OIKOS 47: 211–222. Copenhagen 1986

Size variability and competition in plant monocultures

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Weiner, J. and Thomas, S. C. 1986. Size variability and competition in plant monocultures. – Oikos 47: 211–222.

For most ecological and evolutionary questions, variability in plant size is best evaluated through measures of inequality such as the Gini Coefficient or the coefficient of variation. Models in which competition is "two-sided" ("resource depletion") predict unchanged or lower size inequality at higher densities after a given period of growth. Models in which competition is "one-sided" ("asymmetric competition") predict higher size inequality at higher densities. Of 16 published experiments which present data on the effects of density on size distributions in monocultures, 14 support the hypothesis that competition between plants is asymmetric.

During the development of an even-aged monospecific stand, size inequality increases over time until the onset of self-thinning, then inequality decreases as self-thinning progresses. In two independent data sets we found a linear relationship with a slope near −0.2 between size inequality (as measured by the Gini Coefficient) and log mean plant weight during self-thinning. This trend is also consistent with the asymmetric competition hypothesis.

Plant competition is usually "one-sided", and we suggest that this asymmetry is primarily due to competition for light.

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Для решения большей части экологических и эвлюционных вопросов, вариации размеров растений лучше всего определяются такими показателями, как коэффициент Джини или коеффициент вариации. Модели с "двусторонней" конкуренцией ("нехватка ресурсов") предсказывают неизменяющиеся или небольшие различия приболее высоких плотностях популяций при данной продолжительности периода роста. Модели, в которых конкуренция "односторонняя" ("асимметричная конкуренция") предполагают возрастание различий при повышении плотности популяций. Из 16 описанных опытов, где получены данные по влиянию плотности на распределение размеров в монокультурах, 14 поддерживают гипотезу о том, что конкуренция между растениями исходно асимметрична. В течение развития одновозрастного одновидового насаждения размерные различия увеличиваются со временем до начала самоизреживания, а затем неравномерность снижается, как и прогрессия самоизреживания. В 2-х независимых сериях данных мы нашли линейную зависимость от угла наклона - примерно 0,2 между величиной неравенства (по коеффициенту Джини) и логарифмом среднего веса растений в течение процесса самоизреживания. Эта тенденция сочетается с гипотезой асимметричной конкуренции. Конкуренция растений обычно "односторонняя", и мы полагаем, что эта асимметрия определяется изначально конкуренцией за свет.

Accepted 24 October 1985

1. Introduction

Within a population, plants vary in size. Larger individuals are more likely to continue to live than smaller individuals (Hiroi and Monsi 1966, Watkinson et al. 1983) and large individuals have more offspring than small individuals (Leverich and Levin 1979, Solbrig 1981). Thus, if allelic frequencies among the large plants are different from those in the rest of the population, size differences will have a major effect on allelic frequencies in subsequent generations. Future genetic makeup of a population will be determined by which plants are large, not just which plants survive. Size differences within plant populations may be determined by several factors, some of which affect plants' growth rates while some affect size in other ways. Differences in size may be determined by (1) age differences, (2) genetic differences, (3) environmental heterogeneity, (4) maternal effects, (5) differential effects of herbivores, parasites or pathogens, or (6) competition. In most cases, size distributions will be the result of interactions among these factors. This paper addresses the effect of competition on size variability in even-aged plant monocultures. In the first section, we discuss the statistical evaluation of size variability. The second section looks at models of plant growth and interference and the predictions these models make concerning competition and size distributions. Finally we examine the available empirical data on the relationship between competition and size variability in even-aged plant populations.

2. Analysis and interpretation of size variability

There has been considerable confusion about the analysis of size variability in plant populations. Many ecological and agronomic questions concerning size distributions are posed in terms of "plant-to-plant variation". The central parameters describing variation in classical statistics are the variance and the standard deviation. Since these parameters measure absolute rather than relative variation, they are inappropriate for most questions in plant population ecology. For example, we would expect a population of large plants to have a greater absolute variance in sizes than a population of small plants. The standard measurement of relative variation is the coefficient of variation (CV = standard deviation/mean, usually expressed as a percent). The coefficient of variation has been used by agronomists who are concerned with crop uniformity to look at the effects of various factors on it (Edmeades and Daynard 1979, Hedley et al. 1983). Some plant ecologists have also used CV to look at plant population structure (e.g. Naylor 1976). However, the discovery that most plant populations consist of many small individuals and relatively few large ones has focused research on the asymmetry or skewness of plant size distributions. Many recent studies have addressed the issue of skewness to the exclusion of relative variation. There has been little discussion of what positive skewness of a size distribution means biologically. It has been assumed by many researchers that all plant populations except those in the seed or seedling stage have highly skewed size distributions, but there are several reports of distributions which do not differ significantly from normal. Naylor (1976) and Windle and Franz (1979) reported normal distributions of shoot weights in barley at every harvest, and Hedley et al.'s (1983) size distributions for "leafless" peas (see below) are also not significantly different from normal. Andrzejewska and Falinska (1983) state that normal size distributions occur in stable populations under favorable invironmental conditions. Some researchers believe that skewness is the result of competition, and it has been proposed that skewness be used as a measure of interference (Higgins et al. 1984). In some cases researchers (Rabinowitz 1979, Hawthorn and Cavers 1982) have even calculated skewness for log distributions. The biological meaning of such a statistic is totally obscure, yet skewness is somehow believed to reflect a biologically important attribute. Highly variable, skewed size distributions have been called "size hierarchies" since the differences in size are thought to reflect "hierarchy of exploitation" (Harper 1977).

