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Bimodal distributions of seedling weight in relation to density of *Festuca paradoxa* Desv.

THE degree to which plants growing together interfere with one another by competing for resources such as light, moisture and nutrients is difficult to determine by direct measurement of resource depletion[1]. Plant ecologists have therefore looked for indicators of interference in population structure[2,3]. One proposed measure of interference is the shift that occurs from the 'normal' distribution of seed weight to a 'log-normal' distribution of the weight of seedlings grown from those seeds in an even-aged monoculture. This shift presumably reflects the emergence of a few large and dominant individuals and the suppression of larger numbers of small individuals. Recently Ford[4] and Newbould[5] have proposed that distributions of plant weight in competing populations are actually bimodal, resulting from the presence of distinct populations of large individuals with positive relative growth rates and small individuals with nearly zero growth rates. Even-aged plantations of *Picea sitchensis* demonstrate such disjunct growth rates, and mortality is confined to the smaller individuals[4]. Size distributions in naturally thinning populations of *Abies balsamea* and *Prunus pensylvanica* are also bimodal[6]. We have studied the distribution of seedling weight in even-aged stands of *Festuca paradoxa*, a native North American prairie grass[7], and report here that although the distribution is bimodal, the bimodality is more striking at lower densities, where interference is less severe. This result is the reverse of that expected if the extent of bimodality were a direct indication of the magnitude of interference. Therefore, although bimodality may be an eventual outcome of interference, it cannot be used as a measure of the strength of interaction between individuals.

At the highest density (16 seeds cm^{-2}), distributions of ln-transformed seedling weight (Fig. 1) are only slightly or not at all bimodal. The distributions become increasingly bimodal as density increases. At the lowest density (1 seed cm^{-2}), the distribution appears most strongly bimodal. All distributions are significantly different from the normal distribution at the 5% level (*G*-tests[8]). Only the distributions at 16 seeds cm^{-2} show significant skewness (to the right[9]), but all are significantly platykurtic (flat-topped[9]). Platykurtosis is not sufficient to demonstrate bimodality, but bimodal distributions are platykurtic. There is no direct statistical measure of bimodality.

The bimodality in the weight distributions is not due to an underlying bimodality of seed weight, either for the intact diaspore or for the caryopsis without accessory tissues (Fig. 2). Neither distribution deviates significantly from the normal distribution (*G*-tests[8]), and neither is skewed or kurtotic. The
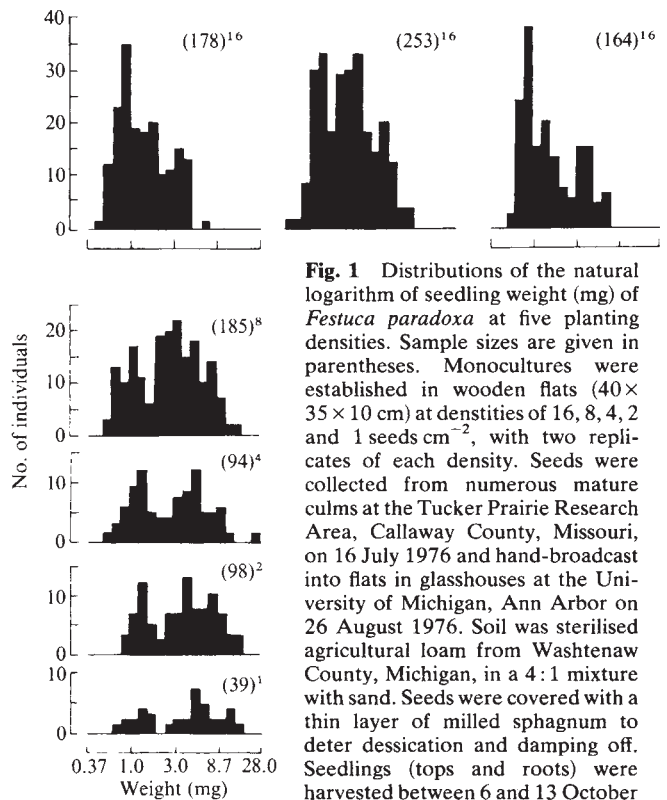
Fig. 1 Distributions of the natural logarithm of seedling weight (mg) of *Festuca paradoxa* at five planting densities. Sample sizes are given in parentheses. Monocultures were established in wooden flats (40 × 35 × 10 cm) at denstities of 16, 8, 4, 2 and 1 seeds cm^{-2}, with two replicates of each density. Seeds were collected from numerous mature culms at the Tucker Prairie Research Area, Callaway County, Missouri, on 16 July 1976 and hand-broadcast into flats in glasshouses at the University of Michigan, Ann Arbor on 26 August 1976. Soil was sterilised agricultural loam from Washtenaw County, Michigan, in a 4:1 mixture with sand. Seeds were covered with a thin layer of milled sphagnum to deter dessication and damping off. Seedlings (tops and roots) were harvested between 6 and 13 October 1976 in randomly-placed 5 × 5 cm plots, 3 for each density, washed to remove soil from the roots, dried at 80 °C for 24 h, and weighed on a Cahn electrobalance. For 8, 4, 2 and 1 seeds cm^{-2}, one-way anovas[8] showed no differences in seedling weight among the three replicates at the 10% level. Consequently, the replicates were lumped, and one distribution is shown. At 16 seeds cm^{-2}, the replicates differed at the 1% level ($F_s = 4.87$) and are shown separately. Distributions at 8, 4, 2 and 1 seeds cm^{-2} are all significantly different from the distributions at 16 seeds cm^{-2} (χ^2 tests[8]).

