

5. VARIATION IN THE PERFORMANCE OF INDIVIDUALS IN PLANT POPULATIONS

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SUMMARY

1 Within plant populations there is much variation in size. This variation is extremely important, because size is correlated with both survivorship and fecundity, and therefore with Darwinian fitness.

2 Size variability can be evaluated with measures of inequality, such as the coefficient of variation or the Gini coefficient. Variation in size results from the interactions between several factors, about which very little is known.

3 Monocultures grown at high densities show greater variability in size than those grown at lower densities, supporting the hypothesis that competition is asymmetric. There is experimental evidence that this asymmetry is primarily due to competition for light. During density-dependent mortality (self-thinning) size variation among the survivors decreases, and this is also consistent with the hypothesis that asymmetric competition (and density-dependent mortality itself) are driven by shading.

4 Age differences are a primary determinant of size variation in populations with large variation in age. Even small age differences can act indirectly by establishing size differences, which then become exaggerated by competition or other factors. The fact that plant growth is sigmoidal has important implications for size differences in populations comprised of mixed age groups.

5 Herbivores may increase size variation by generating size differences which can persist or become exacerbated, but they may also reduce variation by removing large individuals or by reducing the intensity of competition. The most important effects of herbivory and disease on size variation may occur through interactions with competition.

6 There are two contrasting views of the role of size variation in the evolution of plant populations. Size differences may be a reflection of genotypic differences, in which case size (and resultant fecundity) variation will be a vehicle by which natural selection acts. Alternatively, size differences may be due to non-genetic factors, and result in genetic drift.

INTRODUCTION

Variation within a population is central to the Darwinian view of evolution. Darwin's theory of evolution by natural selection has two axioms:

- 1 There is heritable variation within the population.
- 2 Variants differ in their survival and reproduction, and consequently leave different numbers of descendants.

Genetic variability is necessary if natural selection is to operate, but differential survival and reproduction of genotypes must be expressed through the phenotype. Thus, when one is studying variation in the performance of individuals within populations, one is looking at a central process in Darwinian evolution. In plants, performance suggests growth or vigour, but in the evolutionary context it is perhaps best thought of as survivorship and fecundity, which encompass most of what we think of as fitness. Within a population of plants, size is highly correlated with survivorship (Solbrig 1981) and reproductive output (Samson & Werk 1986), and in this chapter I will consider size variation to be a reflection of variation in Darwinian fitness.

Size variation within species which have indeterminate, modular growth such as plants is much greater, and fundamentally different in its causes and implications, than size variation in non-modular organisms such as most animals. While larger individuals have an advantage over smaller individuals in many animal species (e.g. it is the large dominant bull sea-lion which has the largest harem), the nature of this advantage may be quite different. Plants grow by producing more modules, and plants increase fecundity by producing more reproductive modules. Thus there is an almost inevitable correlation between size (module number) and fecundity. Size advantage within a population of non-modular organisms may not be a direct result of their growth form, but may occur through more indirect mechanisms.

This chapter will attempt to review what is known about the causes of size variability in plants, discuss the implications of variation in size for the evolution of plant populations, and look towards some of the most critical questions for current research efforts.

CAUSES AND MEASURES OF SIZE VARIATION

Differences in the sizes of plants within a population will be determined by the following factors and interactions between them: (1) interference (competition), (2) age differences, (3) differential effects of herbivores,

parasites or pathogens, (4) genetic differences, (5) environmental heterogeneity, (6) maternal effects.

Very little is known about most of these factors, and even less is known about their interactions (which may be more important than the direct effects of each). We are at the point in the study of size variation where we are often able to say only that X has an effect on size differences, without yet knowing how this comes about. It is quite easy to show that something has an effect on something else, and ecologists spend much effort demonstrating this for one factor after another. Most things do 'have an effect', but we need to go further and understand the mechanisms which produce the effect if we are to make population biology a predictive science. At this point we can make only the most general predictions.

The most common measures of variation are the variance and the standard deviation (S.D.). Since these are measures of absolute rather than relative variation, they are usually inappropriate for the evaluation of size variability. One would expect a population of large plants to have larger absolute variation in size than a population of smaller plants. What is needed is a measure of relative variation, such as the coefficient of variation

$$\text{C.V.} = \text{standard deviation/mean}$$

usually expressed as a percent. It has been argued that variability in size is synonymous with size inequality (Weiner & Solbrig 1984), and is best evaluated by measures of inequality. Measures of inequality include the coefficient of variation, the Gini coefficient, the S.D. log-transformed values, and Theil's index (Sen 1973). Each of these measures has specific advantages and disadvantages, but all such measures of inequality are highly correlated. Thus, the relative merits of each may be of more interest mathematically than biologically. Measures of skewness or asymmetry of the size distribution are not measures of variability and are only weakly correlated with them. Although the biological meaning of the skewness of a size distribution is obscure, it is used by some researchers as a measure of variation.

There is a need for mathematical methods to evaluate variability in size and survival together. When reproductive output is the measure of performance, it would seem reasonable to look at inequality in cumulative life-time fecundity. Individuals which die before reproducing have zero contribution to population reproductive output. But when size is the measure of performance the evaluation of the survival and size variability together is more problematic. Mortality is often concentrated among small plants, decreasing variability among survivors. This confuses the interpretation of studies in which there is significant size variability and mortality.

Taking a reductionist approach, which may not be the ideal approach

(Levins & Lewontin 1985), but is perhaps the best currently available, I will review what is known about the first four of the above-mentioned factors which influence individual variation (even less is known about the last two), using simple models and available data. The next step for researchers is to study the interactions among these factors, which ultimately determine differences in the performance of individuals. Finally, I consider the role of size variation in the evolution of plant populations.