Starting with the somewhat vague concept of a size hierarchy as thought of by plant ecologists, Weiner and Solbrig (1984) showed that positive skewness of the size distribution reflects something very different. They proposed that it is the concept of inequality, such as studied by economists, which is synonymous with the concept of a size hierarchy. They went further and proposed the use of specific methods, the Lorenz curve and Gini Coefficient, to evaluate size inequalities. Inequality seems to be more relevant to ecological and evolutionary questions than is skewness. For example, Levin (1978) and Begon (1984) discuss the fact that size hierarchies and resultant fecundity variation will tend to reduce the effective population size (since many individuals may be too small to reproduce) and therefore should be expected to reduce genetic variation within the population. There will also be differences in size among those which are large enough to reproduce. Among those plants which do reproduce, large variation in fecundity will have a similar, although less extreme, effect to the "genetic mortality" of those individuals which do not reproduce at all. The concentration of genetic representation in the next generation by the most fecund individuals is exactly what is meant by inequality in fecundity. Since size is correlated with fecundity, size inequality is also of interest to the study of evolution. In terms of biomass, inequality represents the degree to which the biomass is concentrated within a small fraction of the population. This may be a useful thing for ecologists, agronomists and foresters to know. Since skewness is not a measure of inequality, researchers may have been looking at a parameter whose behaviour is weakly correlated with what is important.

Sen (1973) discusses the relative merits of different measures of inequality in studying distributions of wealth and income. Reasonable measures of inequality include the coefficient of variation, the standard deviation of the logs, Theil's measure of entropy and the Gini Coefficient. All these measures of inequality will be highly correlated. For example, for the 28 size distributions presented by Weiner (1985), the correlation between the Gini Coefficient and the coefficient of variation is 0.99.

There has also been some discussion of bimodality in plant size distributions. Bimodality has been reported in *Tagetes patula* (Ford 1975) at high density and in *Festuca paradoxa* (Rabinowitz 1979) at low density. Several authors have stated that bimodality can result from asymmetric competition, which produces distinct dominant and suppressed classes (Aikman and Watkinson 1980, Ford and Diggle 1981). Bimodality has not been defined statistically; therefore there is no statistical test for bimodality. Its visual appearance in a histogram is very sensitive to the number of size classes used. We do not find bimodality to be a generally occurring phenomenon in our examination of the published literature on size distributions of even-aged monospecific populations, but further study awaits clarification of vague concepts and the development of appropriate statistical tools.

3. Models of the interaction between competition and size distributions

We distinguish between two basic types of models of the interaction between competition and size distributions. We consider "resource depletion" or "two-sided" models to be those in which competition acts on all individuals equally or in proportion to their size. In the latter case, although large plants will have a greater effect on small plants than vice versa, small plants will reduce the growth or size of large plants in proportion to their relative sizes. In "resource pre-emption" or "one-sided" models, large plants suppress the growth of small plants more than they are suppressed, and this effect is greater than would be expected from their relative sizes. In most extreme form of "one-sided" competition, the growth of large plants would not be reduced at all by smaller individuals.

3.1. "Resource depletion" models of competition

3.1.1. An exponential "resource depletion" model

The first model of the generation of size distributions in plant populations comes from the work of Blackman (1919) and was further developed by Koyama and Kira (1956). Koyama and Kira considered a population of seedlings which were either equal in size or normally distributed. Each individual grows exponentially. Relative growth rates of individuals are also either equal or normally distributed. Thus, the size distribution of an even-aged population of plants is a function of (1) the distribution of initial sizes, (2) the distribution of relative growth rates, and (3) the length of time the plants grow. For such a model Koyama and Kira demonstrated that (1) if initial sizes are normally distributed but relative growth rates are all equal, the size distribution remains normal. (2) If initial sizes are all equal and relative growth rates are normally distributed, a log-normal size distribution develops. Combining the normal distribution of initial sizes and the normal distribution of relative growth rates gave similar results to (2). We have repeated Koyama and Kira's simulations with a computer program. Even if there is a correlation between the initial size of an individual and its relative growth rate, the effect of variance in growth rate seems to overwhelm any effect due to differences in initial size. In their model, the rate with which inequality (and skewness) develop is a function of the variance (in the strict statistical sense) in growth rates (Koch 1966). Only the variance in growth rates, not their mean value, determines the inequality and skewness of the size distribution after a given period of growth. Koyama and Kira clearly demonstrate that interference is not required for the development of skewed, highly unequal size distributions in even-aged populations.

The model of Koyama and Kira can be extended into a "resource depletion" model of plant interference (Turner and Rabinowitz 1983). In such a model, plants grow exponentially, and they vary in their relative growth rates. Competition acts to reduce the relative growth rates of all individuals by the same proportion. In doing so, it also reduces the variance in growth rates, and this reduces the variation in sizes which results from the growth rate differences. Plants experiencing competition will simply grow the same way as plants which are not competing, only more slowly. For a given period of growth, this model predicts that plants at high density will be smaller and show a less unequal size distribution than plants at lower density. Competition is "two-sided", and interference is like any other factor that reduces plants' growth rates.

There has been much confusion about the relationship between differences in plant size and differences in growth rate. It is true, of course, that plants attain whatever size they have through a process of growth from a smaller size. But this does not mean that questions of size variation can be simply reduced to questions of growth rate. The term "relative growth rate" (RGR) has two very different meanings in biology, and they are often confused. In one usage, the term RGR refers to the actual proportional increase in size over a given period of time. Observed RGRs are valuable descriptors of plant growth. In its other use, RGR is assumed to be constant and therefore an exponential model of growth is implied. Plant growth is exponential only in its earliest phase and the growth of individual plants is better modelled by asymptotic functions such as logistic, Richards or Gompertz equations (Hunt 1982). As in population growth theory, exponential models are only valid under a relatively restrictive set of conditions or for a relatively short period of time. It is true that much variation in size within a population is the result of variation in growth rates in the broad sense, but this does not seem to clarify the issue much if plant growth is not exponential. The generation of plant size distributions will ultimately be understood in terms of the utilization of resources. Resource utilization determines a plant's RGR, and is influenced by the abiotic and biotic environment, the latter including effects of neighbors through specific mechanisms of interference. RGR may be a useful descriptor of plant growth, but it is a result rather than a cause of growth.

