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A Model for Growth and Self-thinning in Even-aged Monocultures of Plants

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ABSTRACT

A theoretical model is derived from simple postulates to describe the rates of growth and mortality of plants in populations of different densities. The growth rate is described by a modification of the logistic growth differential equation in which the increase in weight of an individual plant depends on its area, s_i , rather than on its weight. The effective area for growth of a plant is reduced by an empirical function, $f(s_i)$, with two terms: one term expresses the constraint imposed upon the increasing total area of plants by the limited physical area of the plot; the other term allows for a competitive advantage or disadvantage for plants of varying sizes. Depending on the value of the parameter controlling the relative competitive advantage term, intrinsic variability between plants can be amplified or suppressed. An individual plant dies if the $f(s_i)$ results in a negative growth rate for that plant. Computer simulations of the growth and survival of plants at different population densities were run. The results exhibit characteristics that appear realistic upon comparison with published data: a survival of the fittest occurring during thinning; a line of slope close to $-\frac{3}{2}$ bounding the graphs of log weight versus log density; and the occurrence of bimodality, associated with subsequent mortality, on frequency distribution of log weight.

Key words: computer logistic model, growth differential equation, density-effect, competition, mortality, self-thinning.

INTRODUCTION

Growth in a population of plants may involve change in the size of individual plants, change in the form and change in the number of plants (Hunt, 1978). These three processes are closely interlinked. As plants in a population develop, the biomass produced becomes limited by the rate of availability of resources, and neighbouring plants interfere with each other's activities according to their age, size and distance apart (Harper, 1977). Such 'density stress' results in a forced sharing of limiting resources with a compensating plastic reduction in individual plant development and an increase in the risk of mortality to whole plants. The rate of death and the growth rate of survivors are interrelated.

A number of mathematical models have been used to describe the relationship between yield and plant density (Bleasdale and Nelder, 1960; Willey and Heath, 1969; Barnes, 1977) but few have attempted to describe the rates of growth and mortality of plants in populations of different densities. The paper of Barnes (1977) is, however, particularly relevant to the model presented in this paper for the growth and self-thinning of plants in an even-aged monoculture, as also is a paper by Yoda *et al.* (1963).

Yoda *et al.* presented data on the average weight per surviving plant and the numbers surviving per unit area in self-thinning populations. For each of a number of species, the data could be fitted approximately by a straight line on a log versus log plot with a slope close to $-\frac{3}{2}$. This appears to be a quite general relationship for trees and for biennial and annual herbs (White and Harper, 1970; White, 1975). Hence, in a self-thinning population, the average weight per plant, \bar{w} , is seen to be roughly proportional to $\bar{s}^{\frac{3}{2}}$, where \bar{s} is the average area per plant, the reciprocal of the number of plants per unit area, ρ .

Barnes (1977) tested a number of theoretical models against observed data for the growth of crop plants at densities sufficient to result in a reduction in growth rate but no mortality. In essence, to predict the rate of growth of plants in a crop, he used differential equations of the form

$$dw/dt = k \cdot g(w) \cdot h(y),$$

where w is the weight per plant; y is the yield per unit area, given by $y = wp$; k is, for simplicity, a constant although a time-dependent function, $k(t)$, might be more general; $g(w)$ describes the growth rate of the isolated plant; and $h(y)$ represents the effect of the current biomass per unit area on the growth of the individual plant.

The forms of $g(w)$ tested were those of linear growth, of exponential growth and of logistic growth. The function $h(y)$ related the reduction in growth rate of plants to a maximum yield per unit area, Y . The particular forms of $h(y)$ tested were either a linear reduction effect

$$h(y) = \left(1 - \frac{y}{Y}\right),$$

or a more generalized expression such as

$$h(y) = \left(1 - \left(\frac{y}{Y}\right)^{\theta}\right).$$

The most generally satisfactory model to describe the time dependence of the yield per unit area over a range of densities was found to be that in which the logistic growth equation was combined with a generalized limiting function.

