

A Model of Interference Within Plant Monocultures

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(Received 4 February 1985, and in revised form 10 May 1985)

Simulation models are developed which can mimic all the responses to density that are commonly observed in monocultures of plants. These simulations are based upon a model describing the relationship between the size of an individual plant and the area of resources available to it after accounting for interference from neighbours. Within simulated plant populations, both the mean yield–density function and the distribution of individual plant yield vary with age-structure, the resource utilization efficiency of individual plants and the degree of competitive advantage gained by older, larger individuals.

The simulation model is extended to mimic the time-course of plant monocultures by including simple sub-models for plant growth and mortality. These simulations display realistic hierarchy development, changing mean yield–density responses and self-thinning. The relevance of these models to our understanding of density-dependence in plant populations is discussed.

Introduction

In an otherwise uniform population of plants, the growth and survival of each individual plant depends upon the local density (Mack & Harper, 1977) and upon its emergence time relative to neighbouring plants (Ross & Harper, 1972; Watkinson, Lonsdale & Firbank, 1983). Size hierarchies are quickly established in crowded monocultures, and are maintained by the competitive advantages gained by the older, larger plants. The structure of this hierarchy is affected by density and by the age of the plants, and as the plants grow, the smallest ones may die through self-thinning (Obeid, Machin & Harper, 1967; Ford, 1975).

Density is important in determining yield because the resources available to the plant stand as a whole are restricted. Therefore, both the probability of survival and the mean yield of surviving plants decrease with increasing densities within plant monocultures. Empirical equations have been formulated to model such density-dependence. Mean yield per plant can be

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described using the reciprocal equation

$$\bar{w} = \bar{w}_m(1 + aN)^{-b} \quad (1)$$

where \bar{w} is the mean yield per plant, \bar{w}_m is the mean yield of isolated plants grown in the same habitat for the same time, N is the density of plants at harvest and a and b are fitted parameters (Watkinson, 1980). Density-dependent mortality due to self-thinning can be described by the empirical equation

$$N = N_i(1 + mN_i)^{-1} \quad (2)$$

in which N_i is the initial density and m^{-1} is the maximum density that the habitat can support (Yoda *et al.*, 1963; Watkinson, 1980). The parameter m changes with time as the plants grow according to the empirical relationship

$$w = cm^k \quad (3)$$

which is more usually written in the form

$$w = cN^{-k} \quad (4)$$

where c and k are fitted parameters, k usually having a value of approximately 1.5 (Yoda *et al.*, 1963; White 1981). This relationship, the $-3/2$ power law, describes the limits to the combinations of weight and density that can be attained by plant populations (Yoda *et al.*, 1963; White, 1981). No combinations of density and biomass occur beyond it for autotrophic stands, and so this relationship truncates the mean yield-density response.

Our understanding of these empirically-defined responses to density has been increased by the use of simulation models which mimic certain aspects of density-dependence. These models may be used to test hypotheses about the nature of interference between plants. For example, models by Diggle (1976), Gates (1978) and Ford & Diggle (1981) show that size hierarchy development as observed in many monocultures cannot be simulated by assuming that the effectiveness of resource capture is the same for all plants: the larger plants must have some form of competitive advantage if satisfactory simulations are to be generated. This assumption also allows the simulation of the $-3/2$ power law (Aikman & Watkinson, 1980).

As yet, no general model has been published which mimics all the usual features of density-dependence. The interactions between neighbourhood relationships, hierarchy development, self-thinning and the mean yield-density response can therefore not yet be explored at a detailed, theoretical level. In this paper, we present a simulation model of a generalized plant monoculture to fill this gap in our understanding. A static model is first

described, in which individual plant yield is determined as a function of resource availability. The behaviour of the mean yield-density response is explored. The usefulness of this model is restricted, however, since mortality is dynamic process. The static simulation is therefore developed further by including sub-models for plant growth and death. The resulting dynamic simulations closely mimic self-thinning and hierarchy development as observed in natural populations.