INTERFERENCE

There has been much interest in the effect of competition or interference on size differences within plant populations. Significant progress has been made and a general picture may be emerging. Benjamin & Hardwick (1986) discuss models of interference in their recent review of variation in even-aged plant stands, and Weiner & Thomas (1986) have reviewed the available data on the effect of intraspecific competition on size variability. My goal here will be to summarize briefly what is known, discuss some recent work, and indicate some important unanswered questions.

The study of competition begins with the relationship between mean plant size and density. This relationship has been studied in two ways (Weiner & Thomas 1986):

- 1 Density as the independent variable—the effect of density on mean plant size. Populations are grown at different planting densities and, after a given period of growth, mean size (usually weight) is evaluated as a function of density. Several quantitative models of the relationship between mean plant weight and density have been developed (Holliday 1960; Watkinson 1980; Vandermeer 1984).

- 2 Time as the independent variable—correlated changes in mean plant size (or total biomass) and density as density-dependent mortality (self-thinning) occurs. Populations of the same initial density are harvested or measured at different ages and the relationship between density and mean plant weight of survivors is studied. The ‘self-thinning rule’, a quantitative relationship between density and mean weight of survivors, has been described (Yoda *et al.* 1963; White 1980; Westoby 1984) and criticized (Weller 1987).

The first goal in studying the relationship between competition and size variability is to extend our understanding of density-dependence beyond mean plant performance to include changes in size variation. Numerous models have been built to describe changes in the distribution of plant sizes by simulating the growth and interaction of individual plants (or size classes). While a review of these models is beyond the scope of this chapter (see Benjamin & Hardwick 1986), two basic types of models can be distinguished:

1 'Two-sided' or 'resource depletion' models are those in which plants are able to obtain resources equally or in proportion to their size. Examples include models in which competition is effected through competition coefficients which are constant (or proportional to size (Weiner & Thomas 1986)), and models in which resources are proportional to area available to individual plants (e.g. Mithen, Harper & Weiner 1984).

2 'One-sided' or 'asymmetric' models are those in which larger plants are able to obtain more than their share of resources (based on relative size) and suppress the growth of smaller plants. In some one-sided models, competition is modelled by an equation which gives large plants a disproportionate advantage over small plants (Aikman & Watkinson 1980). In other models, plants are affected only by larger neighbours; smaller plants have no effect on larger plants (Ford & Diggle 1981). The latter case is an example of total asymmetry.

Asymmetric models predict that, after a given period of growth, populations grown at high density will show greater size inequality than those grown at lower density (if there is no density-dependent mortality), as differences in size are exaggerated by asymmetric competition. Two-sided models, on the other hand, usually predict that plants grown at high density will show lower or unchanged size variability when compared to plants grown at lower density. This is because (two-sided) competition does not exaggerate size differences, but slows the divergence in size between larger and smaller individuals.

I have not yet found an exception to the claim that one-sided models predict higher size inequality in populations grown at higher densities, but I have found an exception to the generalization that two-sided models predict lower or unchanged inequality at higher densities. In two-sided spatial models, non-uniform dispersion of individuals will result in variation in local density which can result in variation in size (Benjamin & Hardwick 1976; T. Miller, personal communication). In such a model, size variation may be greater at densities at which many plants are interfering than at very low densities at which few plants are experiencing interference. This effect occurs only at low densities. At densities above which all plants are interacting, the usual prediction holds: increases in density result in lower or unchanged size variability when competition is two-sided.

How do the available data correspond to the predictions of the two types of models? Weiner & Thomas (1986) found that increases in density resulted in increased size inequality in fourteen out of the sixteen relevant studies they could identify. The only cases in which size variation did not increase with density were experiments in which the plants were grown from seed for very short periods of time (less than 44 days). Since our review, several more

studies have been published, and the results are the same: populations growing for more than a few weeks show increased size inequality at higher densities. In one of the most rigorous studies, Knox (1987) has looked at variation in trunk volume in a density series of *Pinus taeda* in the Duke Forest in North Carolina. He found highly significant correlations between size inequality and density (Fig. 5.1).

Since the only experiments which do not show increased size variation at higher densities are those in which plants are grown from seed for a very short period, this suggests that early plant interference is two-sided, whereas later plant interference is one-sided. This hypothesis is supported by experiments on *Zea* by Edmeades & Daynard (1979, Fig. 5.2). Early in the growth period, there is no apparent relationship between the coefficient of variation of plant sizes and the planting density, but by the end of the experiment the coefficient of variation goes up directly with density. To explain the difference between earlier and later plant interference, I have advanced the hypothesis that competition for light is asymmetric and will result in an increase in size inequality whereas competition for nutrients is two-sided and will reduce or have no effect on size variation. Competition for nutrients can begin immediately after germination if the density is high enough, but shading occurs only after the population's leaf area index (the ratio of leaf to ground area) reaches a certain level.

