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SIZE HIERARCHIES IN EXPERIMENTAL POPULATIONS OF ANNUAL PLANTS[1]

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Abstract. The effects of inter- and intraspecific interference on size hierarchies (size inequalities) were investigated in populations of the annual plants *Trifolium incarnatum* and *Lolium multiflorum*. Variables experimentally manipulated included plant density, species proportions, soil fertility, and spatial pattern of plantings. Densities were below those for extensive density-dependent mortality.

Size inequality always increased with increasing density. Plants grown individually showed very low inequality, while plants grown at the highest density had the most developed hierarchies. Size inequality usually increased with an increase in productivity when interference was occurring. When dominant in mixtures, *Lolium* showed less size inequality than in monoculture, while the suppressed species, *Trifolium*, usually displayed an increase in inequality. Spatial pattern appeared to be less important than other factors in causing size inequalities; plants sown in a uniform spatial pattern showed significantly lower size inequality than plants sown in a random pattern in only one out of four cases. Inequality in reproductive output of *Trifolium*, as estimated by dry mass of flower heads, was always greater than inequality in plant dry mass.

The results support a model of plant interference in which large plants are able to usurp resources and suppress the growth of smaller individuals more than they themselves are suppressed. While interference decreases mean plant mass, it increases both the relative variation in plant mass and the concentration of mass within a small fraction of the population.

Key words: competition; dominance; interference; Lolium multiflorum; *size distribution; size hierarchy; size inequality; suppression;* Trifolium incarnatum.

INTRODUCTION

Within a population, plants vary in their size. Most plant populations consist of relatively few large individuals and many small ones, and the few large individuals contain most of the population's biomass (Obeid et al. 1967, Ogden 1970, Mohler et al. 1978). Such size distributions have been called "size hierarchies." The ecological and evolutionary significance of size hierarchies is enormous. For example, it is the smallest plants that suffer density-dependent mortality. Also, within a population, size appears to be correlated with fitness (Werner and Caswell 1977, Solbrig 1981), and large individuals may contribute inordinately to the gene pool of the next generation. If gene frequencies within the large individuals are different from those of the population as a whole, evolutionary change will occur.

There are several possible causes of size inequality. Size differences may be caused directly or through differences in growth rates due to (1) age difference, (2) genetic variation, (3) heterogeneity of resources or other environmental factors, or (4) effects of herbivores, parasites, or pathogens. Finally, (5) competition may cause or exaggerate size differences. The relative importance of each of these factors is not known for any population, and these factors may interact with each other.

There is controversy over the effect of interference or competition on size distributions. Two basic models have so far been advanced.

In Model 1 the size distribution of an even-aged monospecific stand is attributed to variation in growth rates due to factors other than interference. Koyama and Kira (1956) observed that if plant growth is exponential, highly skewed size distributions will be generated from variation in the growth rates of seedlings. For example, if exponential growth rates are normally distributed and seedlings are of equal size or normally distributed, the distribution of plants after a period of growth will be log-normal (Koch 1966). If competition acts to reduce the growth rates of all individuals by the same proportion, it will reduce the variance in exponential growth rates and, therefore, the relative variation in sizes that is generated by these growth rate differences. In its most general form this model requires only that (1) plant growth is exponential, (2) there is variation in growth rates, and (3) competition reduces the variance in growth rates.

In Model 2 ("dominance and suppression"), differences in size are exacerbated as large plants usurp resources and grow at the expense of small plants. The hierarchy of sizes represents a hierarchy of exploitation (Harper 1977). Large plants grow larger while small plants grow little. This results in a highly skewed, unequal size distribution. When mean plant size approaches the limit described by the $-3/2$ thinning rule ($w = Kd^{-3/2}$ where w is mean plant mass, d is density, and K is a constant), smaller plants die. A second version of the dominance-and-suppression model holds

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that interference results in a bimodal distribution of sizes with distinct dominant and suppressed classes (Ford 1975, Ford and Diggle 1981).

Although the two general models lead to different and incompatible predictions, both the available data and their interpretation have been problematic. Two major difficulties have arisen.

First, it has been unclear how to evaluate size hierarchies. Koyama and Kira (1956) and other workers (White and Harper 1970, Turner and Rabinowitz 1983) have used measures of skewness to interpret size distributions. Skewness has even been suggested as a measure of interference by some supporters of the dominance and suppression model (Higgins et al. 1984). Weiner and Solbrig (1984) demonstrated that skewness and size hierarchy are very different in meaning. They have argued that size hierarchy is synonymous with size inequality or concentration, and they have urged the use of methods developed in economics, the Lorenz curve and Gini coefficient, to evaluate size hierarchies.

A second problem with the interpretation of size distribution data occurs because one of the effects of interference is density-dependent mortality (self-thinning). Mortality tends to be concentrated among the smaller individuals, and this changes the size distribution. A size distribution is then the result of both growth and mortality of plants. For example, positive skewness of the size distribution may be the result of variation in exponential growth rates due to interference or other factors, or it may reflect truncation of the size distribution through mortality of the smallest individuals (Turner and Rabinowitz 1983). The problem of truncation is reduced if one evaluates inequality rather than skewness of the distribution. While truncation may increase skewness, it will reduce inequality by reducing the variance in sizes.

A series of experiments was designed to compare the two models of population structure. To avoid the abovementioned problems, size and reproductive inequalities were evaluated, as suggested by Weiner and Solbrig (1984), and plants were grown at densities at which competition would be important, but below those at which there would be much self-thinning.

