Plant Competition and Its Course Through Time

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Mean plant weight and density in competing populations can be related using the competition-density effect and reciprocal equations, and the −3/2 power law. Application of these equations, their interrelationships, and conditions under which their properties alter or fail to apply are discussed. Their importance in teaching ecology is briefly considered. *(Accepted for publication 20 February 1981)*

General statements in ecology are usually of a qualitative nature; the variety of organisms, habitats, and limiting factors in the environment preclude precise quantitative expression of biological phenomena. When an ecological phenomenon can be expressed mathematically, it is often more important to understand the implications of the expression, rather than its derivation.

There has been widespread interest in mathematical expressions describing the relationships between mean weight and density in populations of competing plants—the so-called −3/2 power law and its associated equations. Misunderstanding these equations and their full implications by many university undergraduates specializing in ecology may be due to their limited mathematical background and the fact that no single research paper has provided a suitable comprehensive treatment of the subject (but see Harper 1977, Willey and Heath 1969). We aim to (a) review these expressions and describe their use in the interpretation of data, (b) offer avenues for exploring further relevant literature, (c) encourage the use of illustrative experiments as teaching aids. Finally, a thorough understanding of this material can provide new insights into related areas of plant ecology.

GROWTH OF A POPULATION OF COMPETING PLANTS

Although different members of a plant population may be at very different stages of growth, the manner of accumulation of biomass through time by a population often closely parallels that for a single plant; the growth curve is sigmoid (Figure 1). Increase in biomass is slow early in growth, but as time passes it gathers momentum and enters an exponential phase. Eventually, as their sizes increase, plants begin to interfere with each other's growth by competing for the same essential resources, and the maximum potential growth rate of the population will not be maintained. Plant competition may be defined as "the tendency of neighbouring plants to utilise the same quantum of light, ion of a mineral nutrient, molecule of water, or volume of space" (Grime 1973). Under competitive conditions the form or size of a plant may be modified without leading to the death of the plant; these modifications are known as plastic responses. If the capacity of a plant to withstand competition by its plastic responses is exceeded, it will die.

As the population continues to grow, a point is reached when the habitat may support no more biomass; carrying capacity of the habitat has been reached, and any further growth can occur only at the expense of some biomass already present. Thus, parts of plants or even whole plants will be lost from the population. In the case of woody species, if dead support tissues are included in the measurement of biomass, the maximum biomass achieved will depend strongly on the species and may not be reached for a long time.

This broad description of plant population growth, competition, and death conceals several characteristic features of the growth of individuals in the population. In a population of seedlings there is a wide range of growth rates, even before competition occurs, because of differences in seed size, time of germination, and individual genotype. This range of growth rates, which increases through time, leads to an alteration in the frequency distribution of plant weight. Whereas the distribution of the weights of individual seeds and young seedlings is normal, it becomes progressively more positively skewed as growth proceeds (Obeid et al. 1967), and often achieves log-normality under competitive conditions. Thus, the population consists of many small plants and a few large plants—the dominance hierarchy characteristic of competing populations.

The increase in skewness is a direct result of the plasticity of plants. Eventually, further development of skewness is prevented by the death of those plants under the greatest competitive stress—the smallest in the population (White and Harper 1970). Although weight skewness develops, the height frequency distribution remains normal or becomes negatively skewed, demonstrating that low weight plants, which may be of low competitive ability, grow tall and still manage to intercept some light (Figure 2). A fuller account of the details of changes in weight skewness has recently been provided by Mohler et al. (1978).

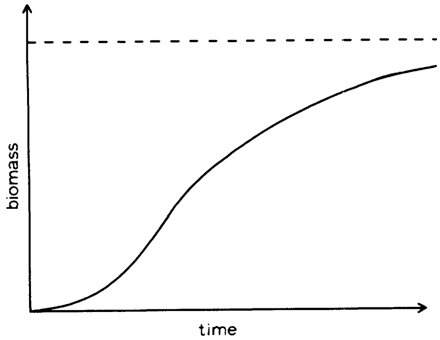

Figure 1. Model graph of the course of biomass accumulation in a plant population. Dashed line represents the carrying capacity of the habitat.