3.1.2. A "resource depletion" model with sigmoid growth

Since plant growth is only exponential for a relatively short period and since modelling competition through reduction in exponential growth rates is somewhat arbitrary, it is reasonable to ask if similar results are obtained from a "resource depletion" model based on sigmoid growth of competing individual plants. One way to model growth and competition of individual plants based upon sigmoid growth is to use Lotka-Volterra competition equations. These were developed to model competing populations, (e.g. May 1981) but have also been used to model total production of plants in monocultures versus mixtures (Vandermeer 1981). In applying the Lotka-Volterra equations to growth of individuals, plants are viewed as populations of modules which grow logistically and interact through competition coefficients which quantify the effect of each individual on every other individual.

We have implemented such a model with a computer program. In implementing the model, we make the following assumptions: 1) Each individual, in the absence of competition, grows logistically: $dN/dt = rN\,(1-N/K)$ where N is the size or module number of a plant, r is its intrinsic rate of increase and K is its maximum size. Each of the parameters, r, K and N_0 (initial size) are independently distributed in a random, normal fashion within the population. We have used mean values of 1.0, 10,000 and 1.0, respectively for these parameters and a coefficient of variation of 20% for each of them. 2) When individuals are competing, the relationships between them are expressed through competition coefficients, which quantify the effect of each individual on every other individual. For each individual, N_i:

$$dN_i/dt = r_iN_i(1 - \sum_{i=1}^{n} \alpha_{ij}N_j/K_i)$$

where every individual is represented by an N_j, α_{ij} is the effect of individual j on individual i (α_{ii} is equal to 1.0), and n is the number of individuals. The competition coefficients also have an independent random normal distribution with a mean of 1.0 and a CV of 20%. This insures that the "law of constant yield" is in effect,

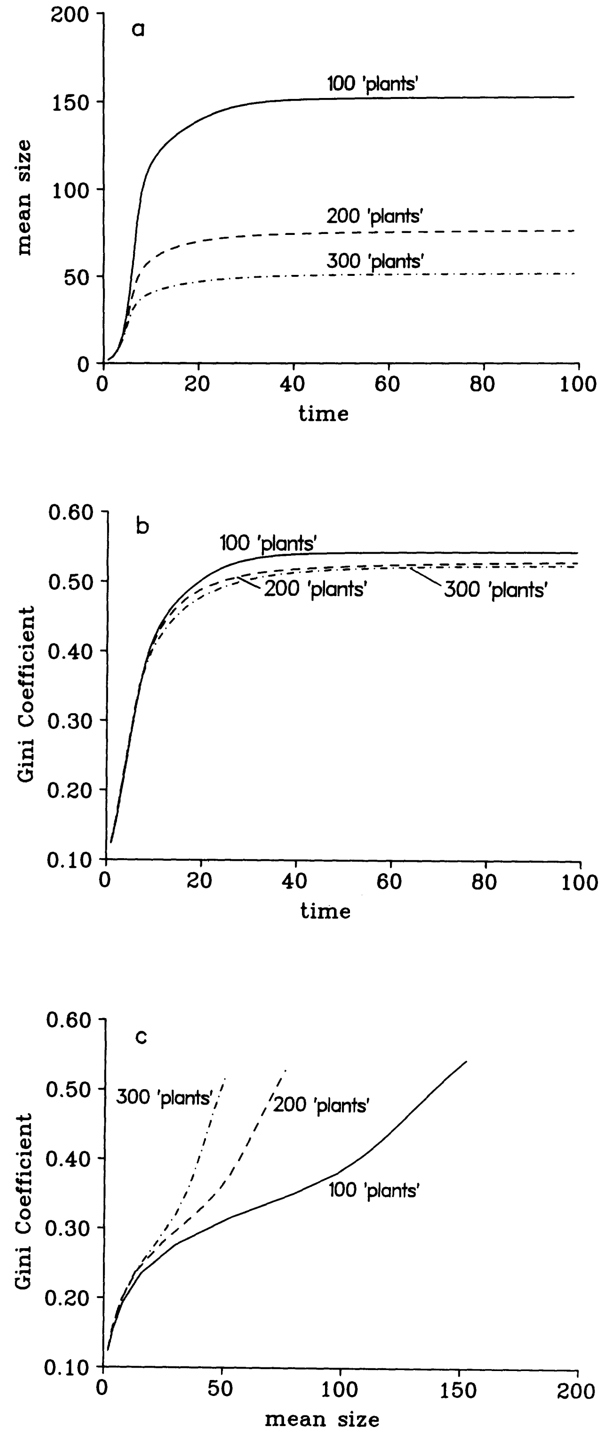

Fig. 1. Effects of density on size inequality in a »resource depletion« model based upon Lotka-Volterra dynamics. Initial sizes, relative growth rates, carrying capacities and competition coefficients are all distributed independently in a random normal fashion with a coefficient of variation of 20%. (a) changes in mean plant weight over time; (b) changes in size inequality over time; (c) relationship between mean plant weight and size inequality (see text).

i.e. increases in density (the number of populations of modules) will not result in increases in total yield. The plants cannot have negative growth rates and they maintain whatever size they achieve (if the Lotka-Volterra equations result in $dN_i/dt < 0$, dN_i/dt is set equal to 0).

The effect of three densities (100, 200, and 300 "plants") are shown in Fig. 1. At higher densities, mean plant weight at equilibrium is lower (Fig. 1a). Size inequality at equilibrium is also lower at higher densities (Fig. 1b). For a given mean plant size, higher density has higher inequality, but higher densities do not achieve high mean plant sizes (Fig. 1c). We have repeated these simulations using different mean values for the parameters (including a lower mean competition coefficient so that inter-individual competition will not be as severe as intra-individual competition). Increasing the number of competing individuals either decreases size inequality at equilibrium or has no significant effect on it. This model is similar to the exponential "resource depletion" outlined above in that competition is "two-sided"; it differs in that (1) plants are modeled by a sigmoid rather than an exponential growth function, and (2) the concept of competition is given more meaning through the use of carrying capacities and competition coefficients. We conclude that "two-sided" models of competition without mortality, whether exponential or sigmoid, predict lower or unchanged size inequality at higher density after a given period of growth.