According to the dominance-and-suppression model, increased density will result in increased size inequality, since interference increases with density, almost by definition. Increases in productivity would also be expected to result in increased size inequality. In high-productivity situations, plants will grow more quickly to the point at which they interfere with each other, and the development of a size hierarchy through dominance and suppression will occur more quickly. In lower productivity environments, factors other than plant interference will retard plant growth and interference will be less important.

If, as Model 2 proposes, intraspecific competition increases size concentration, we would expect interspecific competition to do the same. Thus, if plants are grown in mixtures of a given overall density in which one species is competitively superior to the other, we would expect the competitive dominant to have a more equal size distribution than it would have in a monospecific stand at the same density. Conversely, the suppressed species would be expected to have a more unequal distribution than it would in monoculture.

If competition is important in the generation of size inequality, we would expect the spatial pattern of plants to have an effect on size distributions. Plants do not respond to overall density but to local neighbor conditions (Mack and Harper 1977, Weiner 1982). One of the factors determining a plant's growth is the area available to it (Mithen et al. 1984). Plants with many or close neighbors will grow less than plants with few or distant neighbors (Weiner 1984). Thus, if plants are sown in a regular pattern there should be less of a size hierarchy than if plants are grown in a random pattern at the same density.

Model 1, which involves variance in exponential growth rates, leads to different predictions. Under this model, increased density should result in decreased size inequality because competition reduces all growth rates and therefore the variance in growth rates. While both models predict increases in size inequality with increased productivity, this effect should be more pronounced at lower densities in Model 1, but should be more pronounced at high density in Model 2. If competition reduces the variance in growth rates, we would expect a competitively dominant species to show an increase in its size inequality in mixture, while the inferior competitor should display a less developed size hierarchy than in monoculture.

MATERIALS AND METHODS

The annuals *Trifolium incarnatum* L. (Fabaceae) and *Lolium multiflorum* Lam. (Poaceae) were grown in monocultures and in mixtures in large, 15 cm deep flats in a greenhouse at the Penn-Y-Ffridd Station of the University College of North Wales in Bangor, Wales. Plants were grown in 59 × 45 cm plots. The factorial design included two densities: 200 and 1200 individuals/m^2 (= 52 and 312 plants per plot, respectively); two fertility levels: with and without N-P-K fertilizer; three species proportions: two monocultures and a 50:50 mixture; and three replicates of each combination of factors. In addition to this factoral design, monocultures of each species were also grown at 1200 plants/m^2 in a regular hexagonal pattern at both fertility levels. Nine plants of each species at each fertility level were grown individually in well-spaced 8-L plastic containers so that the size distribution of plants grown without interference could be observed.

The high-fertility soil was John Innes number 1 mixture, and the low-fertility soil was the same mixture without its standard N-P-K components. Plants were sown in plots through holes in templates that were arranged in a random or regular pattern. The low-density random pattern was a random subset of the high-density random pattern. Plots were assigned randomly within each bench. Half the area of each plot, a 7.4 cm wide border area, was a buffer zone; plants within this area were not harvested. Seeds were sown from 31 January to 6 February 1982. A few days after sowing, plants were watered with a suspension of *Rhizobium*. The soil was kept moist throughout the duration of the experiments. Ninety three days after sowing, plants were harvested individually at ground level, put in paper bags, dried, and weighed. *L. multiflorum* individuals did not flower but *T. incarnatum* flower heads were removed and weighed separately to give a measure of reproductive output. Some populations were destroyed by disease; data from these populations were not considered in the analysis.

Lorenz curves and Gini coefficients (G) were calculated for each population (Weiner and Solbrig 1984). In the Lorenz curve, individuals are ranked from the smallest to the largest. The cumulative fraction of the population is plotted against the cumulative fraction of the variable whose inequality is to be evaluated, in this case biomass. If all individuals are equal with respect to the specified variable, the result is a diagonal line from the origin (0% of the population contains 0% of the biomass) to the upper right corner (100% of the population contains 100% of the biomass). Any inequality results in a curve below the diagonal. The fraction of the area below the diagonal that is between the curve and the diagonal is the Gini coefficient, a measure of inequality. It has a minimum of 0 and a theoretical maximum of 1.0. The Gini coefficient is equal to one-half of the relative mean difference, i.e., the arithmetic average of the differences between all pairs of individuals (Sen 1973):

$$G = \sum_{i=1}^{n} \sum_{j=1}^{n} |x_i - x_j|/(2n^2\bar{x}).$$

Calculated G values were multiplied by $n/(n - 1)$ to give unbiased values (G′). Confidence intervals for Gini coefficients were determined using a "bootstrapping" technique (Efron 1981, Diaconis and Efron 1983). In this technique, G′ 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 G′ values are determined from the distribution of G′ values for these bootstrapped samples using a bias-corrected percentile method (Efron 1982).

De Wit replacement diagrams (de Wit 1960, Harper 1977) were constructed in the standard fashion except that mean individual yield rather than total yield was used to determine relative yield. This minor modification of the de Wit procedure was made to minimize any bias in the results due to unequal mortality of the two species in low-density mixtures.