There is, however, a gap between these two approaches: the models of Barnes do not include self-thinning, and the allometric equation of Yoda *et al.* does not describe the time-course along the self-thinning relation, nor does it describe the processes of growth before the onset of thinning. An understanding of such processes is essential if one is to relate the yield of a population, whether this is measured in terms of biomass or seed production, to the initial density of the population. In this paper, a model is presented which simulates the time course of growth including self-thinning for even-aged monocultures.

The model

The model may be derived from a set of quasi-logical postulates.

(1) The $\frac{3}{2}$ power law or self-thinning rule is assumed to be associated with a simple volume/area allometry for plants of a constant shape and specific gravity (Yoda *et al.*, 1963; White and Harper, 1970). This implies that a plant of given weight depends on a certain area for its growth and survival, although this area may represent a 'zone of influence' (Mitchell, 1969) rather than the physical area of leaf canopy or root extension.

(2) The differential equation for logistic growth, limiting the growth of an isolated plant to an eventual maximum size, W , may be regarded as being produced by the sum of two terms, one positive and one negative, depending on differing powers of the current weight w . This equation may be written as

$$\frac{dw}{dt} = aw \left(1 - \frac{w}{W}\right) \quad \text{or} \quad \frac{dw}{dt} = aw^1 - \frac{a}{W}w^2$$

where a is a constant. Net growth occurs if the algebraic sum of the two terms is positive and would cease if w reached W . A modification of the logistic growth equation, which expresses a dependence of growth on area, will be used in the model. For the growth rate of the isolated plant

$$dw/dt = as - bw^2$$

where $s = (w/K)^{\frac{2}{3}}$ and $b = (a/W^2)$. $(W/K)^{\frac{2}{3}} = aW^{-\frac{2}{3}} K^{-\frac{2}{3}}$. K is a constant which relates the area or zone of influence, s , to the weight of the plant, w , and might vary between species and between environments. The constants a and b govern an area-dependent growth process and a weight squared dependent loss process respectively and result in a final predicted weight W for plants of that species.

Richards (1969) has shown how altering the power of the second term in the logistic growth equation can generate a family of growth equations including the Gompertz equation and the 'Monomolecular' or exponential saturation model. Here we have altered the power of the first term from 1 to $\frac{2}{3}$ to relate the positive growth term to area and, for simplicity, have left the second term unaltered as the square. More generally the two powers might be expressed as empirical parameters to be evaluated from observed data (Bertalanffy, 1957).

(3) There is variation between plants. Following Koyama and Kira (1956) the model used independent Gaussian distributions for the initial weights of the individual plants, $\{(w_i)_{t=0}\}$, and for their growth constants, $\{a_i\}$. For the i th plant

$$a_i \in \text{N.D.} (\mu_a, \sigma_a^2)$$

and

$$(w_i)_{t=0} \in \text{N.D.} (\mu_{w_0}, \sigma_{w_0}^2)$$

(4) Competition amongst plants leads to a reduction in growth. The model assumes that a plant can effectively utilize only a fraction of the area that it would utilize in the absence of other plants. A function, $f(s_i)$, will be used to predict this fraction. Hence, for the i th plant

$$dw_i/dt = a_i s_i f(s_i) - b_i w_i^2$$

Before the function $f(s_i)$ is discussed in detail, it is apparent that the above equation associates the competition effects with one term of the growth equation. Hence, if $f(s_i)$ falls sufficiently below the value 1, that is if competition results in a plant being unable to utilize an adequate fraction of its area, dw_i/dt then becomes negative. A simple self-thinning procedure is to assume that a plant experiencing a negative growth rate dies immediately. Doubtless this is an oversimplification (see Mahmoud and Grime, 1974) but as a plant loses mass it would experience a progressively greater competitive disadvantage and an increasing probability of mortality.