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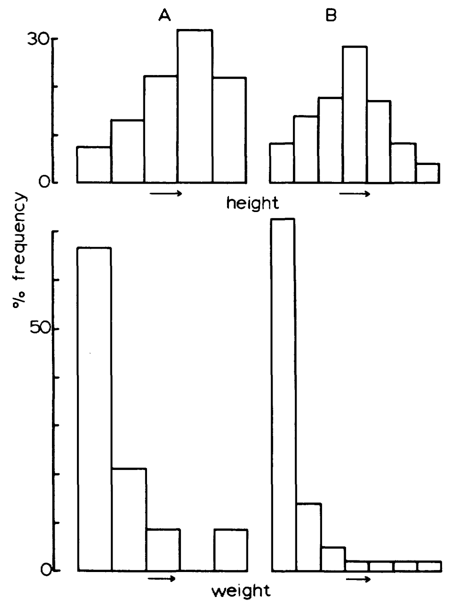

Figure 2. Frequency distribution of plant height and plant fresh weight in two monocultures of ragweed. A: = on fertile soil. B: = on infertile soil. Re-drawn from Koyama & Kira (1956).

COMPETITION-DENSITY (C-D) EFFECT EQUATION

Consider a set of plant populations, each population growing under the same habitat conditions, but starting growth at a different density. After a certain period of growth, when the populations begin to exhibit plasticity in mean plant weight as a response to the onset of competition, the competing populations can all be fitted to a hyperbolic curve that relates mean plant weight and density of survivors (Kira et al. 1953), (Figure 3a). Although the equation relating the competing populations changes with time, it can be generalized as follows:

$$w = Kd^{-a} \quad (1)$$

where w = mean plant weight, d = plant density, and a, K are constants. This equation can be represented linearly (Figure 3b) by plotting on double logarithmic axes, when it can be expressed in the following form:

$$\log w = \log K - a \log d \quad (2)$$

Equation (1) is termed the competition-density equation (C-D equation), and the constant a is termed the C-D index. Through time, the value of a increases; at the seed and early seedling stages it is zero, implying that mean plant weight is independent of density. Given sufficiently intense competition, the C-D index eventually rises to 1, which indicates complete compensation for higher density by lower mean weight, resulting in all populations having the same total biomass. At this stage, the C-D effect equation has the following form:

$$w = Kd^{-1} \quad (3)$$

The gradient of this relationship, on double logarithmic axes is −1, and the angle of the slope is 45° (Figure 3b). Thus when a is unity and equation (3) applies wd = K, and since yield Y equals the sum of the weight of the plants per unit area (or Y = wd), it follows that yield is constant in all populations at this stage of growth.

RECIPROCAL EQUATIONS

The major drawback in describing population weight–density relationships with the C-D equation is that it assumes that the density at which the effect of competition becomes discernible in plant populations is clearly defined. For example, (Figure 3b) a plastic response in mean weight per plant occurs above the density marked X after 21 days of growth. It seems probable, however, that there is a smooth transition from low densities, where there is no effect of competition, to high density ranges, over which competition exerts an ever-greater effect, and that this region on the graph should be represented by a curve. A suitable equation to describe this situation was presented by Shinozaki and Kira (1956). The correspondence between curves produced by this equation and data from a wide range of experiments appears good in nearly every case investigated. Once again, the data are graphed in double-logarithmic form, but an equation of the form:

$$\frac{1}{w} = Ad + B \quad (4)$$

is used to fit a curve to the points. In this equation w = mean weight per plant, d = plant density, and A and B are constants. Shinozaki and Kira (1956) provide further information about the identity of these constants.

Equation (4) was termed the reciprocal equation of the C-D effect. By dividing throughout by density, d, an equation (the reciprocal equation of the yield-density effect) can be obtained, representing the relationship between yield and density:

$$\frac{1}{wd} = \frac{1}{Y} = A + \frac{B}{d} \quad (5)$$

Application of equation (4) to the set of data graphed in Figure 3 is shown in Figure 4.

It must be emphasized that all the above equations refer to the relationships between mean plant weight and density for populations of different densities, but after the same growing period.