3.2. "Resource pre-emption" models of competition

An alternative to "resource depletion" models of plant interference has been variously called "resource pre-emption", "one-sided competition", "asymmetric competition" (Begon 1984), and "dominance and suppression". Such models assume that larger individuals are able to get more than their proportional share of resources based upon their relative size and grow "at the expense" (Harper 1977) of smaller individuals. Competition does not reduce plant growth in the same way as other factors which reduce resource levels. One such model was developed by Aikman and Watkinson (1980). They used a modified Richards equation for individual plant growth and a complex competition function in which large plants have an advantage over small plants. In their competition function, the growth rate of individuals is (1) reduced as the total "area" covered by the population (defined as weight $^{2/3}$) approaches the available area and (2) affected by the individual's relative size within the population. Their model generated size distributions which are similar to those in Ford's (1975) experiments with *Tagetes patula.* Aikman and Watkinson's model differs from the Lotka-Volterra model presented above in that a different sigmoid growth function is used and, more importantly, competition is "one-sided" in their model. Another "one-sided" model of plant interference was presented by Ford and Diggle (1981). In their model, competition occurs between individual plants in space and is determined by differences in plant height. Taller plants suppress the growth of shorter plants but not vice versa; thus their model is totally "one-sided". Their model generated bimodality in the heights of individuals in the population. Both Aikman and Watkinson, and Ford and Diggle used their models to ask questions about changes in the size distribution as a stand develops, but they did not discuss the effects of initial density on size distributions. Their formulations would be expected to produce higher inequality at higher densities after a given period of growth (in the absence of significant mortality) since the "one-sided" interactions would begin sooner at higher density. "One-sided" models based on overlapping "zones of influence" (e.g. Gates 1982) do show increases in inequality with increases in density (Weiner, unpubl.). We conclude, on the basis of the available evidence, that "one-sided" models predict greater inequality at higher densities after a given period of growth.

3.3. Analytic versus mechanistic models of stand development

Several powerful analytic methods for simulating changes in plant size distributions over time have been developed by Japanese researchers. Simulation models have been based upon distribution density functions (Hozumi et al. 1968), finite difference equations (Yamakura and Shinozaki 1980), and diffusion equations (Hara 1984a, b). These models can be fit to data and predictions can be made about stand development. Similarly, Westoby (1982) suggests that we look at changes in size distributions as the result of the operation of "distribution modifying functions" (DMF's) acting upon size distributions. These are functions relating the increment of a size measure to the same size measure across all individuals in the stand at a point in time. This approach assumes that growth rate in the presence of competition is primarily a function of relative size and (if the DMF's are to be tractable) that the relationship between growth rate and relative size does not change as plants grow. The flexibility of these methods is such that they can be used to simulate many possible dynamics of stand development, including "one-sided" or two-sided" competition. Thus they do not make specific predictions concerning the effect of density on size variability. They represent analytic tools which can be used to analyze data and test theoretical models, but they are not explanatory theories.

Hara (1984a, b) has developed stochastic analytic models of changes in plant size distributions based on the mean growth rate of individuals of the same size (G(t,x) function or DMF) and the variance in growth rate of individuals of the same size (D(t, x) function). He has fit this model to data from experimental populations of *Helianthus annuus.* His model shows increases in the coefficient of variation of size with time and with density (Hara, unpubl.).

Questions of size distributions and interference must

Tab. 1. The effect of density on size inequality in even-aged plant monocultures. Measures of inequality: Coefficient of Variation (CV); Gini Coefficient (G); Theil's Index (T). G has been calculated from published or raw data whenever possible; other measures of inequality are those published. Ind. grown: each plant in its own container.
+ G calculated from raw data provided by authors
* G calculated from published data

Species	Densities (ind m^{-2})	Max age (d)	self-thinning?	Results	Notes	Author & date
Linum usitatissimum	60 1440 3600	"maturity"	?	G increases with density at each harvest*	no sample sizes; frequencies do not add to 100%	Obeid et al. (1967)
Lolium perenne	600 1200 2400	189	yes	CV increases with density and time		Naylor (1976)
Zea mays	5 10 15 20	130	no	CV increases with density at later harvests		Edmeades and Daynard (1979)
Plantago major *P. rugelii*	400 2000 10000	76	no <15% <74%	G incr with density$^+$	Fig. 2	Hawthorn and Cavers (1982)
Pisum sativum var. "leafless"	100 123 156 204 277	"maturity"	no	G and CV increase with density in all 12 cases*	3 genotypes grown at 5 densities; Fig. 3	Hedley et al. (1983); Ambrose and Hedley (1984)
Danthonia caespitosa	ind. grown 500 1100	122	no	G and CV increase with density in 19 and 20 out of 24 cases$^+$	seeds from 4 populations grown under 3 temp. regimes	Quinn and Hodgkinson (1983)
Festuca paradoxa	10000 20000 40000 80000 100000	41	no	no trend in G with density*		Rabinowitz (1979)
F. paradoxa	ind. grown 80000	44	?	G higher for ind. grown*		Turner and Rabinowitz (1983)
Trifolium subterraneum	400 1600 3600	160	no no some	CV increase with density after 90 days		Stern (1965)
Trifolium incarnatum *Lolium multiflorum*	ind. grown 200 1200	92	no no <20%	G increase with density in all 8 cases	2 fertility levels	Weiner (1985)
Lychnis flos-cuculi	100 1000	56	little or none	T increase with density in all 4 cases	2 fertility and 2 moisture levels	Andel et al. (1984)
Urtica dioica	ind. grown 9 per pot	91	no some	T higher with interference after 63 days		"
Helianthus annuus	200 400 800 1600	67	yes	CV increases with density when self-thinning is not occurring		Hara (1984b) Hara (unpub.)
Picea sitchensis	0.003 0.05 0.08 0.15 0.30	21 years	no	G correlated with density ($p<.05$)*	trees thinned to different densities at 11 years, data collected 9 years later	Jack (1971)

eventually be reduced to questions of the mechanisms of growth and interference. Some mechanisms of interference (e.g. some forms of root competition) may fit within the resource depletion model, whereas other competitive mechanisms (e.g. shading) may result in resource pre-emption. A reductionist model for the generation of plant size distributions should (1) describe the growth of individuals in terms of resource utilization in the absence of interference and (2) describe how the interactions between plants changes the growth of individuals through mechanisms of resource reduction, and other neighbor effects. Such models will provide the basis for understanding and predicting observed relationships between competition and size inequality.