bimodality is not due to an underlying bimodality in germination time (Fig. 3). This distribution is significantly right-skewed and leptokurtic.

Mean seedling weight increases with decreasing density (Table 1), indicating that resource limitation is occurring at higher densities. The bimodal pattern emerges before density-dependent mortality. The ratio of seedlings harvested to seeds planted is not significantly different for the different densities (one-way anova with arcsine transform[8]). Mortality, if occurring, is uniform among the densities.

Interference is *a priori* more severe at higher densities. Our finding that bimodality is weaker at higher density suggests that at high density, the manifestations of interference in population structure are delayed and that the interaction between individuals is slowed. At the highest density, all individuals may

Table 1 Seedling weight of *Festuca paradoxa* at five planting densities

Planting density (seeds cm^{-2})	Sample size	Geometric mean of seedling weight ±s.d. (mg)	Skewness g_1	Kurtosis g_2
16	178	1.40 ± 2.23	0.444*	−0.881*
16	164	1.58 ± 1.95	0.620*	−0.893*
16	253	1.73 ± 1.88	0.258†	−0.745*
8	189	2.78 ± 2.73	−0.086	−0.935*
4	94	2.82 ± 3.29	0.125	−0.946*
2	98	3.71 ± 3.38	−0.165	−1.133*
1	39	3.92 ± 3.82	−0.318	−1.032†

Skewness (g_1) and kurtosis (g_2) are calculated for the ln-transformed distributions shown in Fig. 1.
*$P < 0.01$; †$P < 0.05$.
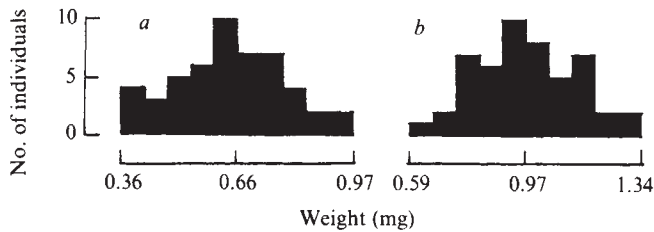
Fig. 2 Distributions of weights of excised caryopses (*a*) and intact diaspores (caryopses with lemmas and paleas) (*b*), obtained on a Cahn electrobalance. Arithmetic scale, sample size is 50 in both cases. For the intact diaspores, $\bar{x} = 0.967$ mg, $s = 0.170$, $g_1 = 0.129$ (not significantly different from zero[9]), and $g_2 = -0.576$ (NS). For the excised caryopses, $\bar{x} = 0.639$ mg, $s = 0.143$, $g_1 = 0.008$ (NS), and $g_2 = -0.502$ (NS). Neither distribution is significantly different from the normal distribution (*G*-test[8]).

suffer from more severe resource limitation; this idea is supported by the right skew in the data at 16 seeds cm^{-2}. The appearance of dominant individuals may be postponed. At lower densities, because resource limitation is less severe, growth is more rapid, individuals are larger, and the emergence of dominant individuals (and hence the bimodality) is more rapid.