THE −3/2 POWER LAW

As each population continues to grow, the capacity of some individuals to absorb competition by plastic responses will be exceeded. Once this point has been reached, plasticity and mortality occur simultaneously in the population. Over the time that the population is undergoing density-dependent mortality

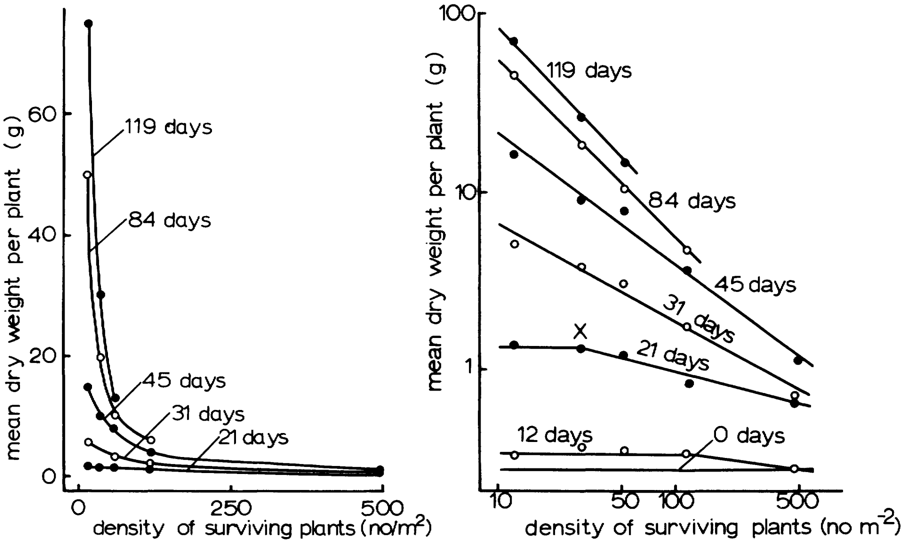

Figure 3. a. Graph of the changing relationship between mean weight per plant and plant density for populations of soybean at different densities. Recalculated from Kira et al. (1953). **b.** The same relationship plotted on double logarithmic axes. The competition-density equation applies to the inclined part of the relationship. The point X on the line for 21 days is explained in the text. Re-drawn from Kira et al. (1953).

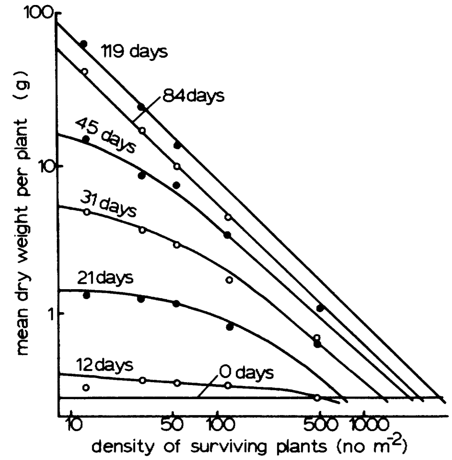

Figure 4. The changing relationship between mean weight per plant and plant density for soybean populations at different densities. The data are the same as in Fig. 3. The curves are derived from the reciprocal equation (equation (4) in text). Re-drawn from Shinozaki & Kira (1956).

as a result of continuing growth, the equation relating the points on the graph is:

$$w = Kd^{-3/2} \qquad (6)$$

$$\text{or } \log w = \log K - 1.5 \log d$$

From equation (6), $wd = Kd^{-1/2}$, therefore

$$Y = Kd^{-1/2} \qquad (7)$$

Equation (6) is termed the $-3/2$ power equation, or the $-3/2$ power law (Yoda et al. 1963). Its gradient is approximately 56°. The reason for the exponent term being $-3/2$ is not known, although it is now fairly clear that the limitation upon biomass accumulation represented by this gradient is a reaction against packing more biomass into a given volume. An explanation of the exponent was proposed by Yoda et al. (1963), based on a simple geometrical model with two assumptions. Firstly, all plants of a given species are geometrically similar, regardless of size and growing conditions. The average ground area or space s occupied by a plant will then be proportional to the square of a linear dimension of the plant, L, in such a way that $s \propto L^2$, and its weight w will be proportional to the volume of space which the plant occupies; in terms of the same linear dimension then, $w \propto L^3$. Thus, the space occupied by a plant and its weight can be related by the equation.

$$s \propto w^{2/3} \qquad (8)$$

Secondly, mortality in the population occurs when the percentage cover of the plants exceeds 100%, and operates in a fashion which maintains 100% cover. The area occupied by a plant and the density of survivors are then related by the expression:

$$\propto \frac{1}{d} \qquad (9)$$

Combining (8) and (9) it can be seen that $(1/d) \propto w^{2/3}$. Therefore, $w \propto d^{-3/2}$, or $w = Kd^{-3/2}$. An alternative derivation relating the power law to equations for measuring spatial pattern in plant populations has been presented by White and Harper (1970).