I tested the hypothesis that root interference is two-sided while shoot interference is one-sided by separating root and shoot interference in experimental populations of morning-glory vines (*Ipomoea tricolor*, Weiner 1986). Plants were grown (1) without interference, (2) with shoots but not roots interfering, (3) with roots but not shoots interfering, and (4) with both roots and shoots interfering. While competition for nutrients was much more

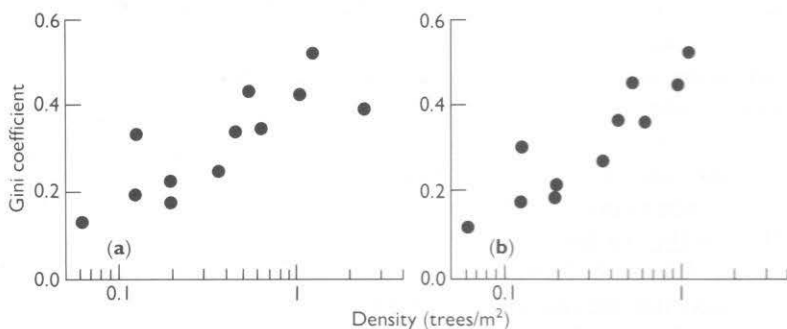


FIG. 5.1 Inequality in stem volume (as measured by the Gini coefficient) versus density for a density series of *Pinus taeda* in the Duke Forest in North Carolina (a) at 10 years ($r = 0.81$, $P < 0.01$); (b) at 13 years ($r = 0.91$, $P < 0.001$) (data from Knox 1987).

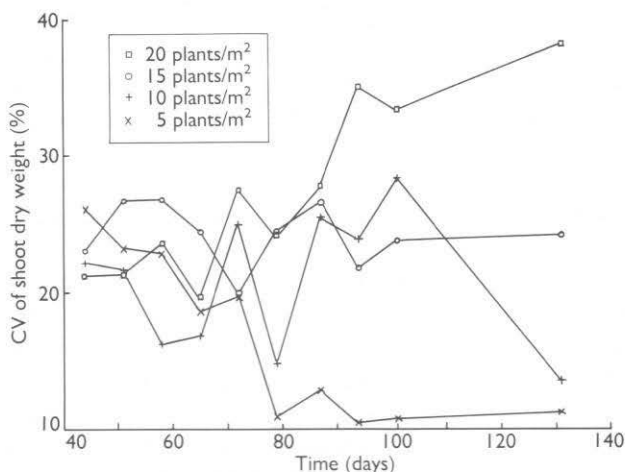


FIG. 5.2 Changes in the coefficient of variation of above-ground dry weight of *Zea mays* grown at four densities (data from Edmeades & Daynard 1979).

severe than competition for light in that it had a much larger effect on mean plant weight, competition for light resulted in a significant increase in size variability, whereas competition for nutrients did not (Table 5.1). Plants grown with both roots and shoots competing were not significantly smaller than those with only roots competing, but they showed the greatest size inequality. In populations competing both above and below ground, nutrient competition accounted for the decrease in mean plant size, whereas light

TABLE 5.1. The effect of root and shoot interference on mean size and size inequality in 57 day old experimental populations of *Ipomoea tricolor*. Means are significantly different ($P < .05$) except those connected by a line. Significant differences in the Gini coefficient (G) and the coefficient of variation (CV) are denoted by * ($P < .05$) and ** ($P < .01$) (data from Weiner 1986).

| | Treatment | | | |
|----------|--------------------|-------------------|------------------|--------------------------|
| | Individually grown | Shoot competition | Root competition | Shoot + root competition |
| N | 21 | 24 | 21 | 29 |
| mean (g) | 6.34 | 4.84 | 1.42 | 1.29 |
| G | 0.081 | 0.139 | 0.112 | 0.143 |
| | * ———— | | * ———— | |
| | ↑ ———— | | ↑ ———— | |
| CV (%) | 14.0 | 24.5 | 19.4 | 25.1 |
| | * ———— | | * ———— | |
| | ↑ ———— | | ↑ ———— | |

competition accounted for the increase in size inequality. There may be situations in which competition for nutrients is also asymmetric, i.e. plants with larger roots are able to get a disproportionate amount of soil resources. It remains to be seen whether root interference is generally symmetric or asymmetric.

Additional evidence that asymmetric competition is due to shading comes from the study of size variability and density-dependent mortality (self-thinning). Weiner & Thomas (1986) found only two data sets which contain information on changes in plant size distributions during the process of self-thinning. The first data set was from forestry yield tables for *Pinus ponderosa* stands in the western USA, and the second from data on wave-regenerated *Abies balsamea* populations (Sprugel 1984, unpublished data). In both cases size inequality increased over time until the onset of self-thinning and decreased thereafter. To obtain data on size variation and self-thinning in herbaceous plants, Weiner & Whigham performed a sequential harvest study of self-thinning in wild rice (*Zizania aquatica*) occurring naturally in Maryland (Weiner & Whigham 1988). As in the forest studies, size inequality decreased as self-thinning progressed (Fig. 5.3).

The decrease in size inequality during the course of self-thinning provides strong support for the hypothesis that asymmetric competition (and self-thinning itself) are primarily due to competition for light (Weiner & Thomas 1986). Before plants are large enough to compete for light they acquire light in proportion to some aspect of their size. When plants get larger the canopy closes, and plants begin to shade one another. Larger plants will then receive more than their share of the light energy. For example, an individual which is half the size of its neighbour will receive less than half the amount of solar energy (Fig. 5.4). After the community's leaf area index has reached its

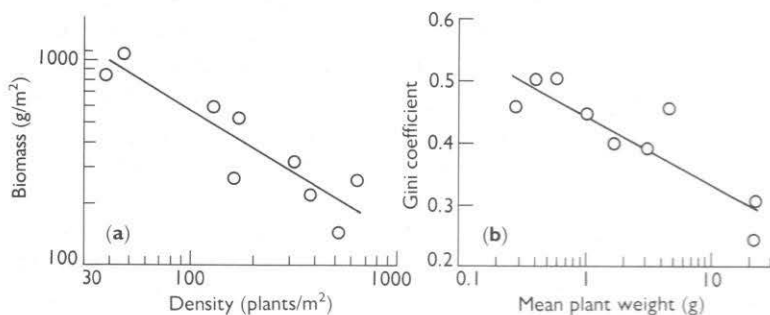


FIG. 5.3 Changes in size inequality during self-thinning in wild-rice, *Zizania aquatica*: (a) biomass versus density of survivors, (b) in equality in size versus mean plant weight of survivors (data from Weiner & Whigham 1988).