RESULTS

Mortality was very low (<5%) for low-density populations, averaged 5–10% in high-density populations,

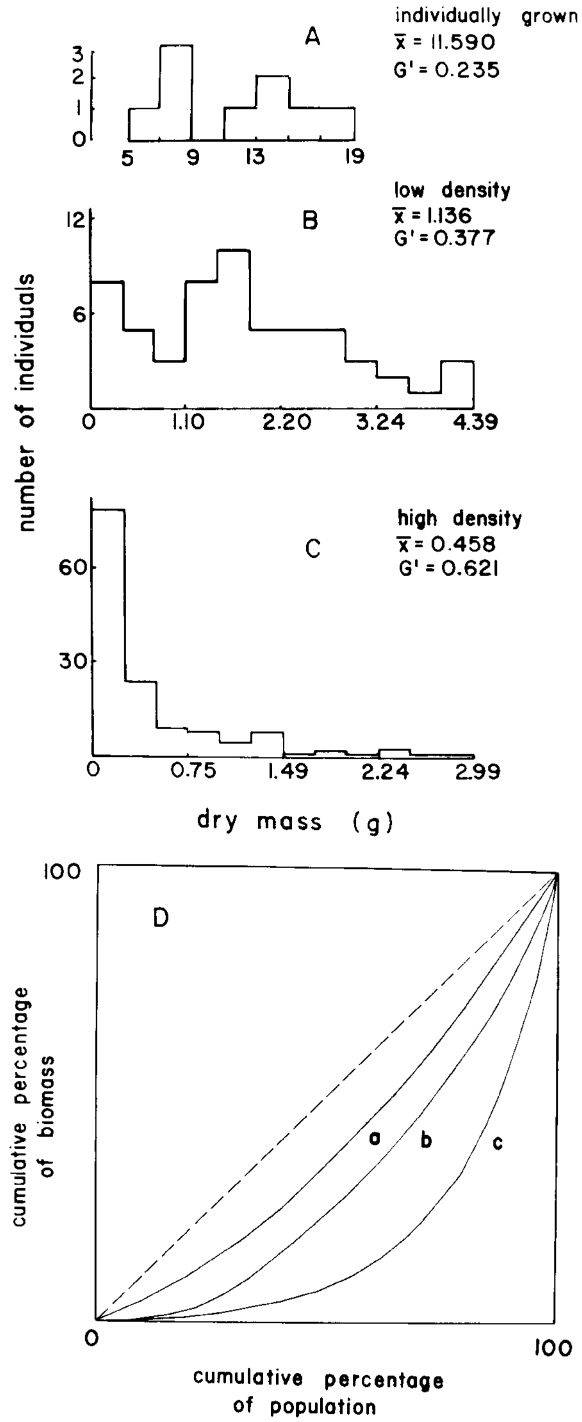

FIG. 1. Dry mass distributions (with inequality measured by the unbiased Gini coefficient G′) and Lorenz curves for monospecific populations of *Trifolium incarnatum* grown in low-fertility soil. (A) individually grown; (B) low density (200 individuals/m^2); (C) high density (1200 individuals/m^2); (D) Lorenz curves for (A), (B), and (C).

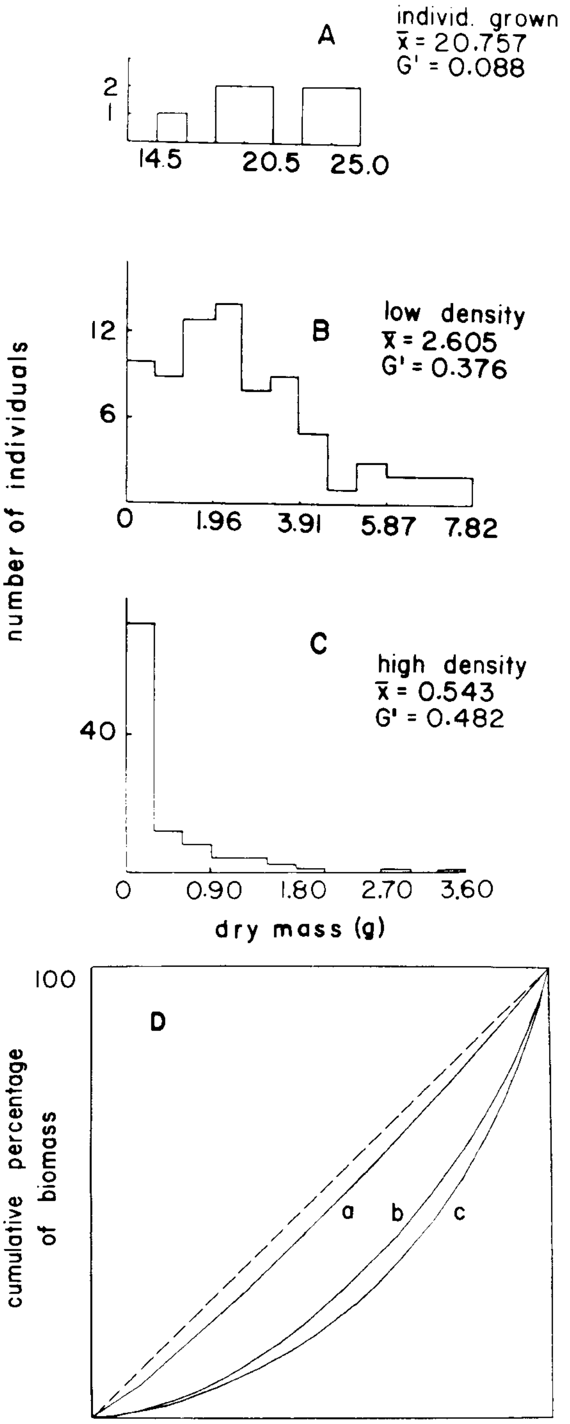

FIG. 2. Dry mass distributions (with inequality measured by the unbiased Gini coefficient G') and Lorenz curves for monospecific populations of *Trifolium incarnatum* grown in high-fertility soil. (A) individually grown; (B) low density (200 individuals/m^2); (C) high density (1200 individuals/m^2); (D) Lorenz curves for (A), (B), and (C).