(5) Competition between plants becomes increasingly severe as the sum of the areas of the individual surviving plants, Σs_i , approaches the total area of the plot, S . However, a larger than average plant is assumed to have a competitive advantage over its smaller contemporaries, competition between plants affecting the smaller plants to a greater extent than it does the larger ones.

The particular form of $f(s_i)$ chosen for the model was

$$\left[1 + \left(\frac{\Sigma s_i}{S} \right)^{\phi_1} \left(\frac{\bar{s}}{s_i} \right)^{\phi_2} \right]^{-1}$$

Expressions of the form $(1 + (x/x_c)^r)^{-1}$ are described by Thornley (1976) for threshold response curves of the switch-off type. These functions are equal to 1 for $x \ll x_c$ and fall monotonically, tending to zero for $x \gg x_c$, and passing through the value $\frac{1}{2}$ for $x = x_c$. The higher the value of r , the higher the value of the function for $x < x_c$ the sharper the fall in the region $x \simeq x_c$, and the smaller the function for $x > x_c$. For an infinitely high value of r , the function abruptly changes from 1 to 0 at $x = x_c$.

In $f(s_i)$ the term $\Sigma s_i/S$ is associated with a decrease in growth rate as Σs_i approaches the area of the plot, S , and the other term \bar{s}/s_i allows for a variation in the effect of competition on plants of differing relative size. ϕ_1 and ϕ_2 allow for the severities of the

two processes. The ratio $\Sigma s_i/S$ can also be expressed as $\bar{s}\rho$ where \bar{s} is the average area required per plant and $1/\rho$ is the average area available. The expression used for $f(s_i)$ also bears some relation to existing yield-density equations. This is shown in Appendix I.

Hence, for a surviving plant

$$\frac{dw_i}{dt} = a_i s_i f(s_i) - b_i w_i^2,$$

where

$$s_i = \left(\frac{w_i}{K}\right)^{\frac{2}{3}} \quad \text{and} \quad b_i = \frac{a_i}{W^2} \left(\frac{W}{K}\right)^{\frac{2}{3}}$$

$$f(s_i) = \left[1 + \left(\frac{\Sigma s_i}{S^1}\right)^{\phi_1} \left(\frac{s}{s_i}\right)^{\phi_2}\right]^{-1}$$

$$a_i \in \text{N.D. } (\mu_a, \sigma_a)$$

$$(w_i)_{t=0} \in \text{N.D. } (\mu_{w_0}, \sigma_{w_0}).$$

K , W and S do not vary with time nor from plant to plant. A plant dies if $dw_i/dt < 0$.

Computer simulation

A program using the model with its growth-increment equation and self-thinning algorithm was run with a range of initial densities. The effect of various values of ϕ_1 and ϕ_2 was investigated in an exploration of the behaviour of the model. The values of the other parameters as given in Table 1 were used in all but one of the simulations reported here.

Figure 1 (a)–(e) presents some calculated values for the average weight per plant plotted against the density of surviving plants. Note that for Fig. 1 (d) the variability on intrinsic growth, σ_a , has been set to zero. Figure 2 presents some calculated results for the distributions of relative weights of individual plants which are compared with some distributions reported from real plants (Ford, 1975). Although a selection was made from a limited number of simulations there has been no systematic attempt to obtain a best fit.

TABLE 1. *List of values used in simulations of the model run on a computer using an integration increment of Δt*

$K = 7 \text{ kg m}^{-3}$	$W_{max} = 0.1 \text{ kg}$
$\mu_{w_0} = 10 \text{ mg}$	$\sigma_{w_0} = 0.05 \mu_{w_0}$
$\mu_a = 25 \text{ g m}^{-2} \text{ d}^{-1}$	$\sigma_a = 0.05 \mu_a$
$S = 1-10^{-4} \text{ m}^2$	$\Delta t = 0.1 \text{ d}$

Initial number of plants, 100–600, such that surviving number $\simeq 100$ after 50 days.