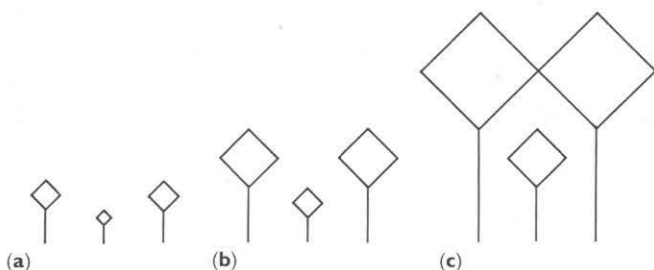


FIG. 5.4 Schematic diagram demonstrating the decrease in light available to smaller plants as mean plant size increases. Although the relative size differences are the same, the relative amount of light available to smaller individuals decreases as plants get larger.

maximum, plants continue to grow, although total community photosynthesis cannot increase further. When plants are very large, an individual which is half the size of its neighbours will get very little of the available light, and its photosynthetic rate may fall below the compensation point. Because light intercepts a two-dimensional surface, but shading occurs in a third dimension, the same relative size differences will result in an increase in shading as plants increase in size (Fig. 5.4). Thus, less relative size variation can be tolerated as plants increase in size. While plant geometry is important in determining the self-thinning trajectory, geometry alone cannot account for the decrease in size variability during self-thinning. Self-thinning and asymmetric competition can only be examined in terms of the interaction between geometry (or allometry) and shading.

Further evidence for this view of asymmetric competition and self-thinning comes from studies on *Salicornia* by Ellison (1987). *Salicornia* is a leafless plant which often grows in dense, monospecific stands but does not undergo asymmetric competition or self-thinning. This is because, at high density it grows in one dimension only, growing taller but not wider. *Salicornia* is the exception that proves the rule that asymmetric competition and self-thinning are due to the interaction between geometry and competition for light. I would predict the same results for palms, tree ferns, cycads and other plants which grow in one dimension after a certain point. (Perhaps competition was more symmetric and self-thinning did not occur in the Permian.)

These results lead to a working theory of stand structure, which I call the 'Light Competition and Allometry Theory'. According to the theory, competition for light determines the form of the competitive interactions between individuals ('altered form' model of Morris & Myerscough 1984), while competition for nutrients primarily affects the rate at which these interactions occur ('altered speed' model). Plants grow at a certain rate given

their genotype and available resources. Competition for nutrients has an important influence on this rate. When competition for light becomes important, it not only slows plants' growth but it does so in an asymmetric manner, and alters plant allometry (Weiner & Thomas, unpublished data). Stand structure is determined by the interaction between plant allometry and competition for light. The starting point for such a reductionist model of stand structure is the growth of individual plants in the absence of interference. This growth is altered in predictable ways by interference from neighbours.

What is needed in studies of plant interference are mechanistic (functional) models of the interactions between individuals (Tilman 1987). Organisms do not affect one another abstractly, but by altering each other's environment. Empirical models (e.g. 'curve-fitting') may enable us to make predictions about plant behaviour in some cases, but they do not provide explanations in the scientific sense and therefore are not theories (see Loehle 1983). A good example of the move from empirical to mechanistic models can be seen in the work of Toshihiko Hara. Using different diffusion equations, Hara (1984a,b) has built the best and most general empirical models available to follow changes in the size distributions of plants over time. At each point in time, plants of a particular size class have a certain mean growth rate ($G(t,x)$ function), and a certain variance in growth rate ($D(t,x)$ function). By fitting a sequence of size distributions to these functions, one can obtain a mathematical description of stand development. In his more recent work, however, Hara (1986) has begun to look at growth, interference and resultant size distribution change ($G(t,x)$ and $D(t,x)$ curves) as products of the functional processes of light interception, extinction and resultant photosynthesis. We should follow Hara's example and look for the mechanistic bases for observed phenomena and begin to build truly theoretical, rather than purely descriptive, models.

AGE DIFFERENCES

Age differences are among the most important factors determining size distributions in natural populations. In multi-aged plant populations size is correlated with age. For example, foresters routinely use tree size as a measure of age in describing stands. Age is clearly a primary determinant of size within plant populations but the indeterminate nature of plant growth means that age is not necessarily the overwhelmingly important demographic parameter that it is for many animals. For example, asymmetric competition acts to exacerbate size differences, but age seems to be one of the most important sources of initial differences in size (e.g. Ross & Harper 1972;

Firbank & Watkinson 1987). It is surprising that ecologists have made very few attempts to model the relationship between size and age in plant populations. We can start by modelling the effect of age alone on size, and then look at the interactions of age and other factors.

The simplest models of plant (or population) growth are exponential: $dN/dt = rN$, where N is the size or module number of a plant and r is the instantaneous growth rate. We can start by noting that Koyama & Kira's (1956) simple yet much-misunderstood model of the effect of variation in relative growth rate of size distributions, can also be applied to variation in age, since both r and t occupy the same position in the integral version of the exponential model:

$$N_t = N_0 e^{rt}$$

Koyama and Kira considered a population of seedlings which were growing exponentially. Initial sizes were equal or distributed normally. Relative growth rates (r) were also equal or normally distributed. In such a model, the size distribution of an even-aged population is a function of (1) the distribution of initial sizes, (2) the distribution of relative growth rates, and (3) the length of the growth period. If initial sizes are normally distributed and the relative growth rates are equal, the distribution of sizes remains normal. If initial sizes are equal and relative growth rates are normally distributed, the result is a log-normal size distribution, which is high in variability. If both the distribution of initial sizes and the distribution of relative growth rates are normal the effect of the growth rate distribution is much more important than the initial size distribution.