The equations described above are normally used to illustrate weight–density relationships in monocultures. The conditions that must be satisfied for them to apply are minimal. For the C-D and reciprocal equations, the populations must have been growing for the same length of time and there should be no environmental gradients within or between the populations. The $-3/2$ power law describes the weight-density relationships in a population at different times as thinning proceeds. It can also describe the relationship between populations on plots of different fertility which are undergoing thinning, but only when light intensity is the same for all plots.

Both situations are illustrated in the experiment upon *Erigeron canadensis* carried out by Yoda et al. (1963). Experimental monocultures of this species were established from a fixed, high-sowing density on plots with a wide range of soil fertilities. Plants were harvested from the treatments six times after establishment, and mean weight and density of surviving plants were recorded. As time passed the mean weight of surviving plants increased and their density dropped in such a way that the data collected from all the experimental plots fell along the same thinning line (Figure 5). However, on the more fertile plots growth was faster, resulting in greater competition and higher mortality, so at any given harvest date the data points for the more fertile plots appear further along the thinning line (i.e. diagonally to the left) than those for the less fertile plots (Figure 5). On more fertile plots the density of surviving plants was lower, but their mean weight and total plot yield were greater. These differences among plots of different fertility levels increased as time passed.

Further relationships between mean weight of whole plants or plant parts and density, in pure and mixed stands, have been proposed by Bleasdale (1967), Bleasdale and Nelder (1960), Farazdaghi and Harris (1968), and Holliday (1960a) *inter alia*. These have not proved to be such valuable general statements as the equations given above.

VALUE OF THE C-D, RECIPROCAL, AND −3/2 POWER LAW EQUATIONS

The best comprehensive illustration of the importance of these equations and their interrelationships is provided by the experiment upon buckwheat reported by Yoda et al. (1963) (see Figures 6a and b). In this experiment, replicate populations were established at initial densities of 25, 100, 2000, 10000 and 50000 seeds m^{-2}. The density and mean dry weight of surviving plants were determined for populations sampled after 21, 34, 49 and 63 days of growth.

At the beginning of growth, mean weight (i.e. seed weight) is the same for all populations, regardless of starting density. When the changing relationship between mean weight and density is plotted on double logarithmic axes (Figure 6a), the initial locus of movement of the less dense populations on the graph is vertical. This occurs for a shorter length of time in more dense populations. As time passes, competition begins to take place and exerts continually depressing effect upon the rate of increase in the mean weight of plants. Thus, in competing populations, weight plasticity develops, along with the changes in distribution of weights and heights described above. At first, only the densest populations exhibit plasticity, but as the plants

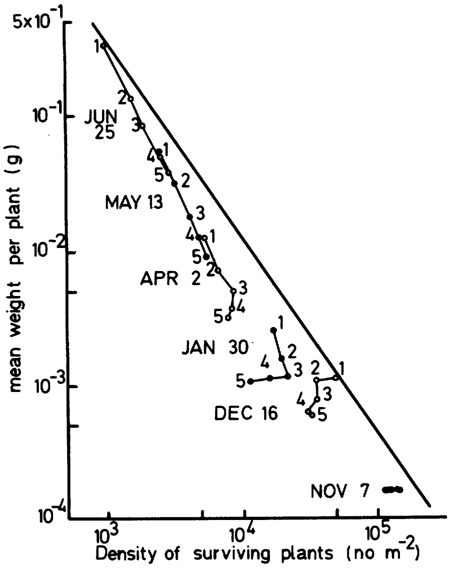

Figure 5. Changes in number of survivors and mean plant weight through time in monocultures of *Erigeron canadensis*. Numbers 1–5 represent data collected from plots of different fertility. 1 = highest fertility, 5 = lowest fertility. Separate harvests are indicated by their dates and the results from a single harvest date are joined by solid lines. The straight line has a gradient of $-3/2$. Re-drawn and adapted from Yoda et al. (1963).

continue to grow, the effect of competition is observed in the less dense populations. In other words, as plant size increases, fewer plants per unit area are required for competition to result. The change in mean weight per plant over a given period of time is smaller for more densely planted populations.

A curve based on the reciprocal equation (4) may be drawn connecting all populations which have had the same period of growth (solid lines in Figure 6a). At the highest planting densities, the gradient of this curve reaches the value of -1, indicating that biomass is the same on these plots at a given time. Thus, there is a completely reciprocal relationship between mean plant weight and density. Each successive date of harvesting reveals that the position of the -1 gradient has risen, showing that biomass has accumulated between harvests, but that the relationship between the populations has not changed.