A Model of Individual Plant Yield

In the absence of interference, the size of a plant depends upon its age and genotype, the habitat conditions and the action of herbivores and pathogens. The area of resources required by the plant is, of course, finite, and so the growth of the plant is not affected by other plants taking up light, water and nutrients from outside this zone, termed the ecological neighbourhood area, q (Antonovics & Levin, 1980). At higher densities, the resources within this zone are likely to be poached by neighbouring plants. The area of resources left to the plant can be termed the zone of influence, z (Opie, 1968), where $z \leq q$. The yield of an individual plant, w , is therefore a function of z , q and the yield it would have had in the absence of interference, w_m

$$w = w_m f(z/q). \quad (5)$$

When $z = q$,

$$w = w_m. \quad (6)$$

The yield of a plant is not necessarily directly proportional to the zone of influence. The morphology and physiology of the plant may dictate that not all of the resources within the zone can be utilized. The efficiency of resource utilization, r , must be included as a parameter of individual plant yield. Hence

$$w = w_m (z/q)^r. \quad (7)$$

The yield of each plant in a population as described by equation (7) may be summed to give the mean yield per plant

$$\bar{w} = N^{-1} \sum_{i=1}^N w_{mi} (z_i/q_i)^r. \quad (8)$$

The behaviour of equation (8) may be explored using hypothetical plant populations. Suppose that there are N identical plants growing in a uniform habitat of unit area and that $r = 1$. The mean value of z is calculated by

dividing the total area occupied by the plants by N . If q is small, the proportion of the habitat which is not occupied by zones of influence (P_0) can be estimated from the Poisson distribution

$$P_0 = e^{-qN}. \quad (9)$$

The remaining area, $1 - e^{-qN}$, is occupied by the plants. Therefore

$$\bar{z} = N^{-1}(1 - e^{-qN}). \quad (10)$$

Assuming that r equals one, it follows from equation (7) that

$$\frac{\bar{w}}{w_m} = \frac{1 - e^{-qN}}{qN}. \quad (11)$$

The behaviour of this equation can be investigated by using different values of q . The mean yield-density function

$$\bar{w} = \bar{w}_m(1 + aN)^{-b} \quad (1)$$

can then be fitted to data points generated by equation (11). For created data for which $w_m = 1$ and $r = 1$, the fitted parameters of equation (1) tend to the values $\bar{w}_m = 1$ and $b = 1$ as the range and number of data points increase (see Fig. 1; n.b. \bar{w}_m is estimated from the asymptotic mean yield per plant at low densities and b from the gradient of the mean yield-density response at high densities). Furthermore the parameter a is estimated by the reciprocal of the density at which the effects of density become apparent, i.e. at the shoulder of the curve which approximately coincides with a density of q^{-1} (Fig. 1). Therefore a provides an estimate of q . The close (but not perfect) agreement between equations (1) and (11) when $b = r = w_m = 1$ and $a = q$ (Fig. 1) shows that equation (8) can be used to describe

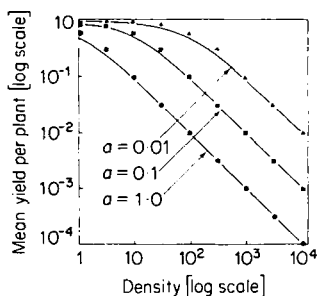


FIG. 1. The relationship between mean yield per plant and density according to two models. The points represent values according to equation (11) where $w_m = 1$, $r = 1$ and $q = 1.0$ (●), 0.1 (■) and 0.01 (▲). The lines show the relationship according to equation (1) where $w_m = 1$, $b = 1$ and a is given the values indicated. Density is given per unit area, and the units of yield are arbitrary. See text for details.

mean plant yield, and suggests that the assumptions implicit in the model are reasonable.