4. Empirical studies

The classical way of studying the effects of competition on plant populations is to look at the relationship between mean plant weight and density. This relationship has been studied in two contexts:

(1) Density as the independent variable – the effect of density on mean plant weight. Populations are grown at different planting densities and, after a given period of growth, mean plant weights are compared. Several quantitative relationships have been described (reviewed by Harper 1977 and Watkinson 1980).

(2) Time as the independent variable – correlated changes in mean plant weight and density as density-dependent mortality (self-thinning) occurs. Populations are harvested or measured at different ages and the relationship between density and mean plant weight of survivors is studied. The self-thinning rule has been described, and its generality and theoretical basis have been debated (Yoda et al. 1963, White and Harper 1970, White 1980, Westoby 1984).

Our goal is to extend these analyses to address the question of size variability. Taking a reductionist approach, it seems reasonable to (a) study the effect of density on size distributions in the absence of self-thinning, and (b) study the relationship between self-thinning and size distributions. The ultimate goal is to build a comprehensive model which addresses both these issues.

4.1. Density and size inequality

With respect to specific hypotheses addressing the behaviour of size distributions with changes in density, we conclude that models in which competition is symmetric, (i.e. in which a plant's ability to compete is proportional to its size, such as the Lotka-Volterra model presented above) predict decreased or unchanged inequality with increased density. Models in which competition is asymmetric (e.g. Aikman and Watkinson 1980, Ford and Diggle 1981) predict increased inequality with increased density.

While there are numerous agricultural and ecological studies in which density is the independent variable, size distribution data are available for relatively few. In reviewing studies in which size distribution data have been published, we have encountered two major problems. First, inequality has not been calculated, and often the data are presented in a way which does not permit an estimate of inequality to be calculated. Many authors present size distributions as a specified number of equal size classes without units (e.g. Koyama and Kira 1956, White and Harper 1970, Ford 1975, Bazzaz and Harper 1976, Mohler et al. 1978). In these cases the raw data must be obtained and analyzed if inequality is to be estimated. Self-thinning poses a second problem. Density dependent mortality is concentrated among the smallest individuals, and will reduce size variability and therefore inequality (see Sect. 4.2 below). Since we are observing the outcome of two opposing factors, it is impossible to assign exact roles to each factor. Thus, we limit ourselves to studies in which density is the independent variable and in which mortality is less than 20%.

Tab. 1 summarizes the results of sixteen experiments in fourteen studies in which density is an independent variable and for which size distribution data or size inequality measures are available. In some cases the authors have calculated a measure of inequality (usually the Coefficient of Variation). Whenever possible we have calculated the Gini Coefficient from published histograms or, when authors have provided them to us, from the raw data.

One of the most frequently cited studies on size distributions and competition is Obeid et al.'s 1967 study on flax. Their data for three densities and three harvest dates does show increases in inequality with density at each harvest. However, we must be cautious in interpreting their results because their paper provides no sample sizes, no information on mortality and in only four of the nine size frequency distributions presented do the frequencies add up to between 96 and 100%. Still, such typographical errors are unlikely to affect the general trend or their conclusions. Results of Hawtorn and Cavers (1982, Fig. 2) are typical. Despite mortality, which will tend to reduce inequality, inequality is higher at higher density. Hedley et al.'s (1983) results for "leafless" peas (Fig. 3) are of special interest. The size distributions of this variety are seen as one of its major agronomic advantages. The populations are not highly skewed and skewness does not increase with density. Inequality, however, does increase with density. While the range of densities they studied is appropriate for the agronomic questions they are addressing, it would be considered narrow for an ecological study.

Of the sixteen experiments cited in Tab. 1, fourteen show increases in inequality at higher densities. We must reject the hypothesis that interference acts like any other factor which reduces resource levels ("resource depletion"). From the point of view of a living, growing plant, resource reduction caused by another living, growing plant is very different from resource reduction