DISCUSSION

The values of ϕ_1 and ϕ_2 chosen for Fig. 1 (a) impose a sharp restriction ($\phi_1 = 20$) upon the growth of the hypothetical plants as Σs_i approaches the area of the plot, S , but give no relative advantage to the larger plants ($\phi_2 = 0$). This results in a severe reduction on growth as the plants reach a sufficient size to fill the area, the critical size depending on the density. No self-thinning occurs with these particular parameters since the growth of the larger plants is slowed up rather more than that of the smaller ones. However, at the highest density there is initially insufficient area per plant to support survival and, in the simulation, all are killed off.

In Fig. 1 (b) the parameter ϕ_2 , which is set at 20, gives a strong size advantage and with the severe area constraint ($\phi_1 = 20$) drastic self-thinning occurs, eliminating the smaller plants rather than appreciably checking the growth of the larger surviving plants.

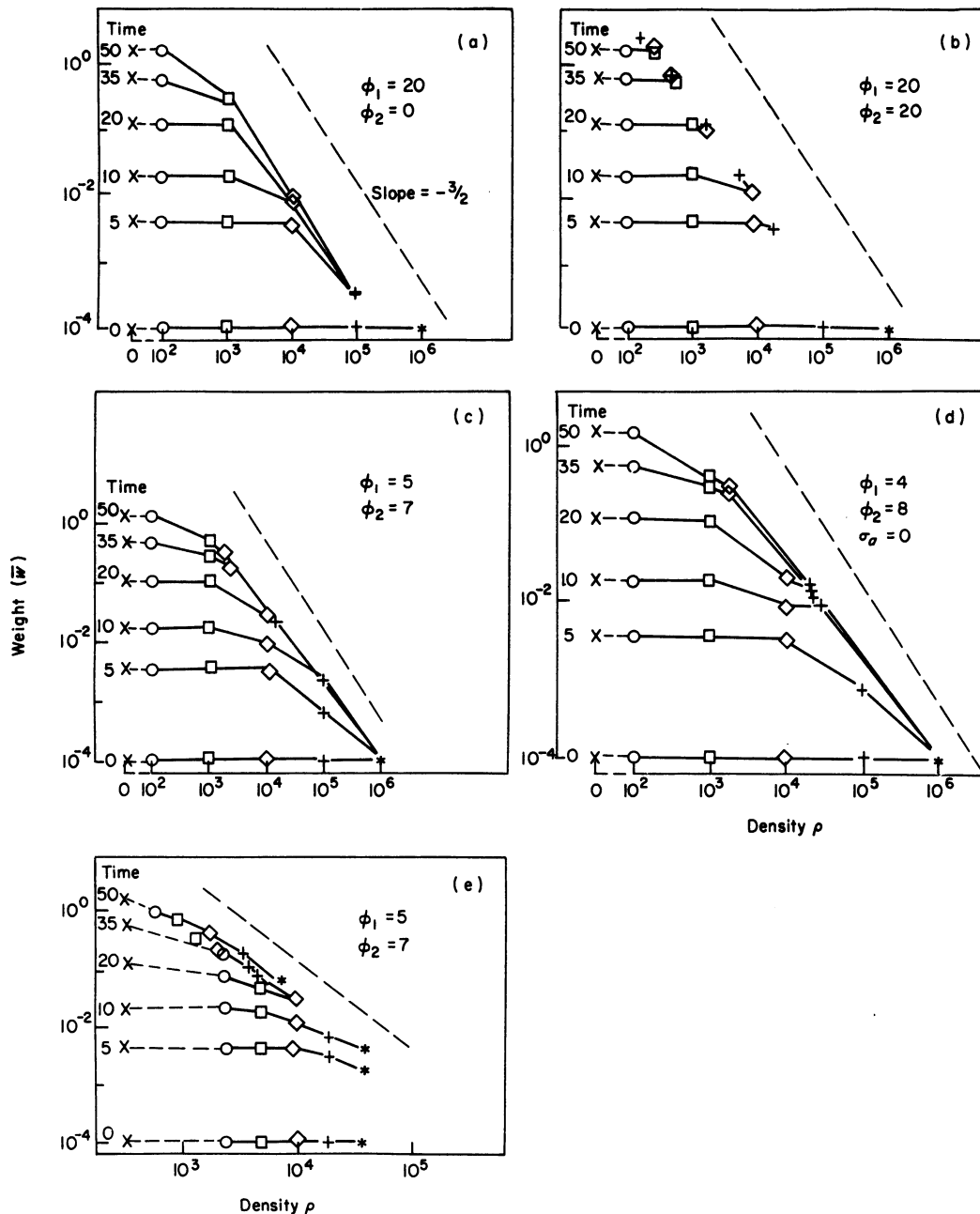


FIG. 1. Results obtained from simulations of the plant growth and self-thinning model. The density of surviving plants per square metre, ρ , and their average weights in grams, \bar{w} , for times 0, 5, 10, 20, 35 and 50 days are plotted on logarithmic axes. The dashed lines have a slope of $-3/2$. The value used for ϕ_1 and ϕ_2 are indicated in each graph. Note that the density scale has been changed in (e) and that σ_a has been set to zero rather than $0.05 \mu_a$ for (d). The values of the other parameters are given in Table 1.

Indeed with the initial variability and the operation of a 'survival of the fittest', those plants surviving from higher initial densities are those with the highest values of the parameters $(w_i)_{t=0}$ and a_i . These may, on average, be larger than the plants from lower densities where selection has not operated significantly! Of course, competition has reduced the growth that those same surviving plants would have made if they had been grown at a lower density but the more important effect is the self-thinning.

Figure 1(c) shows a simulation generated by less severe limitations from the parameters ϕ_1 and ϕ_2 producing a less extreme behaviour. The simulation has a similarity to published experimental results (e.g. Kays and Harper, 1974).

For Fig. 1(d), the model has been run with plants assumed to have no variability in their intrinsic growth rate, a . That is, the only variation between the plants is in their initial weight, w_0 . With the higher value of ϕ_2 , the competition effects on the smaller plants amplify the variation and produce an outcome similar to that given in Fig. 1(c).