If the distribution of the parameter z (the zone of influence) is understood, then the distribution of the yields of individual plants can also be described. The value of z for a given plant depends upon the outcome of interference with its neighbours. Suppose that there are two identical plants A and B growing in a uniform habitat. The total area available to these plants is the area encompassed by the two ecological neighbourhood areas. If these areas do not overlap, there is no interference and each plant has complete access to its ecological neighbourhood. On the other hand, if the ecological neighbourhood areas overlap, and the plants cannot respond by extending the boundaries of the zones of influence beyond the boundaries of the ecological neighbourhood areas, then interference must take place. In this case, the yield of each plant depends not only upon the size of the ecological neighbourhood area but also upon the proportion of resources that it can obtain from the region of overlap. If the resources in the region of overlap are shared equally between the plants, then

$$z_A = z_B = \bar{z}. \quad (12)$$

This type of interference is known as two-sided competition (Diggle, 1976). It is however possible that one of the plants obtains a disproportionate share of the resources, perhaps by shading its neighbour. This form of competition is referred to as being one-sided (Diggle, 1976; Ford & Diggle, 1981). The form of competition clearly has a marked effect on the values of z_A and z_B and hence on the yields of the plants. The mean value of the zone of influence is unaffected.

A Static Simulation Model of a Monoculture of Plants

It is possible to model the yields of any number of plants by assuming that the ecological neighbourhood areas are fixed circles and that each plant competes for the resources within ecological neighbourhood areas of neighbouring plants with which its own area overlaps. Given the density of a hypothetical population of plants together with the distribution of ecological neighbourhood sizes and the form of competition, the outcome of competition within the stand may be simulated.

The algorithm for the simulation model assigned a specified number of plants to random positions within the habitat. Each plant was then allocated a circular ecological neighbourhood area from a normal distribution of possible values. The zone of influence of each plant was calculated by sampling the ecological neighbourhood area. If the sampled location was

not within the ecological neighbourhood area of any other plants the resources present were assigned to the focal plant. Resources at locations within overlap regions were divided amongst the relevant plants. Two-sided competition was simulated by sharing out the resources equally, whilst for one-sided competition, the plant with the largest ecological neighbourhood area was assigned a fraction d , the next largest taking d of the remainder and so on (after Ford & Diggle, 1981). Except when $d = 1$ (complete one-sided competition), not all of the resources were accounted for using this method, but the resulting inaccuracy was negligible. The yield of each plant was calculated from its estimated zone of influence using equation (7).

The model was run with a wide range of initial densities and the effects of various values of r and d on the behaviour of the model were investigated. The yield of each plant was scaled so that a plant with an ecological neighbourhood area of x had a w_m value of x . The variance of q was set at 0.1. The habitat was a closed square of 10 units in area, i.e. plants near the boundary could not take up resources from beyond it. Data are presented from one simulation run for each combination of parameter values.

The complete program was written in FORTRAN77, using a random number generator from the NAG subroutine library.

SIMULATION RESULTS

No mortality occurred in these simulations except in the case of complete one-sided competition (Fig. 2(d)) where at high densities the larger plants prevented the smaller ones from obtaining any of the resources. Some of the smaller plants therefore died. In the other simulations, every plant had access to at least some resources.

Mean yield per plant always followed the expected trend with increasing density. That is, yield was approximately constant at low densities and became a log-linear function of density at high densities. In particular, when competition was two-sided or when $r = 1$, the model

$$\bar{w} = q(1 + qN)^{-r} \quad (13)$$

provided an adequate fit to the generated data (Fig. 2). When one-sided competition was modelled, however, the gradient of the mean yield-density relationship at high densities differed from r (Table 1).

The distribution of the yields of plants within the simulated populations depended upon density, the form of competition and the value of r (Fig. 3). At low densities, where there was little interference, the yield distributions were approximately normal, reflecting the normal distributions of q used to generate the data. Simulations of two-sided competition resulted in