and reached a maximum of 20% in some high-density, high-fertility populations. In treatments without added fertilizer, inequality in *Trifolium* dry mass distributions increased with increasing density (Fig. 1A–C); Lorenz curves were more concave with increasing density (Fig. 1D) and Gini coefficients were significantly different from each other (Table 1). *Trifolium* at high fertility gave similar results (Fig. 2). For both species at both fertility levels, Gini coefficients were significantly lower for individually grown plants than for plants grown at low or high density (Table 1). The Gini coefficient for individually grown *Lolium* plants was significantly different from those for both low- and high-density treatments ($P < .01$; Figs. 3 and 4), but the difference between Gini coefficients for low and high density was only ≈0.03 and was not significant.

De Wit replacement diagrams comparing standardized mean plant yield in mixtures and monocultures for both densities and fertility levels showed that increased total yield in mixture over monoculture occurred in the three out of four cases when *Lolium* benefited and *Trifolium* suffered from the mixture (Fig. 5). In one case (high fertility, high density; Fig. 5d) interspecific competition was equivalent to intraspecific competition according to the de Wit analysis. Biomass distributions and Gini coefficients for mixtures are displayed in Fig. 6. In the three out of four cases in which mean plant mass for *Lolium* was much greater than that of *Trifolium*, the mass distributions of the two species were very different in shape. When mean plant mass for *Lolium* was only 25% greater than that of *Trifolium* the dry mass distributions were similar. Frequency distributions for dry mass of flower heads produced by *Trifolium* individuals showed large variation in the pattern of reproductive output (Fig. 7).

DISCUSSION

Lower inequality for plants grown individually than for plants grown in competition is not consistent with Model 1, which predicts the greatest inequality among plants grown individually. If plant growth is exponential, interference reduces mean growth rate but increases the variance in growth rates. This is a definition of dominance and suppression for an exponential growth model.

Also, while Model 1 assumes that the growth of plants is exponential, this is true only during the earliest phase. Individual plant growth is better modelled by a Richard's equation or logistic function (Causton and Venus 1981), in which plant size levels off at maturity. The distribution of sizes of plants grown to maturity without interference may be a function of the maximum sizes plants can achieve in their environment rather than a function of their initial exponential growth rates. There may be genotypic or environmental factors that cause variation in maximum size, as well as variation in initial growth rates.

The sample size of nine for individually grown plants is low. But the biology of these plants, the behavior of the Gini coefficient, and the specific hypotheses being tested militate against the possibility of a Type I error (rejection of a true null hypothesis) in this case. The small sample size can lead to a Type I error if the G′ of the sample does not reflect the true population G. Since the hypothesis being tested is that the G for individually grown plants is smaller than for plants grown in competition, a Type I error will occur only if the G′ of the small sample of individually grown plants greatly underestimates the true population G for individually grown plants. The true population G could be greatly underestimated by these low-G′ samples if the population contained a small number of very large plants (much larger than any in the sample) that were not sampled. While such a possibility may exist statistically, it is almost inconceivable biologically. Also, although the sample sizes for individually grown plants are small, the difference in G′ between individually grown plants and those grown in competition occurs in all four cases and is quite large in three cases (Table 1).

The biomass distributions of individually grown plants also demonstrate the potential lack of correspondence between skewness and inequality addressed by Weiner and Solbrig (1984). *Lolium* plants individually grown in low-fertility soil have a size distribution that is highly skewed ($g_1 = 1.52$; Fig. 3A), but the coefficient of variation, and therefore the degree of inequality, is very low. These plants range in size from 10 to 17 g, i.e., the largest individual is only 70% larger than the smallest.

Mortality, which occurred in some high-density plots, tends to be concentrated among the smaller individuals (Watkinson et al. 1983), and therefore to reduce inequality. The fact that inequality increased from low to high density despite a similar trend in mortality further supports the dominance-and-suppression model.

In four out of six cases in monocultures (all *Lolium* monocultures plus the high-density, regularly spaced *Trifolium* populations) higher productivity due to high fertility resulted in increased inequality. The level of inequality did not change for *Trifolium* at low density. Inequality decreased with increased fertility in high-density, randomly sown *Trifolium* populations, which had the greatest mortality levels observed (≈20%). While both models predict increased inequality with increased productivity, under Model 1 the increase should be most pronounced in plants grown individually. Size inequality for *Lolium* plants grown individually did increase with fertility, but not signifi-