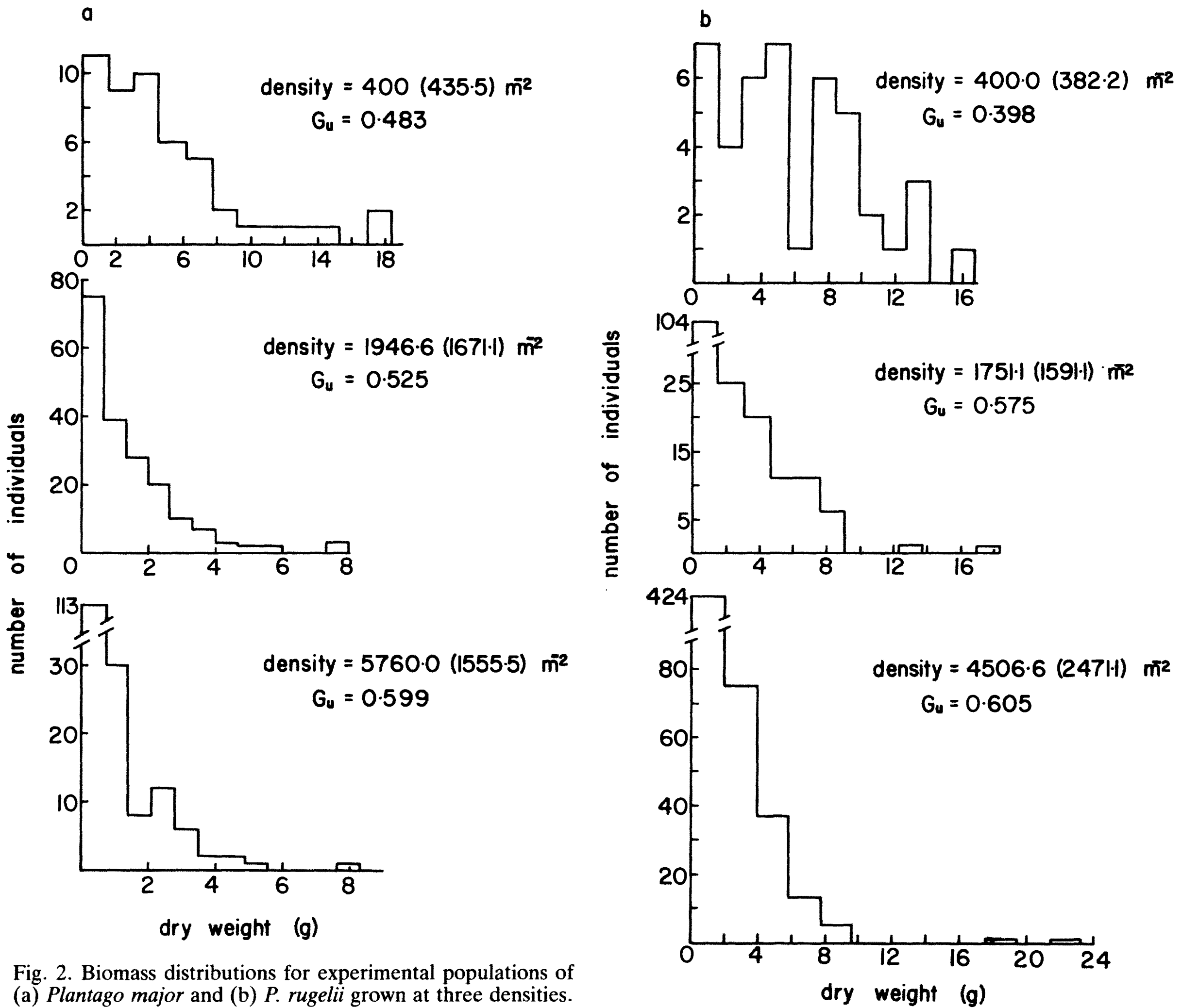

Fig. 2. Biomass distributions for experimental populations of (a) *Plantago major* and (b) *P. rugelii* grown at three densities. Density of survivors is in parentheses. G_u is unbiased estimate of the Gini Coefficient (after Hawthorn and Cavers 1982).

due to abiotic factors. We conclude that density decreases the overall growth rate of plants, but also increases the variance in growth rates. This is the outcome expected from asymmetric competition.

The only results which do not show increasing inequality with increasing density are those of Rabinowitz (1979) and Turner and Rabinowitz (1983) on *Festuca paradoxa*. The most notable difference between these and other studies is that the plants were grown for a relatively short period of time (41 and 44 d, respectively). While interference is occurring in these studies (mean plant weight is lower at higher densities), competition is probably for nutrients, since the plants would probably not be large enough to shade one another. Weiner (1985) suggests that the resource depletion model may apply when competition is not for light, and this may be the case when plants are grown for very short periods. Later, when competition for light develops, dominance and suppression occur. The results of Andel et al. (1984) on *Urtica dioica* are illuminating in this context. They compared inequality in individually grown and competing individuals at five harvest dates. Inequality was higher for individually grown plants after 5 and 7 wk, but inequality was higher for interfering plants after 9, 11 and 13 wk. Thus early plant interference appears to behave according to the resource depletion model, whereas later plant interference results in dominance and suppression. Turner and Rabinowitz suggest that the absence of dominance and suppression in *F. paradoxa* may be due to the graminoid growth form, but dominance and suppression are observed in the studies on grasses by Edmeades and Daynard (1979), Quinn and Hodgkinson (1983) and Weiner (1985). Plant growth form may influence size variability: if dominance and suppression result from competition for light, then we would expect growth forms which

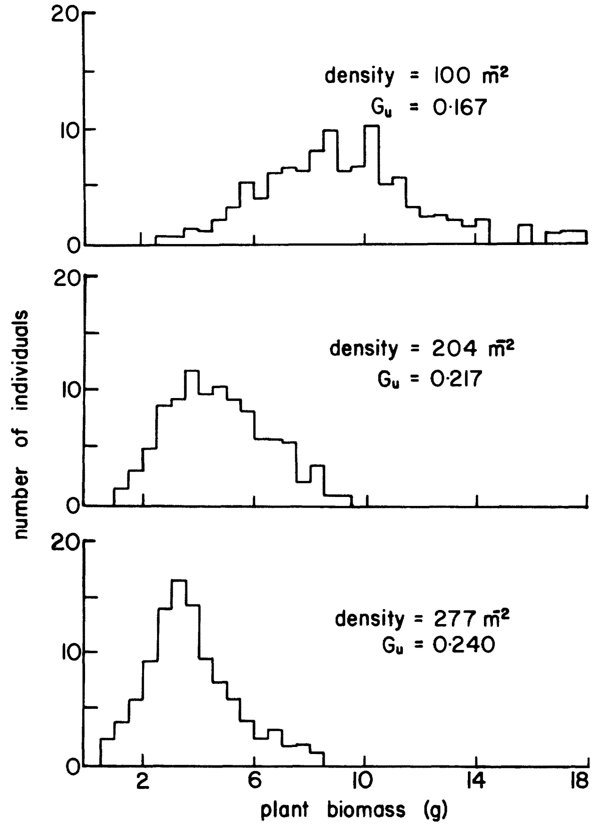

Fig. 3. Biomass distributions for populations of the »leafless« genotype of *Pisum sativum* grown at three densities. G_u is unbiased Gini Coefficient (after Hedley et al. 1983).

result in quicker and/or more extensive shading of individuals by others to result in competition which is more one-sided. Thus we might expect grasses to be less prone to dominance and suppression than broad-leaved plants. But when competition for light does occur, i.e. when the canopy is closed and the community is close to its maximum leaf area index, dominance and suppression will occur. While competition for light may not have been a significant selection pressure in the evolution of certain growth forms, growth form cannot prevent dominance and suppression from occurring when plant size and density make light a limiting factor. Growth form may thus affect the extent, but not the existence, of the asymmetry.