If we modify Koyama and Kira's argument to apply to age differences rather than differences in relative growth rate, the conclusions are similar: if (1) all seedlings are the same size, (2) their relative growth rates are equal, and (3) age (time of germination) is distributed normally, the outcome will be a log-normal distribution of sizes. A normal distribution of sizes at germination does not change this result. Before we question the assumption of exponential growth, let us look at the assumption that ages are normally distributed. Field data on time of germination within one season often show a distorted distribution of germination dates, with a peak followed by a relatively long tail of late starters (e.g. Miller 1987). This means that the distribution of ages within a cohort of plants is negatively skewed. However, if one is looking at a larger scale of time and space, e.g. recruitment of seedlings within a climax forest, a uniform distribution of ages over a large time scale may be a reasonable first approximation. If we start with a uniform distribution of ages and apply Koyama and Kira's argument the outcome would be a log-uniform (i.e. exponentially decaying) distribution.

Although the history of population modelling requires that we start with exponential models, I believe that exponential models of plant growth are more misleading than helpful. Plant growth is exponential for a very short period, as can be seen by looking at whole-plant data (Hunt 1982), and exponential models are incapable of simulating even the most general behaviours of plant populations such as density-yield relationships. For example, in exponential models of plant growth, total yield decreases with increasing density after a certain period of growth, and the higher the density, the sooner the yield of one plant surpasses the combined yield of several competing plants! Some researchers (e.g. Turner & Rabinowitz 1983; Benjamin & Hardwick 1986; Huston & DeAngelis 1987) continue to use exponential models of plant growth, perhaps because exponential growth is mathematically tractable. Sigmoidal models of plant growth, despite their limitations, represent a vast improvement over exponential models in their ability to simulate plant behaviour.

What are the implications of sigmoidal growth for modelling the effects of age on size distributions? If we assume (1) plant growth is sigmoidal (e.g. 'logistic'), (2) recruitment of seedlings is continuous and uniform, and (3) relative growth rates and maximum sizes are normally distributed, the outcome is a bimodal distribution of plant sizes. There is a broad peak reflecting those individuals which have achieved their maximum size, and a narrow peak representing very young individuals (Fig. 5.5). The valley between the peaks is a reflection of the fact that in sigmoidal growth, the growth rate is fastest at intermediate sizes. Put another way, plants spend a relatively short period of time at intermediate sizes. If age is normally

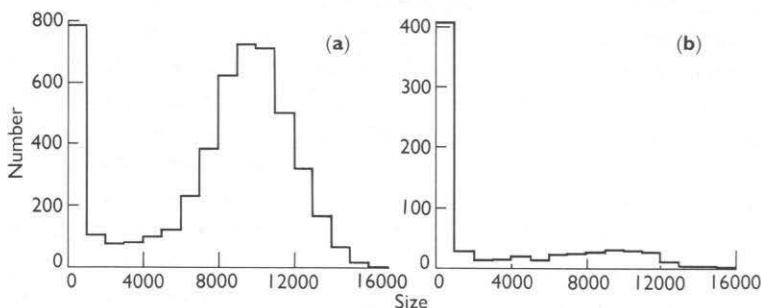


FIG. 5.5 Size distributions resulting from logistic growth with continuous recruitment. Initial sizes, instantaneous growth rates and carrying capacities for 5000 individuals are normally distributed with means of 1, 1, and 10 000 respectively, and coefficient of variation of 20%. (a) All plants live to age 40: continuous recruitment, sigmoid growth, no mortality; (b) constant per capita death-rate (0.15 individuals/individual/unit time): continuous recruitment, sigmoid growth and constant mortality.

distributed and growth is sigmoidal, most plants will diverge in size during the 'exponential' part of their growth, but they will tend to converge as they reach their maximum sizes. The greatest variability in size will occur at intermediate sizes. Remember, however, that these models assume there is no competition between plants. If we add competition to such models the results can be fundamentally altered. Intuitively, if there is large variation in age, asymmetric competition can be expected to produce bimodality, or high mortality of late recruits. Two-sided competition may reduce the effects of age variation on size variation by slowing the growth of older plants, although this has not yet been shown. Our understanding of the interactions between age, competition and size is underdeveloped, and much in need of models and experimental data.

Two sorts of data which bear on the role of age differences in determining variation in performance have been collected. There have been several studies which have looked at the influence of time of emergence on size in fields and glasshouse populations. In most cases, time of germination appears to have a major effect in determining final size or fecundity (e.g. Black & Wilkerson 1963, Ross & Harper 1972; Howell 1981; Waller 1985; Firbank & Watkinson 1987). Often, time of germination is the most important among a group of independent variables in accounting for variation in performance. It is often rank order of emergence, rather than age itself, which is most highly correlated with final size. This suggests that the effects of germination time are mediated by competition, since rank order of emergence may reflect position in the size hierarchy.

The other sort of data which has been collected relating age to plant size are distributions of age and size of trees in temperate forests. Age can be determined from ring counts and size is usually measured as stem diameter. Unfortunately, most of these data are static (i.e. collected at one point in time), and this makes any inferences about the dynamic processes which result in the observed distributions very weak. Data on size-age distributions over periods of even a few years would greatly increase our ability to study the concomitant changes in age and size of individuals which determine population size structure. To date, researchers have either focused on age-dependent survival and fecundity (classical demography) or size, but not both (but see Law 1983). In a given situation, information on both a plant's size and its age may enable us to predict its future performance with a high degree of accuracy.