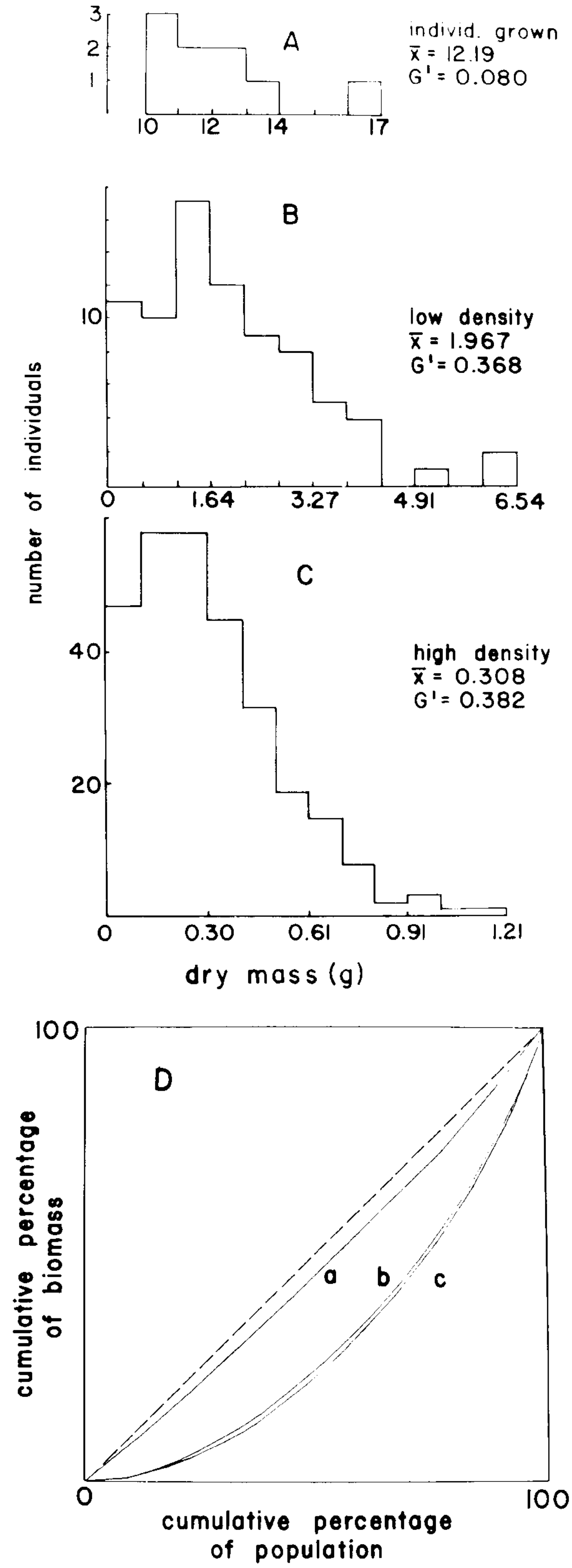

FIG. 3. Dry mass distributions (with inequality measured by the unbiased Gini coefficient G′) and Lorenz curves for monospecific populations of *Lolium multiflorum* grown in low-fertility soil. (A) individually grown; (B) low density (200 individuals/m^2); (C) high density (1200 individuals/m^2); (D) Lorenz curves for (A), (B), and (C).

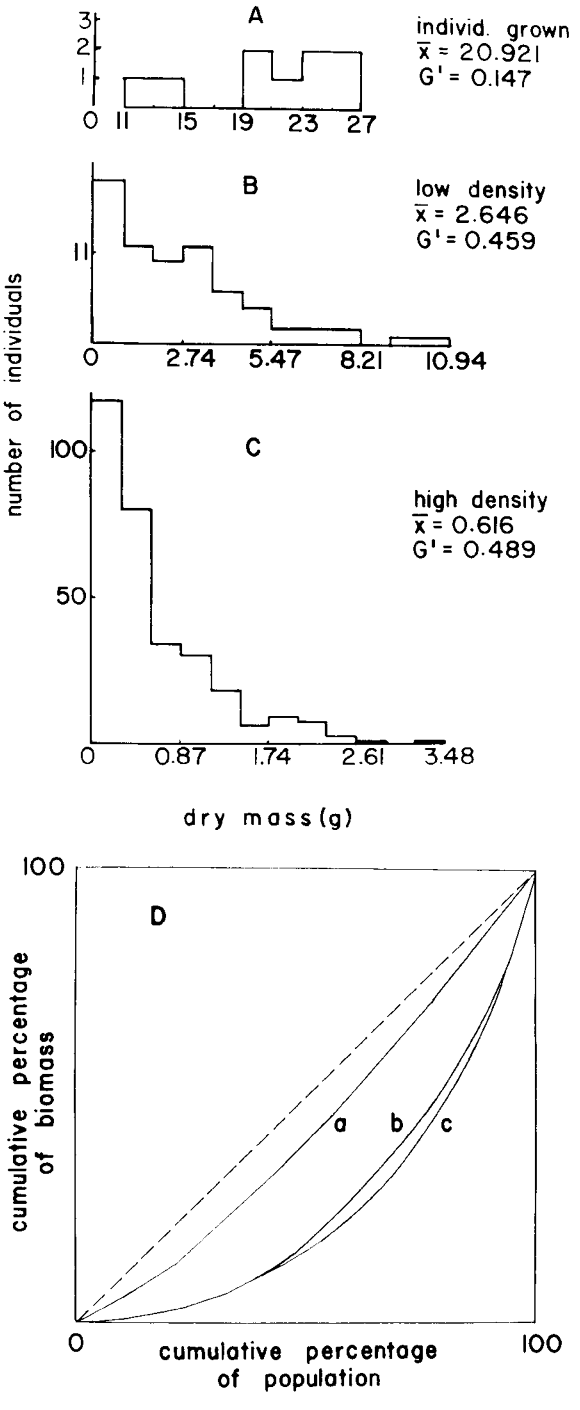

FIG. 4. Dry mass distributions (with inequality measured by the unbiased Gini coefficient G') and Lorenz curves for monospecific populations of *Lolium multiflorum* grown in high-fertility soil. (A) individually grown; (B) low density (200 individuals/m^2); (C) high density (1200 individuals/m^2); (D) Lorenz curves for (A), (B), and (C).

cantly; individually grown *Trifolium* showed a significant decrease in inequality at high fertility. These results are inconsistent with Model 1 and provide further support for the notion that size hierarchies in adult plants are not primarily due to the exponential phase of plant growth. Model 2 makes no claim for changes in size inequality without interference.