Figure 1(e) shows the calculated values of the weights for a more limited range of densities. However, in the case of this simulation, cross-overs occur in which a population from a higher initial density thins to a lower density with a higher average weight than a population from some lower initial weight. Such a behaviour is not apparent in published data on real plants. Possibly, this discrepancy is due to the particular form of $f(s_i)$ chosen. Another possibility is that the mortality process in the simulation is too abrupt.

In all these graphs of $\log w$ versus $\log \rho$, the density-dependent reduction in growth rate occurs as the population approaches a straight line of slope $-\frac{3}{2}$ and/or self-thinning proceeds close to such a line. The higher the values of ϕ_1 and ϕ_2 the closer a fit ensues.

The qualitative agreement between the distributions of weight that can be produced by the model and those reported by Ford (1975), as shown in Fig. 2 is particularly impressive since the authors were unaware of these data when formulating the model. The development of an apparently bimodal distribution for $\{\log w_i\}$ and the reduction in numbers of survivors is evident in both. The distributions for $\{w_i\}$ obtained from most simulations show that an initially symmetrical bell-shaped distribution becomes asymmetric and 'L-shaped'. This transition occurs earlier in time for populations simulated at higher densities. This phenomenon has been reported from observations over a number of species (Koyama and Kira, 1956). In terms of the model presented here, the intrinsic variability of the plants is amplified as competition among them slows up the less vigorous individuals and leads to their mortality.

On the other hand, a lower value of ϕ_2 suppresses the variability in simulations produced by the model. A more uniform population also can result if there is not an initial period of growth with little competition, a period which permits the effects of differing growth rates to be expressed. These latter suggestions might provide an explanation for the observation of Rabinowitz (1979) that, for seedlings of *Festuca paradoxa* Desv., bimodality is less marked at higher densities. These seedlings showed a reduction in average weight at the higher densities but no density-dependent mortality.