Some conifer stands in the Rocky Mountains which have different age distributions appear to have similar size distributions (Knowles & Grant 1983). This suggests that there are ecological factors which are independent of age that act to determine population size structure. Diameter distributions

of lodgepole pine (*Pinus contorta*) in the Sierra Nevada seem to show a good fit to an exponential decay (Fig. 5.6, Parker 1986), although in such a fit most of the variance is due to the first few columns of the size distribution. These are climax forests in which regeneration occurs in canopy gaps. Since a size distribution is a function of recruitment, growth and mortality, static data tend to be consistent with many alternative hypotheses. An attractively

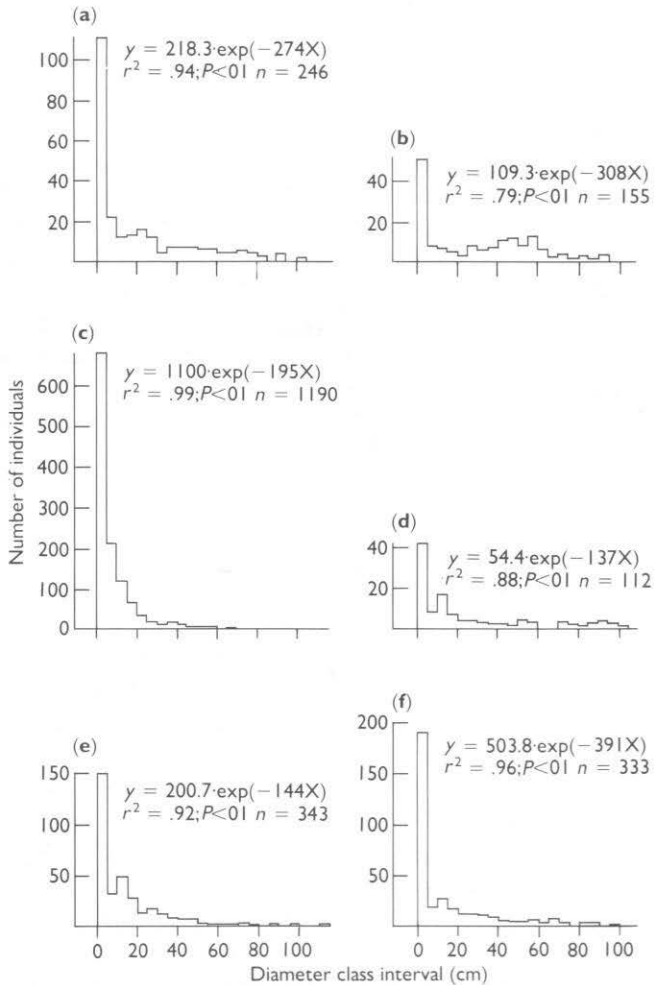


FIG. 5.6 Diameter class distributions for six stands of *Pinus contorta* (lodgepole pine) in the Sierra Nevada. Non-linear regression equations for negative exponential curves are given (y = number of stems per diameter class and x = diameter class midpoint) with their coefficients of determination and levels of significance (data from Parker 1986).

simple hypothesis to explain an exponentially decaying distribution of diameter in forests would be continuous, uniform recruitment, linear (arithmetic) growth in diameter, and a constant per capita death-rate. An equally extreme but less plausible alternative hypothesis would be continuous recruitment (at a lower rate), exponential growth in diameter and no mortality. In between these two extremes lies a continuum of compromise hypotheses. Dynamic demographic and growth data will be required to test these and other alternatives.

Differences in size due to age may, in many cases, have different implications for ultimate performance (i.e. final size or total reproductive output) from differences in size due to other variables. A plant which is small simply because it is young has greater prospects than a plant of the same size which is old but has suffered extensive suppression, herbivory or disease. On the other hand, when size differences are due to competitive suppression of slightly younger plants, relative size may be a good reflection of relative performance. In this case the difference in size is not a direct effect of age but an interaction between age and other factors. From the evolutionary perspective, we want to look at the cumulative performance of an individual over its life, not simply its size at one point in time. Again, the dynamic, demographic approach is necessary if we are to obtain the type of data needed to study this. Non-destructive measures of size are greatly needed so we will be able to follow the performance of individuals over time.

HERBIVORY, PARASITES AND PATHOGENS

Herbivory

The study of herbivory is one of the most exciting areas of active research in plant ecology (Crawley 1983), and researchers are now beginning to study the effects of herbivory on plant size variability (e.g. Windle & Franz 1979; Dirzo & Harper 1980; Cottam 1986). The effects of herbivory can be understood in terms of (1) the initial size distribution of plants, (2) the effect of herbivores on this size distribution (how herbivory modifies the distribution) and (3) the interaction of herbivory and other processes, e.g. herbivore attack may change subsequent patterns of growth and interference.