Dominance/suppression and self-thinning may both be due to competition for light. Competition for light is fundamentally different from competition for other resources in that it is "one-sided" (Watkinson et al. 1983). If a leaf of plant A shades a leaf of plant B, thus reducing the light available to plant B, that leaf of plant B probably does not reduce the sunlight available to the leaf of plant A. Dominance and suppression may occur under such circumstances. Competition for other resources may not result in dominance and suppression, and Model 1 could apply when competition for light is not important. For example, a plant's ability to take up water or nutrients is a function of the surface area of its roots. A small plant with relatively little root surface area will not be able to absorb as much of the soil nutrients as a large plant, but it may be able to take up an amount proportionate to its root surface area, and accordingly to reduce the nutrients available to its large neighbor. However, when competition for light is intense, the effects of interference are not shared in proportion to size; a small plant will not be able to get its share of this resource, and its growth will be reduced disproportionately. Thus, if plants do not grow to the point at which the canopy becomes closed and competition for light is important, we would not expect to see dominance and suppression. This may be why dominance and suppression were not observed in 44-d-old populations of *Festuca paradoxa* (Turner and Rabinowitz 1983).

The observed increase in size inequality with increased fertility in populations experiencing interference is related to the "Sukatschew effect" (Harper 1977): self-thinning occurs at increased rates in higher fertility stands. For equal planting densities, a more productive stand has a lower density of individuals after a period of growth than a less productive stand, although standing biomass is greater. The process of self-thinning is preceded by the formation of a very pronounced size hierarchy, and mortality is concentrated among the smaller, suppressed individuals. Increased productivity accelerates the processes of hierarchy development and self-thinning.

The relationship between self-thinning and population size structure is not understood. Size differences are always being generated by dominance and suppression and reduced by mortality of the smallest individuals. The outcome of these two opposing factors is unclear. While in general there has been great emphasis on investigations at the individual level, as opposed to studying mean plant behavior, the only predictive

TABLE 1. Unbiased Gini coefficients (G′) for dry mass distributions of monocultures. 95% confidence intervals were obtained from the "bootstrapping" procedure, using 1000 estimates of G.

		Plant spacing treatment†						
Soil treatment	Statistic	Individually grown		Low density (random)		High density (random)		High density (hexagonal)
Trifolium								
Low fertility	G′	0.235	*	0.377	**	0.621	**	0.341
	95% CI	(0.172–0.309)		(0.314–0.459)		(0.583–0.662)		(0.303–0.386)
		**		NS		**		**
High fertility	G′	0.088	**	0.376	**	0.482	NS	0.437
	95% CI	(0.053–0.127)		(0.329–0.429)		(0.441–0.529)		(0.400–0.484)
Lolium								
Low fertility	G′	0.080	**	0.368	NS	0.382	NS	0.357
	95% CI	(0.041–0.109)		(0.316–0.425)		(0.355–0.415)		(0.332–0.384)
		NS		NS		**		**
High fertility	G′	0.147	**	0.459	NS	0.489	*	0.545
	95% CI	(0.745–0.210)		(0.403–0.529)		(0.465–0.517)		(0.521–0.573)

† Asterisks denote significant differences between adjacent values based upon 95% and 99% confidence intervals (* $P < .05$; ** $P < .01$); NS denotes nonsignificant difference between adjacent values.

quantitative relationship elucidated so far, the −3/2 thinning rule, is a population-level phenomenon. The −3/2 thinning rule may be a special case of more general laws that can predict not only mean plant size but also fundamental aspects of plant size distributions.

The interaction between *T. incarnatum* and *L. multiflorum* was greatly influenced by density and nutrient levels (Fig. 5), as previously reported (Weiner 1980). Under high-fertility, high-density conditions, the effect of interspecific competition was equivalent to that of intraspecific competition. At low fertility and high density, *Lolium* individuals were, on average, more than twice as large in mixture as they were in monoculture: total yield of the *Lolium* increased when one-half of the *Lolium* population was replaced by *Trifolium*. This "positive neighbor effect," in which benefits to *Lolium* from *Trifolium* outweigh competitive effects, is presumably due to increased availability of nitrogen from *Trifolium*'s nitrogen-fixing symbionts. I reported earlier that total *Lolium* yield increased when one-sixth of the individuals were relaced by *Trifolium* (Weiner 1980).

Analysis of size inequality in mixtures provides additional support for the dominance-and-suppression model. The size distributions of both species in mixture were usually different from those in monoculture. In three of the four density-fertility combinations (Fig. 5a, b, c) *Lolium* benefited and *Trifolium* suffered in mixture as opposed to monoculture. *Lolium* showed decreased inequality in dry mass in mixture vs. monoculture in these three cases, while *Trifolium* displayed increased dry mass inequality in two of the three cases. Thus, changes in species composition of neighbors and changes in density may have similar effects on size distributions. Increases in interference appear to increase size inequality, whether this increase in the intensity of interference is due to a change in the density or the genotype of neighbors. When interspecific competition was indistinguishable from intraspecific competition (high density, high fertility; Fig. 5d) dry mass inequality in *Lolium* was almost the same in monoculture and mixture, while *Trifolium* displayed decreased dry mass inequality in mixture. Size inequality may serve as an index of a population's competitive status.