4.2. Self-thinning and size inequality

Predictable changes in size distributions may accompany self-thinning (Mohler et al. 1978, Weiner 1985). Asymmetric competition and other factors will continually generate and exaggerate size differences, but mortality of the smallest individuals will reduce size variability. Mohler et al. (1978) found that skewness is greatest at the onset of self-thinning and decreases as mortality proceeds. The Coefficient of Variation of sizes goes down during self-thinning in wave-generated *Abies* stands in Japan (Kohyama and Fujita 1981). Analysis of Ford's 1975 data on *Tagetes patula* (Fig. 4) also supports this hypothesis. Size inequality increases before mortality is extensive, then decreases as mortality proceeds.

The only data on size distributions during extensive self-thinning are for coniferous forests. The first of these are the huge data sets on *Pinus ponderosa* collected in the 1930's by Meyer, which have been analyzed by White (1980) to study self-thinning. The data consist of predicted diameter distributions for stands of numerous ages on sites of differing productivities ("site indices") over vast areas of the western U.S. Although

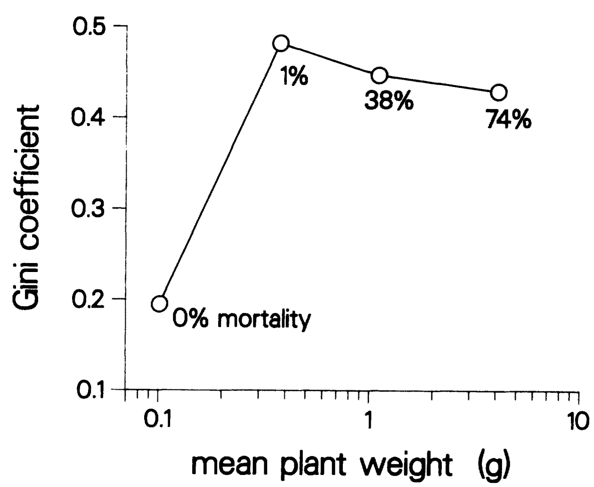

Fig. 4. Changes in Gini Coefficient with mean plant biomass for sequential harvests (2, 4, 6 and 8 wk) of experimental populations of *Tagetes parula* (after Ford 1975).

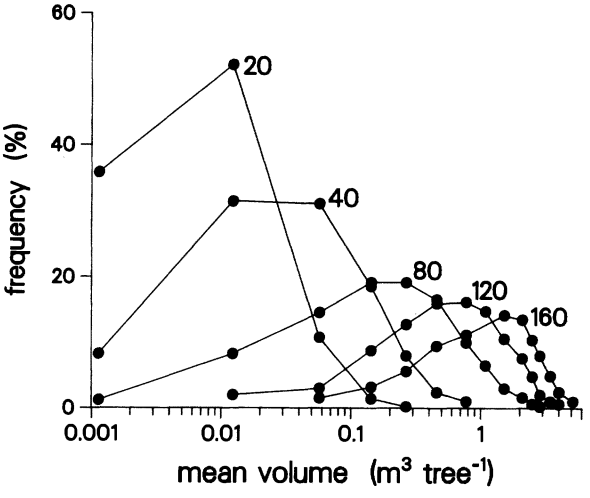

Fig. 5. Size distributions for even-aged stands of *Pinus ponderosa* of site index 80. Numbers are stand ages in years (from J. White, unpublished, data from Meyer 1938).

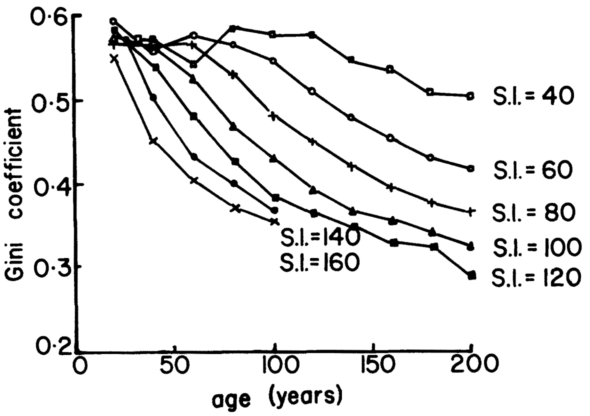

Fig. 6. Changes in the Gini Coefficient with age in even-aged stands of *Pinus ponderosa*. Numbers refer to the "site quality index" (data from Meyer 1938).

Meyer's data are predicted values based on a visual curve fitting procedure which is not clearly described in his paper, the unequalled volume of data, the care with which they were collected, and the fact that his curve-fitting could not have been influenced by recent models such as those we are investigating, make his data sets valuable resources. Fig. 5 shows size distributions (log scale) for some of these stands of site index 80. White (1980) has studied self-thinning in these stands; the slope of the log mean stem volume versus log density relationship is −1.50. The Gini Coefficient decreases as mean stem volume increases and density decreases. The rate of decrease in G in Meyer's *P. ponderosa* stands is faster in the more productive stands (Fig. 6). This is a result of the "Sukatshew effect" (Harper 1977) in which self-thinning proceeds more quickly in more productive stands. When the Gini Coefficient is plotted against log mean stem volume (Fig. 7) for all of Meyer's stands, a linear relationship between log mean plant weight and G develops. The slope of this line is −0.21. This is especially interesting in view of the fact that these stands represent different ages and site qualities and do not even have the same self-thinning trajectories (Westoby 1984). Surprisingly similar results are obtained from data on 31 wave-generated *Abies balsamea* forests (Mohler et al. 1978, Sprugel 1984, Sprugel, unpubl.). These stands show self-thinning with a slope of −1.24 (Sprugel 1984, Fig. 8). G increases with log mean plant weight until self-thinning is extensive, then decreases (Fig. 9). The slope of this decrease is −0.195 which is very close to the slope for Meyer's *Pinus ponderosa* stands. The theoretical basis for this is yet obscure. Just as there are quantitative relationships between mean plant weight and density (self-thinning trajectories), there are also quantitative relationships between mean plant weight and other aspects of the size distribution,

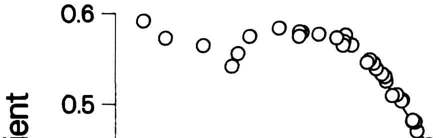

Fig. 7. Relationship between the Gini Coefficient and mean plant weight for 58 stands of *Pinus ponderosa* of different ages and on different quality sites. The least square linear regression for the linear portion of the graph is y = 1.04 – 0.208 log x (data from Meyer 1938).