Many researchers (e.g. Harper 1977; Dirzo 1984) seem to feel that herbivory will increase variation in individual plant performance, but this is not necessarily the case (Table 5.2). If herbivory is random with respect to biomass, i.e. if each unit of biomass is equally likely to be consumed, and if the loss of parts does not result in mortality, then size variability will not be affected: the distribution of sizes will be shifted proportionally. If herbivory

TABLE 5.2. Expected direct effects of herbivory on size variability in plant populations.

| Size-dependence of herbivory | Effect on plant size variability |
|--|----------------------------------|
| Herbivory random with respect to biomass | |
| No mortality | No change |
| Smaller plants more likely to die | Decrease |
| Herbivory concentrated on large individuals | |
| All large individuals removed or reduced in size | Decrease |
| Only some large individuals removed or reduced in size | Increase or decrease |
| Herbivory concentrated on small individuals | |
| Small individuals removed | Decrease |
| Small individuals reduced in size | Increase |

is random but smaller plants are more likely than larger plants to die as a result, then variation in the size of survivors will be reduced as the lower end of the distribution is truncated. If herbivory tends to be concentrated on the largest individuals, such as one might see from a mowing machine or a large vertebrate herbivore, then size variability will tend to be reduced (Crawley 1983), although this depends in part upon the original distribution. If all large individuals are removed, variability will almost certainly be reduced, since truncation of a distribution almost always results in a decrease in relative variation. If, on the other hand, only some of the large individuals are removed, variability may increase or decrease, depending upon the original distribution. These expected effects are summarized in Table 5.2.

These ideas are supported by a recent study on rabbit herbivory by Crawley (in preparation). Winter wheat was sown in October and harvested in June. There were four treatments: (1) no grazing by rabbits, (2) grazing only in November, (3) grazing only in March, and (4) continuous grazing (Fig. 5.7). Herbivory in November had the effect of removing the largest individuals, and size variation decreased relative to the ungrazed controls (Fig. 5.7a,b). March grazing reduced mean plant size more than November grazing, but it had no effect on size inequality (Fig. 5.7c). Continuous grazing kept most of the plants very small and created a highly skewed unequal size distribution (Fig. 5.7d).

Since the effect of a process on a distribution is a function of both the process and the distribution (Westoby 1982), it is perhaps best to think of herbivory as something that modifies a distribution. The effects of a specific regime of herbivory on a population of plants could be summarized in terms of diffusion equations such as developed by Hara (1984a,b; see p. 68) to study

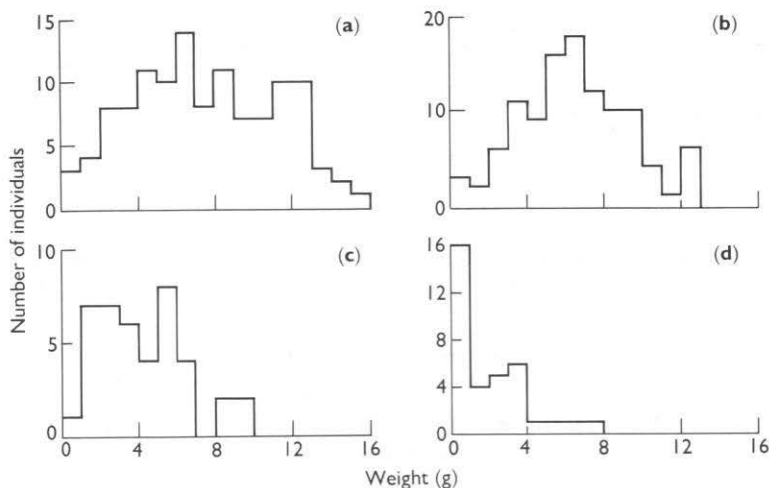


FIG. 5.7 Size distributions for populations of winter wheat sown in October and harvested in March at Silwood Park, UK. There were four rabbit grazing treatments: (a) ungrazed, CV = 52%; (b) grazed in November, CV = 43%; (c) grazed only in March, CV = 52%; (d) continuously grazed, CV = 89% (data from Crawley, unpublished).

growth in plant populations. If herbivory is size-dependent, in a given regime of herbivory each plant of a certain size will suffer a mean amount of loss to herbivores ($G(t, x)$ functions have been called 'distribution modifying functions' by Westoby (1982).

Herbivory may interact with competition to change the population size distribution. Harper (1977) and Dirzo (1984) state that herbivory may generate differences in size which may later be exaggerated by other factors such as competition. But herbivory will tend to reduce resource limitation and, therefore, reduce competition. Thus, although random herbivory will have no direct effect on size variability, it may tend to reduce competition and thus indirectly reduce variability.

We can consider several possible scenarios for the interaction between competition and herbivory. For simplicity, let us consider the relationship between competition for light and herbivory on leaves.

I If competition for light is intense (e.g. the leaf area index is close to its maximum) a limited amount of herbivory on leaves might simply change the distribution of leaf areas among plants without significantly reducing the leaf area index. But even limited herbivory on abundant leaves could have a major effect on competitive interactions if herbivores selectively attack individuals by size. For example if such herbivory were concentrated on certain sizes it could affect variability in two ways: by modifying the distribution directly and by changing the degree of asymmetric competition.

Such a situation might occur if each plant is equally likely to be attacked and the herbivore eats a given amount of foliage. In such a case smaller plants would suffer more than larger plants. An animal that crawls along the ground and climbs stems, such as a slug, could behave in such a manner.

2 If there is extensive defoliation, the leaf area index, and therefore competition for light, may be reduced. In this case selectivity by the herbivore may influence size variability mostly through its direct effect on the size distribution. This could be similar to the case of herbivory when competition is not very intense: the effect of herbivory is direct and not mediated by competition.

In monocultures and mixtures of aphid-resistant and non-resistant cultivars of barley, Windle & Franz (1979) found that size variability increased over time in the presence of aphid herbivory but not its absence. The coefficient of variation of plant sizes was always higher when aphids were present. Unfortunately, Windle and Franz did not look at the distribution of sizes of each cultivar separately when they were grown in mixture, to determine if the increase in size variability in mixtures with aphids was due to inter- or intravariety effects.

