant cover were assessed on 2 September 1981 and 28 July 1982 by methods described in West and Hassan (1985). Soil seed pools were sampled from randomly placed locations with a 5.4 cm diameter soil bulk density sampler driven to 5 cm depth. Twenty samples per plot were taken at each sampling date: 22 September 1981, 11 December 1981, 25 March 1982, and 11 September 1982.

The relationship of soil seed pools to the surrounding plants or "hot" spots (where shrubs were centered before the fire) was determined from a large-scale map of each plot that was drawn within a month after the fire, when the accumulations of ash and stumps of the shrubs were still evident.

All samples were air-dried at room temperatures for 1–2 d and then stored in a cold room (0°–2°C) to prevent germination until separation within 3 mo. "Seeds" are defined here in a general way, with fruits or caryopses counted as "seeds" for some taxa.

Coarse materials were first removed by sieving (0.5-cm mesh). Materials passing through the sieve were then mixed in a high-density salt solution (Malone 1967). After 1 min of agitation, the organic material was skimmed from the top of the solution and washed over a 25-μm mesh sieve. The agitation, flotation, skimming, and rinsing operation was repeated three times for each sample.