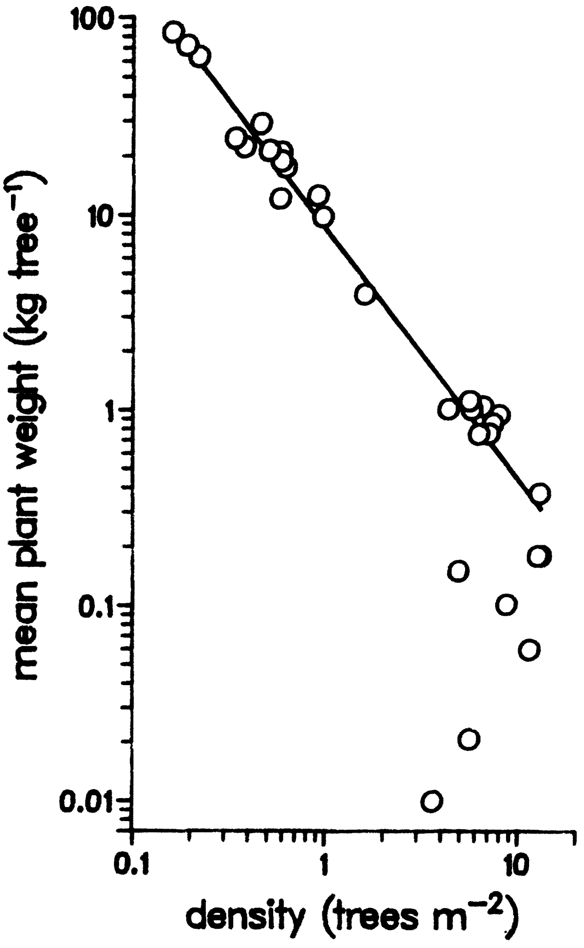

Fig. 8. Self-thinning in 31 wave-regenerated stands of *Abies balsamea* in the Northeastern United States. The slope of the log mean plant weight vs. log density relationship is −1.24 (unpublished data from D. Sprugel).

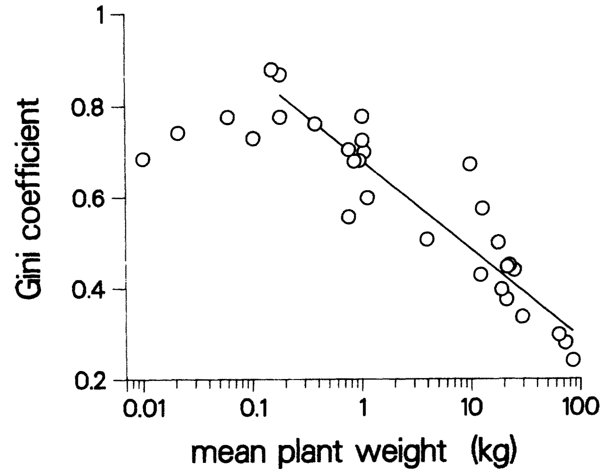

Fig. 9. Relationship between the Gini Coefficient and mean plant weight for *Abies balsamea* stands. The least square linear regression for the descending portion of the graph (excluding the five smallest mean plant weights) is y = 0.68 – 0.195 log x (unpublished data from D. Sprugel).

such as inequality. Size inequality appears to increase until the onset of self-thinning, then decreases as self-thinning progresses.

The observation that size inequality decreases during self-thinning is consistent with the hypothesis that competition asymmetry and self-thinning are due to shading. Before plants compete for light they are able to acquire resources, including light, in proportion to some aspect of their size. When the canopy closes, plants begin to shade each other. Larger plants get more than their share of the light resource. An individual which is half the size of its neighbors will not be able to get half the amount of solar energy, but it may be able to get enough light to survive and grow. After the community's leaf area index has reached its maximum, plants continue to grow although community photosynthesis cannot increase further. When the plants are large, it may be impossible for an individual which is half the size of its neighbors to get sufficient light to survive. For a given density, proportionately smaller individuals will get a smaller proportion of the available light when mean plant size is large than when it is small. Because of the two dimensional nature of the light resource and the three dimensional nature of competition for it, a greater degree of relative size variation can be tolerated when mean size is small than when mean size is large. In a stand of large trees with a fully closed canopy, small individuals may get very little light, unless they are located near canopy gaps. According to this view, we would expect size inequality to decrease after the leaf area index reaches its maximum, as observed.

We conclude that current theory is inadequate to describe or predict the interaction between plant growth, interference and size distributions. Future model building should be based on resource utilization of individual plants, which is changed in predictable ways by interference and determines the distribution of growth and death within a population. A comprehensive theory which explains the relationships between the growth of individual plants, density-yield relationships, size distributions, and self-thinning is waiting to be uncovered.

Acknowledgements – We thank D. Sprugel for unpublished data on *Abies balsamea* displayed in Figs 8 and 9; J. White for providing us with Fig. 5; J. Quinn for raw data on *Danthonia caespitosa* for Tab. 1; W. Hawthorn for raw data on *Plantago* spp. for Tab. 1 and Fig. 2; F. Amador and R. Woodley for help with the computer simulations; T. Hara for unpublished manuscripts; R. Wallach for help with data analysis and artwork. D. Sprugel, M. Hutchings and J. White provided helpful comments on an earlier draft of this paper. This research was supported by a grant from the Research Corporation and Swarthmore College Faculty Research Funds.

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