Hence, the one simple model can generate a range of effects observed in the growth of real plant populations. It appears to provide a basis for developing a clearer understanding and modelling of the effects involved. It is, of course, an over simplification ignoring disease and density-dependent cross-infection and many other phenomena.

Furthermore, the expression chosen for $f(s_i)$ is a convenient empirical one. It describes the result upon the individual plant of a population-average effect rather than of its nearest neighbours. Although some plasticity in the growth of plants may produce an overall population-average effect, such immediate interactions may well be important. In an experiment on the growth of yellow dent corn, Hozumi, Koyama and Kira (1955) found negative correlations between the fresh weights of shoots of immediately neighbouring plants from a linear layout, competitive interactions having resulted in plants

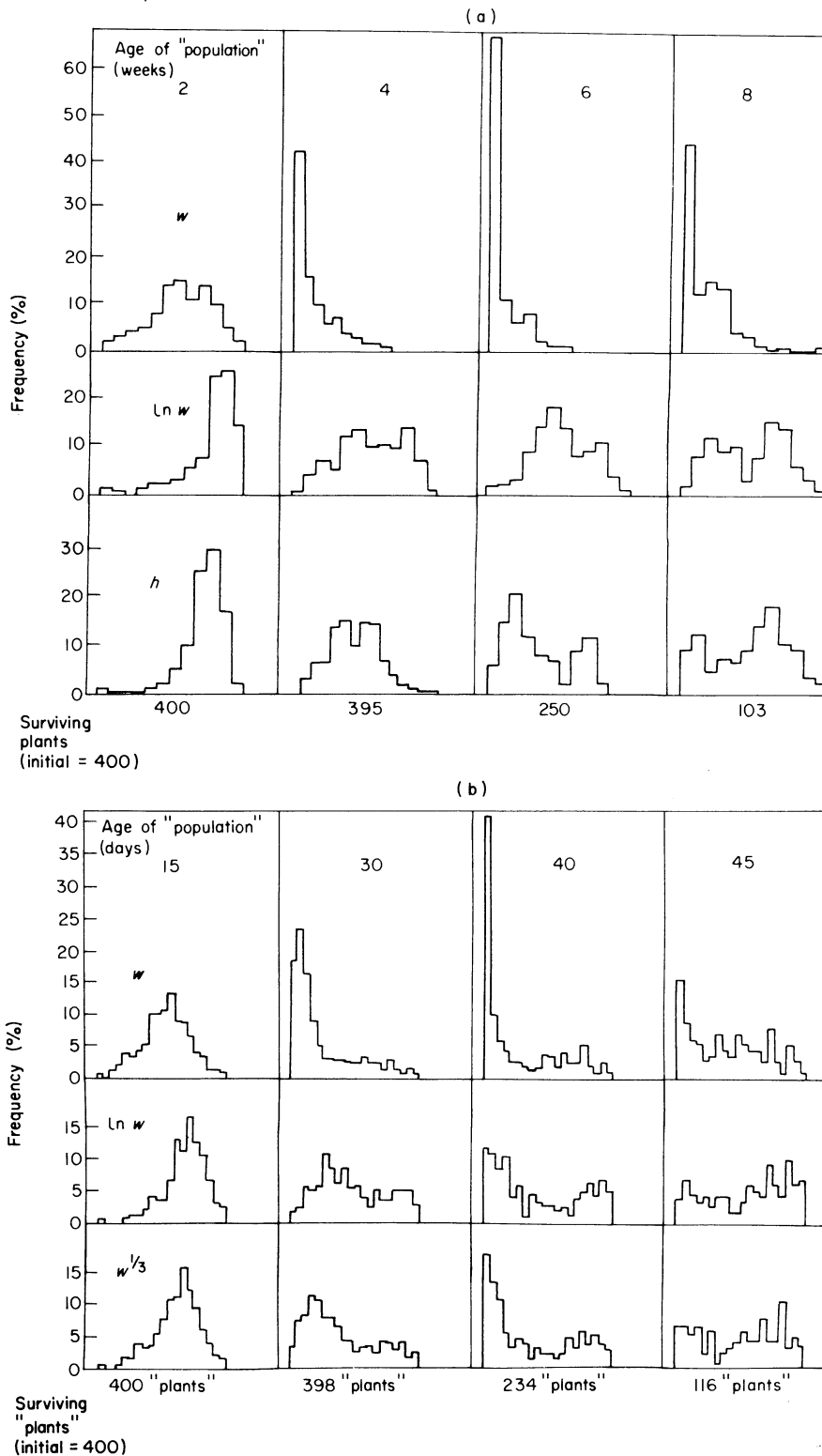


FIG. 2. Results obtained for plant weight distributions. (a) Data from the growth of real plants, *Tagetes patula* L. var. 'Naughty Marietta' reported by Ford (1975). (b) Data from a simulation of the model using $\phi_1 = 5$ and $\phi_2 = 7$ as in Fig. 1(c) and (e). In each case the uppermost set of graphs are histograms for the weights of plants, the middle set are for the log weights and the lowest set are either for the heights of the real plants (a) or for the cube root of weights of the hypothetical plants (b).

that were alternately larger and smaller along the row. Gates (1978) has described a static model for the competition between a pair of plants. Possibly the incorporation of some such mutual shading or competition expression into $f(s_i)$ might give a better theoretical model.

However the present model is quite convenient mathematically and does describe with some plausibility a range of phenomena. It is hoped that it will provide a useful basis for further investigations and analyses.

APPENDIX

The expression for $f(s_i)$ is related but not identical to equations for plant yield and density discussed by Shinozaka and Kira (1956) and by Bleasdale and Nelder (1960).