As time passes, populations exhibit density-dependent mortality, which occurs earlier in more dense populations. The densest populations in Figure 6a have already exhibited mortality before the harvest at 21 days; thus, their curves move diagonally to the left through time rather than vertically. The result of density-dependent mortality is that populations starting growth with widely differing densities gradually converge upon a common density, which will decrease through time (Figure 6b). If the points relating log (mean weight) to log (density of survivors) are joined through time for a single thinning population, the gradient of this line is $-3/2$ (see dotted line in Figure 6a). This line appears to represent a limit on the amount of biomass that can be supported for any given plant density. For high plant densities, when the mean weight is low, biomass is also low; later in growth, when density has fallen, but mean weight of survivors is greater, the total biomass has increased. Thus, as growth proceeds, it appears to be accompanied by an increasingly efficient use of "biological space" (*sensu* Ross and Harper 1972), allowing biomass to be accumulated. An increasing proportion of the biomass of woody species traveling along the thinning line will be dead supporting tissues.

Too low a planting density, or too short a life span or growing period to accumulate the necessary biomass may result in the growth of a population never being constrained by the $-3/2$ thinning line. This is the case with the two lowest planting densities in the present experiment; Figures 6a and b illustrate that they have not been subject during the experiment to the heavy density-dependent mortality characteristic of populations following the thinning line.

As the falling density in the heavily competing populations reaches that of lower density populations, their growth and thinning patterns become identical (Figure 6b). Thus, the time trajectory for lower density populations is the same $-3/2$ thinning line as for populations of higher initial planting densities, but the former reach the thinning line at a higher point on the graph. All populations which reach the thinning line should theoretically converge and move along it at the same rate when they grow under the same conditions, regardless of the densities at which they commenced growth. No points may lie to the right of the thinning line; mortality ensures that as growth proceeds the thinning line is not transgressed.

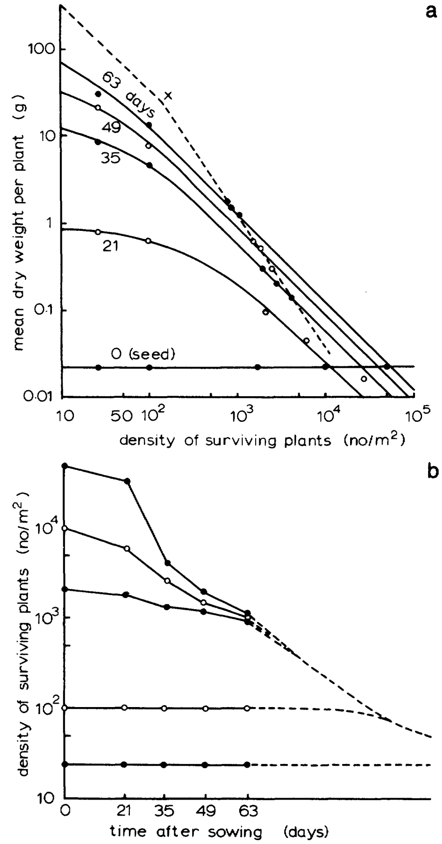

Figure 6. a. Reciprocal equation curves (solid lines) and $-3/2$ power law (dotted line) in buckwheat, showing the inter-relationship between the two. The relationship between the $-3/2$ power law and the maximum weight of biomass which can be supported by the plot is also indicated by the transition point marked on the graph at X. The exact position in which this point of transition has been drawn is arbitrary since it is not based upon collected data. Graph re-drawn and adapted from Yoda et al. (1963). **b.** Time-survival curves in buckwheat populations starting growth at a wide range of densities. Dotted lines indicate the extrapolation from experimental data collected for the first 63 days of plant growth. Graph re-drawn and adapted from Yoda et al. (1963).

Ultimately, if growth continues and the habitat can support no more biomass, the increasing weight of plants must be compensated by an equal loss of biomass through mortality. At this stage of growth all populations under the same growing conditions are at the same point on the graph. Reaching this stage may take hundreds of years for tree species, in which a high proportion of the biomass is woody support structures. As plants continue to grow and self-thin, they now follow a -1 gradient, rather than a $-3/2$ gradient. This -1 gradient represents the ultimate limit upon biomass accumulation for the species concerned under these conditions (see Figure 6a). Thus populations have passed from a stage where they are limited by physical constraints (occupation of biological space), to one where they are limited by the carrying capacity of the habitat.