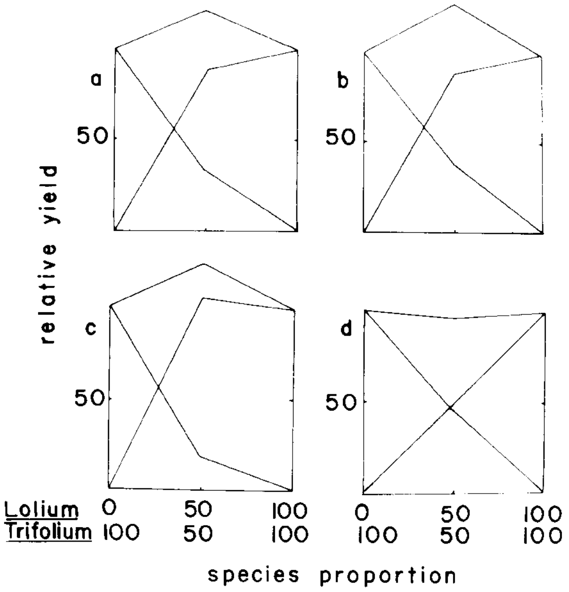

FIG. 5. De Wit replacement diagrams comparing relative yield of *Trifolium incarnatum* and *Lolium multiflorum* in mixtures and monocultures. (a) low fertility, low density; (b) high fertility, low density; (c) low fertility, high density; (d) high fertility, high density.

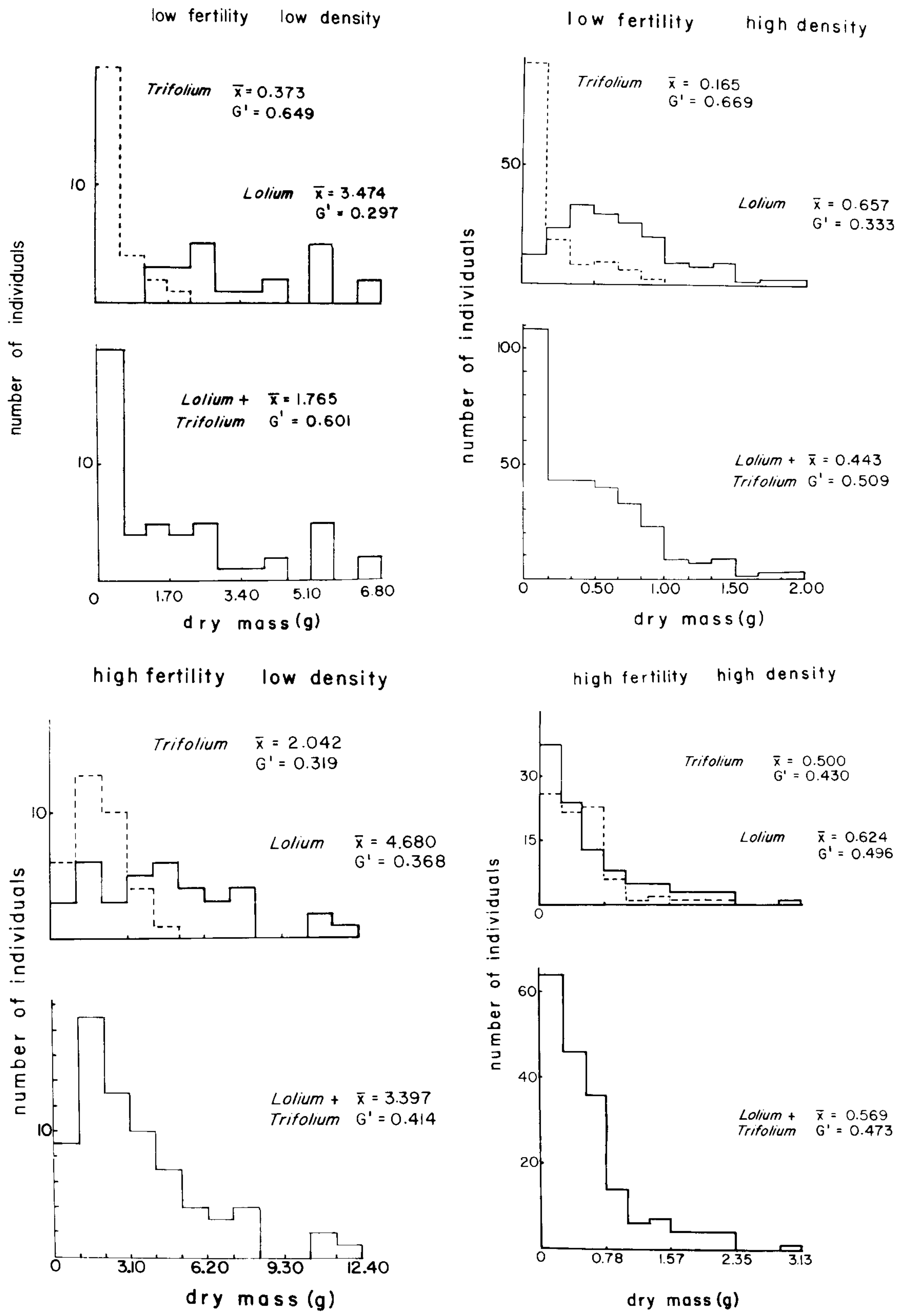

FIG. 6. Dry mass distributions (with inequality measured by the unbiased Gini coefficient G') for mixtures of *Lolium multiflorum* and *Trifolium incarnatum*.