Factors determining which individuals become dominant and which are suppressed remain somewhat obscure. Suppression is probably not due to genetic differences[10]. Seed size[11], order of emergence[12] and neighbourhood effects[13] have been implicated in determining which individuals become dominant.
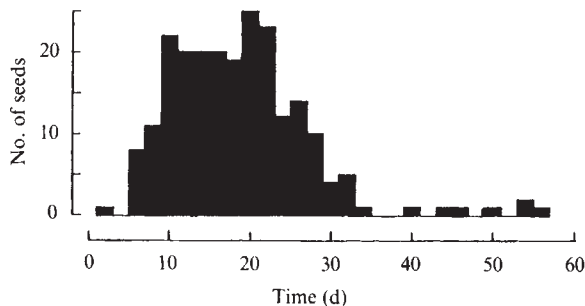
Fig. 3 Distribution of day of germination for excised caryopses of *Festuca paradoxa*. Arithmetic scale, sample size is 222. Excised caryopses between filter paper moistened with distilled water were germinated in the dark at room temperature. $\bar{x} = 18.6$ d, $s = 8.6$, $g_1 = 1.41$ ($P < 0.01$) and $g_2 = 3.78$ ($P < 0.01$).

While intrinsic factors generating bimodality cannot be exhaustively eliminated, the two most likely intrinsic sources (bimodality in seed weight or germination time) have been excluded here. The bimodality is probably a direct result of interference, although the possibility remains that severe interference prevents the expression of an intrinsic bimodality (due to other factors) at high density.

Disjunct populations with zero and positive growth rates are sufficient to generate a bimodality in distributions of ln-transformed individual weight. Bimodality appears to be an eventual structural result of interference and thus is a valuable descriptor of populational attributes. These results demonstrate the need to distinguish between populational attributes which characterise the pace and severity of interference from attributes which describe the outcome of interference.

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A method for culture of micromanipulated sheep embryos and its use to produce monozygotic twins

MICROSURGICAL techniques have proved valuable for investigations of the regulatory capacity of early mammalian embryos, including the developmental potential of single blastomeres from two-, four- and eight-celled embryos (see ref. 1 for review). However, the usefulness of radical microsurgery in experiments on early cleavage stages has been restricted largely to species in which such young embryos may be cultured *in vitro*, notably the mouse, as, in most instances, embryos less advanced than the late morula stage fail to survive *in vivo* if the zona pellucida has been removed or substantially damaged[2-6]. There has been no satisfactory method for culture *in vitro* of early cleavage stages in the sheep, and consequently there have been few reports of attempts to micromanipulate early sheep embryos[7-9]. I describe here a method whereby micromanipulated eggs can be protected during their early development *in vivo* and its use in an investigation of the developmental potential of single blastomeres from two-celled sheep embryos with the aim of producing monozygotic twins. The method involves coating the eggs with agar after microsurgery so as to seal defects produced in the zona pellucida.

In preliminary experiments it was established that young sheep embryos embedded in agar and transferred to rabbit oviducts[10] continued to develop at a normal rate, even when the zona pellucida was extensively damaged, provided that they remained embedded in agar during the culture period. On the basis of this observation, a technique was devised which enabled the production of monozygotic twins.

Two-celled embryos were collected from super-ovulated donor ewes early on day 2 of their oestrous cycle (onset of oestrus: day 0). Embryos were collected, stored, micromanipulated and transferred in an enriched phosphate-buffered saline medium (PBS)[11]. During storage and manipulation the embryos were held at room temperature.

Monozygotic pairs of agar-coated single blastomere eggs were produced as follows. (1) The two-celled egg was held by suction with a capillary pipette, and the zona pellucida was ripped open along the interblastomeric groove for about three-quarters of its circumference with a fine glass needle. (2) The blastomeres were sucked out of the zona with the aid of a Pasteur pipette with a tip diameter sufficiently small to detain the zona while allowing the