To describe the effect of density on the weight per plant, the former used an equation of the form

$$w^{-1} = A\rho + B,$$

where A and B were functions of time. This equation may be rewritten as

$$w = \frac{W}{1 + \frac{A}{B}\rho},$$

where $W = 1/B$. The actual weight attained by plants at a density ρ would be less than the weight W which they would have had if they had been grown without competition.

Bleasdale and Nelder (1960) and Bleasdale (1966) modified the equation to

$$w^{-\theta} = A\rho^{\phi} + B.$$

Bleasdale noted that it is the ratio between the constants θ and ϕ which is important rather than their absolute values. Thus one or other may be set equal to unity and Bleasdale chose to set ϕ to unity. Here, however, we will set θ to unity and rewrite their equation as

$$w = \frac{W}{1 + (A'\rho)^{\phi}} = W[1 + (A'\rho)^{\phi}]^{-1},$$

where $W = 1/B$ and $A' = (A/B)^{1/\phi}$.

The expression $A'\rho$ must be dimensionless and hence A' must have the dimensions of area per plant. In the formulation of Shinozaki and Kira, $1/A'$ would be a function of time, possibly the density at which competition becomes appreciable.

In our model in which self-thinning occurs, we use ρ as the current density at any time and we have chosen to make A' a function of the size attained by the plants.

If $A' = \bar{s}$ then $A'\rho = \bar{s}\rho = \Sigma s_i/S$, where \bar{s} is the average of the areas required by the surviving plants grown on a plot of area S .

An obvious generalization, analogous to that of Bleasdale and Nelder, is to introduce a parameter ϕ_1 as a power of $\bar{s}\rho$ and, for mathematical convenience, the relative size effect may be included in a similar form giving

$$\begin{aligned} f(s_i) &= [1 + (\Sigma s_i/S)^{\phi_1} (\bar{s}/s_i)^{\phi_2}]^{-1} \\ &= [1 + (\bar{s}\rho)^{\phi_1} (\bar{s}/s_i)^{\phi_2}]^{-1}. \end{aligned}$$

If, following Bleasdale (1966), ϕ rather than θ was set to unity, the analogous expression for $f(s_i)$ would have been

$$[(1 + \bar{s}\rho)^{1/\phi_1} (1 + \bar{s}/s_i)^{1/\phi_2}]^{-1}.$$

However, this expression would be somewhat more demanding on time for the innermost operations of the loops of the computer simulation.