The effect of herbivory on size distributions is more complex when we begin to look at plant species mixtures. In species mixtures, one species can benefit from herbivory if another competing species is grazed more. Cottam (1986) found that in mixtures of *Trifolium* and *Dactylis*, grazing by the slug *Deroceras reticulatum*, benefitted *Dactylis*, which actually showed an increase in mean plant size and size inequality when the mixed stand was grazed (Fig. 5.8). The increase in size variability and mean plant weight with grazing suggests that the increase in productivity of *Dactylis* with grazing was mostly due to few very large individuals. Experiments such as Cottam's are very

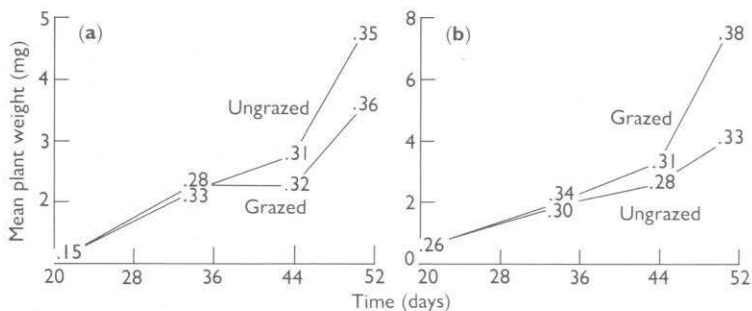


FIG. 5.8 Changes in mean plant weight and weight inequality over time in mixtures of *Trifolium repens* and *Dactylis glomerata* with and without grazing by slugs. (a) *Trifolium*; (b) *Dactylis*. Gini coefficients are used as points (data from Cottam 1986).

exciting, but difficult to interpret because of the large number of variables. Studies on herbivory should include appropriate controls, even if this means reducing the number of variables which can be studied. For example, if herbivory in mixtures is studied, we should also look at herbivory in monocultures at the same density.

Parasites and pathogens

Researchers are also beginning to look at the effect of disease on plant size distributions. Although there were no clear trends with respect to size variability, Burdon *et al.* (1984) showed that rust infection interacted with competition to change the size distributions of mixtures of disease-resistant and susceptible varieties of *Chondrilla juncea*.

The influence of the rust fungus *Puccinia lageniphorae* on populations of *Senecio vulgaris* has been investigated by Paul & Ayers (1986, 1987). In their experiments, rust infection always increased size variability, even though they used inoculation methods which achieve a more uniform distribution of disease than is usually seen in nature (N. D. Paul, personal communication).

GENETIC DIFFERENCES

How much does the variation in individual performance within a population reflect differences in genotype? Although this question is central to understanding the implications of variation in performance for evolution in plant populations, very little is known about the role of genetic differences in determining size difference. While many researchers feel that genetic variation must play an important role in determining variation in individual performance, there is not much evidence to support this view. Gottlieb (1977) found no electrophoretic differences between large and small individuals in a population of *Steganomeria exigua*.

While the limitations of isozyme studies in this context are clear (i.e. the particular loci studied may not have been relevant to plant size) Gottlieb's basic approach cannot be faulted: the null hypothesis must be that there are no genetic differences between large and small plants, and evidence for such differences must be obtained if the importance of genetic factors is to be demonstrated. There are studies showing genotype-dependent survivorship within polymorphic populations (Burdon, Marshall & Brown 1983) and between cultivars in mixture (Bazzaz, Levin & Schmierbach 1982) and these differences in survivorship may reflect differences in size. Heywood & Levin (1984) studied the interaction between genotype and performance in monocultures and pairwise mixtures of *Phlox drummondii*. Because there was

extensive mortality as well as size variation among survivors, their results are difficult to interpret with the methods that are currently available (see above).

Factors over which the individuals' genotype has no apparent influence (e.g. microsite differences) seem to account for much of the variation in performance within populations which have been examined. Although it is likely that differences in genotype play a role in determining size differences, the relationship is not likely to be straightforward. In my view there are probably not genes which determine size or growth rate directly, but rather genes which determine an individual's capacity for growth as a function of the abiotic and biotic environment. There will be trade-offs in the ability to be large in one situation versus another. For example, if there is a trade-off between herbivore defence and growth, different individuals will be large depending upon whether or not herbivores are present. Looking for genes for 'performance' (i.e. size or other measures of fitness) is unlikely to advance our understanding of plant evolution.

There are two alternative views of the role of variation in performance in the evolution of plant populations:

1 Variation in performance as genotypic 'signal'. In this view, genotype plays an important role, although factors which are not influenced by genotype determine much of the variation in individual performance. Differences in performance reflect differences in genotype, although the latter will be difficult to detect because there is also a large stochastic component to plant performance. Evolution by natural selection does not require that genetic differences have large effects relative to other factors, it only requires that these effects exist. In general there are significant, consistent differences in genotype between larger and smaller individuals. Selection mediated by differences in individual performance may be 'Sisyphean' (Williams 1975) in that genotypes which perform well in one generation may perform poorly in the next because of a change in the selection regime, but natural selection is occurring all the time. By favouring different genotypes in different generations Sisyphean selection may be a form of disruptive selection over time, and act to maintain genetic variation within populations.

2 Variation in performance as phenotypic 'noise'. In this view differences in the performance of individuals do not reflect genetic differences, but are due to other factors. Size inequality reduces effective population size (Heywood 1986) and increases genetic drift. Natural selection occurs through differential survivorship, and genetic differences among those that survive and reproduce are essentially random. If natural selection does occur among

survivors, it acts through offspring quality, not quantity. Variation in individual performance may be important to the evolutionary process, but it acts randomly.

The truth probably lies somewhere in between these two extremes. Correlations between genotype and performance may be unusual and episodic, and variation in performance may usually result in genetic drift. Natural selection (as distinct from genetic drift) may be an important, but rare phenomenon in plant populations.

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