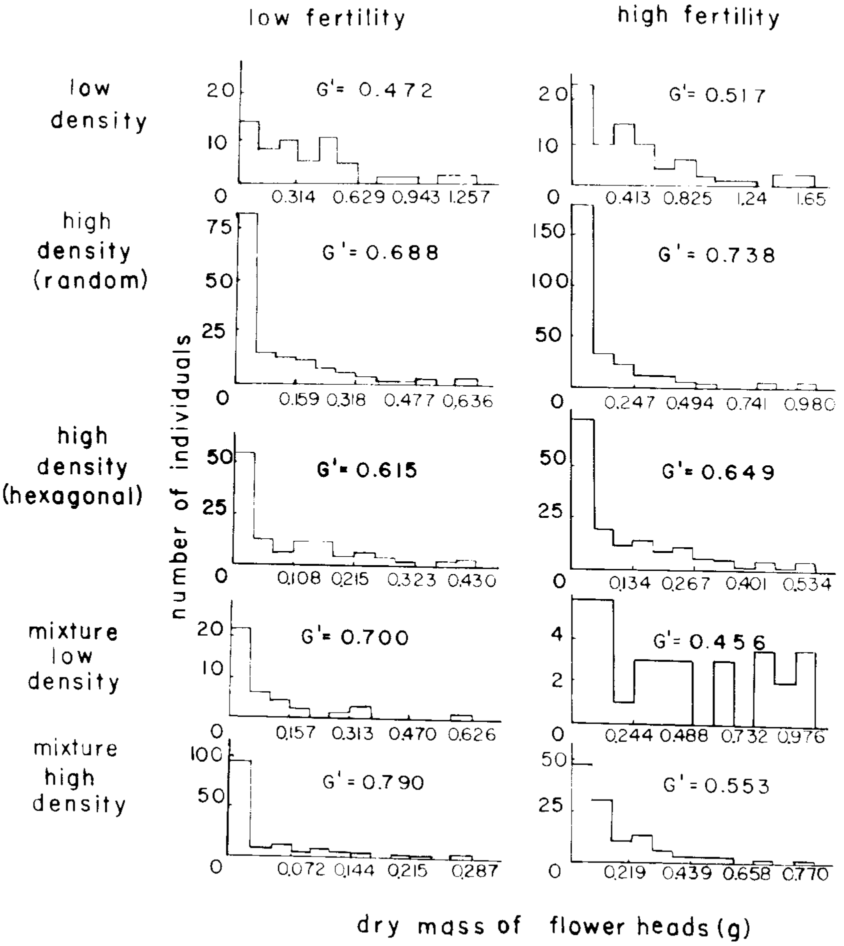

FIG. 7. Dry mass distributions (with inequality measured by the unbiased Gini coefficient G') of flower heads produced by *Trifolium incarnatum* individuals in experimental populations.

An increase in size inequality when a population is suppressed by interspecific interference occurs because the suppression is not shared equally within the population; high inequality occurs when there are a few large individuals. Some individuals escape suppression, perhaps because of local conditions, e.g., some individuals have few neighbors or emerge earlier.

While spatial differences among neighborhoods may be a factor in determining size differences in plants (Mack and Harper 1977, Hickman 1979, Liddle et al. 1982, Waller 1981, Weiner 1982, 1984), highly unequal population structure occurs even in regularly sown populations (Table 1). Plants with the highest leaves in the canopy will shade and suppress their neighbors. Differences in "available area" (Mithen et al. 1984) contribute to size differences, but other factors, such as relative emergence time (Ross and Harper 1972, Howell 1981, Watkinson et al. 1983), may often be more important. Regularly sown populations showed significantly lower size inequality than their randomly sown counterparts in one out of four cases, but randomly sown plants had lower inequality in one case. In these populations spatial pattern was not as important as other factors. This might be because when competition is for light, plants grow towards areas of greatest light availability. Phototropism alters the relative position of leaves with respect to the base of the plant, and this greatly influences the proximity of a plant to its neighbors, and other spatial relationships.

While the distribution of plant sizes was not normal, neither was it log-normal, as some models (e.g., Koyama and Kira 1956) suggest. Size distributions were skewed to the right, but log-size distributions (not shown) were skewed to the left. In 7 of 12 size distributions for monocultures, the hypothesis of log-normality could not be rejected if treated as the null hypothesis. However, this is extremely weak evidence in support of a model predicting log-normality. Bimodality has been reported at low (Rabinowitz 1979) or at high densities (Ford 1975) but there was no evidence for bimodality in these populations.

Size hierarchies are important in the evolution of plant populations because they result in reproductive hierarchies. In the results obtained here (using dry mass of flower heads as a crude measure of *Trifolium*'s reproductive output) inequality in reproductive output was always greater than the inequality in size. This would be expected if a plant must achieve a minimum size to reproduce, and if reproductive output is proportional to size above this minimum. Such a relationship has been observed in crop plants (e.g., Hedley and Ambrose 1981). The presence of nonreproducing plants increases reproductive inequality, as a measure of inequality is always increased by the addition of zero-value individuals to the sample. The existence of plants that are too small to reproduce emphasizes the similarity between size hierarchies and self-thinning. Although these small individuals may be alive physiologically, they have suffered genetic mortality.

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