The position of the $-3/2$ thinning line is not known to be altered by habitat conditions except for light intensity. As light intensity decreases the thinning line falls to the left, and the value of the intercept K, in equation (6) declines. Thus, at any density, less biomass can be produced before thinning will occur (e.g. data on *Helianthus annuus,* Figure 4 in White and Harper 1970). This result reinforces the view that thinning is usually caused by plants' net assimilation rate or their light compensation falling below a critical point, although there is also some evidence to suggest that the dynamics of thinning also alter when light intensity decreases (e.g. White and Harper 1970, Ford 1975). If the nutrient supply is increased, the position of the thinning line is not changed, but it is reached more rapidly, and populations move along it faster as a result of a greater growth rate.

The position of the -1 gradient representing the limit to biomass accumulation depends largely on a particular species' maximum size, which is controlled by its genotype. However, for any species, the position of this line can be modified by the availability of essential resources in the habitat, especially light and nutrients. If the resource supply increases, the position of the line rises, so that it is reached when fewer plants of greater mean size are still surviving in the population. The converse is true if resource supply diminishes.

APPLICABILITY OF THE EQUATIONS

The validity of equation (4) has been demonstrated (Shinozaki and Kira 1956, Holliday 1960b), in particular over the range where $a = 1$. However, there is some evidence to show that over this range it does not always describe the relationship between mean weight and density, especially where the mean weight of *parts* of plants is considered, rather than total plant weight. It has been shown for many crop plants, particularly when products of reproductive growth rather than vegetative growth are considered, that the yield-density relationship is parabolic rather than asymptotic (Figure 7); so yield is not totally independent of density at high densities (Holliday 1960b), and the value of a is greater than unity.

The $-3/2$ power law has been verified for a wide range of species, including many herbs, shrubs, and trees, under both natural and experimental conditions. White (1980) has documented the law for about 80 species. The power law has also been applied to mixed plots and it can be applied to components of plant yield (White and Harper 1970). This final example, however, requires the ratio between the weight of a plant component and the weight of the whole plant to remain constant as population growth proceeds. Mohler et al. (1978) showed that this ratio does not hold for pin cherry and balsam fir, and that the exponent term in the equation varies considerably for different components.

The seasonal growth of clone-forming perennial herbs does not follow the $-3/2$ thinning line (Hutchings 1979, Hutchings and Barkham 1976), although there is a strong connection between mean shoot weight, shoot density and the thinning line in these species. Here the shoot is part of a large plant consisting of several connected shoots, and is alternately the sink and source for large-scale translocations of carbohydrates and other materials. The clonal species investigated by Hutchings mainly exhibit large changes in mean shoot weight until maturity, but little mortality until after maturity. Mean shoot weight stops increasing just at the point when any further increase would result in density-dependent mortality and movement of the population along the thinning line (Figure 6a in Hutchings 1979). Clonal herbs therefore appear to produce a maximum standing crop close to the limit which can be achieved by any plant at the particular density at which they mature, but without undergoing density-dependent mortality; these species are limited by the $-3/2$ thinning line, but do not move along it.

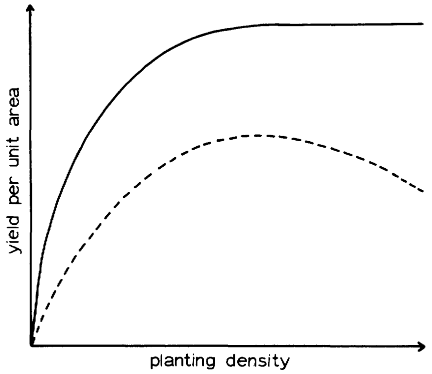

Figure 7. Asymptotic relationship between plant density and yield per unit area expected for total plant weight (solid line), and parabolic relationship between plant density and yield per unit area expected for products of reproductive growth (dotted line). See text for further explanation.

The only environmental variable which appears to alter the $-3/2$ gradient of the mean weight vs. density relationship (as well as altering its position on the graph—see above) is light intensity. Ford (1975) and White and Harper (1970) have presented data which appear to show that as light intensity drops, the gradient of the thinning line falls, approaching -1. However, this relationship may well be an artifact caused by fitting a gradient through points, some of which refer to the $-3/2$ thinning line and some to the ultimate -1 gradient for the plot under the reduced light régime (see Figure 8). This seems possible since the range of light intensities in experimental and natural situations where the power law has been demonstrated have not revealed any systematic variation from a gradient of $-3/2$.