LITERATURE CITED

- BARNES, A., 1977. The influence of the length of the growth period and planting density on total crop yield. *Ann. Bot.* **41**, 883–95.
- BERTALANFFY, L. VON, 1957. Quantitative laws in metabolism and growth. *Q. Rev. Biol.* **32**, 218–31.
- BLEASDALE, J. K. A., 1966. The effects of plant spacing on the yield of bulb onions (*Allium cepa* L.) grown from seed. *J. hort. Sci.* **41**, 145–53.
- and NELDER, J. A., 1960. Plant population and crop yield. *Nature, Lond.* **188**, 342.
- FORD, E. D., 1975. Competition and stand structure in some even-aged plant monocultures. *J. Ecol.* **63**, 311–33.
- GATES, D. J., 1978. Bimodality in even-aged plant monocultures. *J. theor. Biol.* **71**, 525–40.
- HARPER, J. L., 1977. *Population Biology of Plants*, 892 pp. Academic Press, London.
- HOZUMI, K., KOYAMA, H. and KIRA, T., 1955. Intraspecific competition among higher plants. IV. A preliminary account on the interaction between adjacent individuals. *J. Inst. Polytech. Osaka Cy Univ., Ser. D* **6**, 121–30.
- HUNT, R., 1978. *Plant Growth Analysis*, 67 pp. Arnold, London.
- KAYS, S. and HARPER, J. L., 1974. The regulation of plant and tiller density in a grass sward. *J. Ecol.* **62**, 97–105.
- KOYAMA, H. and KIRA, T., 1956. Intraspecific competition among higher plants. VII. Frequency distribution of individual plant weight as affected by the interaction between plants. *J. Inst. Polytech. Osaka Cy Univ., Ser. D* **7**, 73–94.
- MAHMOUD, A. and GRIME, J. P., 1974. A comparison of negative relative growth rates in shaded seedlings. *New Phytol.* **73**, 1215–9.
- MITCHELL, K. J., 1969. Simulation of the growth of even-aged stands of white spruce. *Yale Univ. Bull.* **75**, pp. 48.
- RABINOWITZ, D. (1979). Bimodal distributions of seedling weight in relation to density of *Festuca paradoxa* Desv. *Nature, Lond.* **277**, 297–8.
- RICHARDS, F. J., 1969. The quantitative analysis of growth. In *Plant Physiology*, Vol. VA, ed. F. R. Steward, 435 pp. Academic Press, New York, San Francisco and London.
- SHINOZAKI, K. and KIRA, T., 1956. Intraspecific competition among higher plants. VII. Logistic theory of the C-D effect. *J. Inst. Polytech. Osaka Cy Univ. Ser. D* **7**, 35–72.
- THORNLEY, J. H. M., 1976. *Mathematical Models in Plant Physiology*, 318 pp. Academic Press, London and New York.
- WHITE, J., 1975. Patterns of thinning of plant populations. Twelfth International Botanical Congress, Leningrad.
- and HARPER, J. L., 1970. Correlated changes in plant size and number in plant populations. *J. Ecol.* **58**, 467–85.
- WILLEY, R. W. and HEATH, S. B., 1969. The quantitative relationships between plant populations and crop yield. *Adv. Agron.* **21**, 218–321.
- YODA, K., KIRA, T., OGAWA, H. and HOZUMI, K., 1963. Self-thinning in overcrowded pure stands under cultivated and natural conditions. *J. Biol. Osaka Cy Univ.* **14**, 107–29.