The most important generalization concerning the $-3/2$ power law has been made by White (1980, and see also Gorham 1979). This concerns the relatively constant position of the thinning line for a large number of species, including herbs, shrubs and trees. Virtually all calculated values of log K in the equation lie between 3.5 and 4.3, which is just over a six-fold range in linear terms. Although Harper (1977) suggested that the value of log K might vary in a systematic manner, reflecting the influence of canopy geometry upon thinning and biomass accumulation, no general theory explaining its variations has yet been developed (White 1980). Such detailed interpretation of the value of log K obtained for different species may not be justified by the data on which it is based.

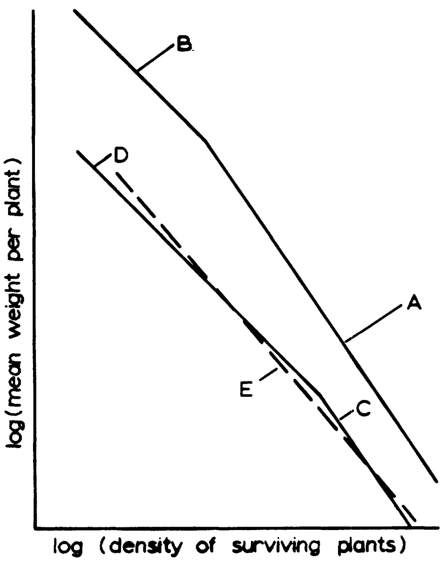

Figure 8. Possible explanation for the failure of the $-3/2$ power law at low light intensities. A: = $-3/2$ thinning line at high light intensity. B: = ultimate yield line (gradient -1) at high light intensity. C: = 3/2 thinning line at low light intensity. D: = ultimate yield line (gradient -1) at low light intensity. E: = regression line plotted through data points on lines C and D.

Gorham (1979) has also clearly demonstrated that the relationship between standing crop and density for a wide range of plants in monocultures (mosses, ferns, gymnosperms, monocotyledons and dicotyledons) of differing size and architecture can be expressed by the simple rule in equation (7), with a value of log K just below 4.0. The subjects used in experiments on which this conclusion was based ranged from large trees (density 0.1 shoots m^{-2}, standing crop $26{,}000 \cdot m^{-2}$) to large mosses (density 10,000 shoots$\cdot m^{-2}$, standing crop 120 $g \cdot m^{-2}$).

RELEVANCE OF THE EQUATIONS IN TEACHING ECOLOGY

Experimental study of growth and self-thinning of plants illustrates several fundamental principles of plant ecology in addition to those outlined in previous sections of this paper. This approach thus provides a basis for deeper understanding of the interactions between the individual plants in populations, and the interactions between the population and its habitat. When supplemented with further data these types of experiments can highlight the struggle for survival between the individual plants in a population. The dominant plants in a population leave more propagules than suppressed plants, and thus stand the best chance of having their genes represented in following generations. Dominance may be achieved because of particular genotypes, or favorable environmental conditions, or a combination of both. Several workers have demonstrated the development of a dominance hierarchy in competing plant populations (e.g. Obeid et al. 1967); the course of events is predictable and can easily be observed. It is also easy to prove that the heaviest mortality risks fall on the smaller plants in the population.

Turning to the interactions between the population and its environment, several important facts can be noted. (1) Rate of growth, rate of reaching the −3/2 thinning line, and rate of thinning depend on habitat conditions. Site fertility and light intensity appear to be the main controlling factors. (2) Thinning proceeds in a density-dependent fashion. (3) In sites of lower light intensity, thinning lines fall to a lower level on the graph, and the ultimate level of biomass that can be supported also falls. Change in fertility level, however, does not appear to alter the position of the thinning line. (4) For a given species, the habitat, rather than the density of planting will usually be the factor controlling the biomass that can be supported, but the major habitat factors of light intensity and fertility exercise different controlling effects. These important lessons, which can be learned from simple laboratory experiments like those conducted by Yoda et al. (1963), provide ample justification for laying heavy emphasis in degree courses on teaching the relationships between plant growth, competition, mortality, and biomass accumulation.

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