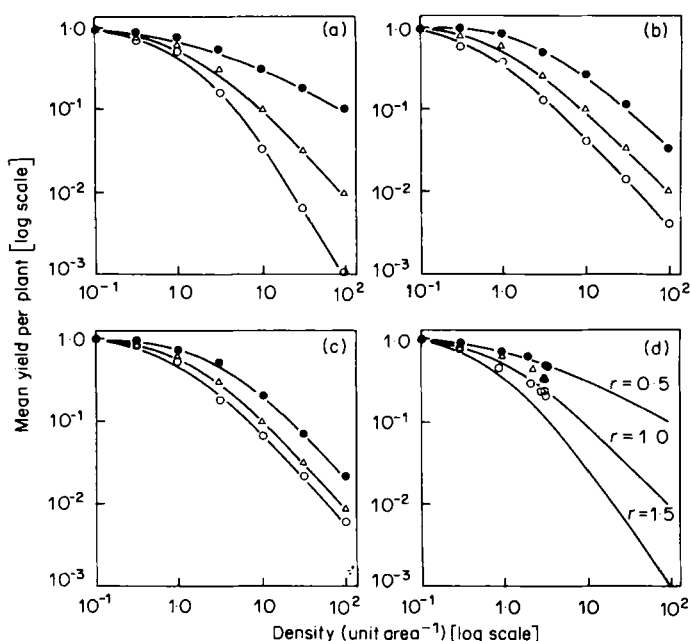


FIG. 2. The response of mean yield per plant to density in simulated plant populations where $w_m = 1$, $q = 1$ with a variance of 0.1 and $r = 0.5$ (●), 1.0 (△) and 1.5 (○) and where competition was (a) two-sided or was one-sided where (b) $d = 0.4$, (c) $d = 0.8$ or (d) $d = 1.0$. The habitat is of 10 units of area. The lines represent the best fits of equation (1) to these relationships, except for (d) where the lines are given by equation (13) using the indicated values of r . The fitted value of w_m is always 1.0, and the other parameter values of these fits are given in Table 1.

normal distributions at any density provided that r equalled one (Fig. 3(ae) and (ah)). When incomplete one-sided competition was modelled, however, the yield distributions were asymmetric with a few large plants and many suppressed individuals. The degree of asymmetry was enhanced by an increase of density (in a manner reminiscent of the populations of *Linum usitatissimum* L. studied by Obeid *et al.* (1967)) and by high values of d and r (Fig. 3(b) and (c)).

The simulations generated a value for the yield of each plant according to its position relative to other plants. It was, therefore, possible to investigate the effects of spatial factors on individual plant yield. When plants were allowed to take up resources from beyond the edge of the habitat, the outermost plants were larger than average, mimicking edge effects in field plots (Table 2). Furthermore, in simulated populations with weak one-sided competition ($d = 0.2$), the largest plants were found to be over-dispersed

TABLE 1

Estimates and standard errors of the estimates of the parameters a and b in equation (1) corresponding to data generated from simulated plant populations where $w_m = 1$, $q = 1$ with a variance of 0.1 and r was set at the values indicated. Asterisks indicate estimates for which the confidence limits exclude the values $a = q$ and $b = r$ (, 95% confidence limits; **, 99%; ***, 99.9%). Competition was (A) two-sided or one-sided where (B) $d = 0.4$ and (C) $d = 0.8$. The area of the habitat was ten units. See Fig. 2, and text for details*

	r	a		b	
		Estimate	Std Error	Estimate	Std Error
A	0.5	0.70	0.11	0.55	0.020
	1.0	0.72	0.12	1.10	0.043
	1.5	0.76	0.10	1.62	0.050
B	0.5	0.30***	0.072	0.98**	0.072
	1.0	0.92	0.14	1.04	0.033
	1.5	2.30*	0.38	1.05***	0.027
C	0.5	0.32***	0.050	1.10***	0.052
	1.0	0.85	0.14	1.07	0.040
	1.5	1.36	0.30	1.08***	0.047

within the habitat ($\chi^2_{29} = 13.38$, $P < 0.01$ using chi-square to test for deviations from a random dispersion amongst the 80 largest plants in a population of 250), as observed in many plant populations (e.g. Ford, 1975).

A Dynamic Model of Plant Monocultures

The static model is helpful in describing many aspects of plant interference, but its usefulness is restricted because it allows combinations of mean yield and density to exist which are beyond the self-thinning boundary. A dynamic model is required to simulate mortality. In order to be satisfactory, such a model must also simulate effectively the growth of individual plants, the increase of total standing crop with time and the effects of interference on plant yield.

GROWTH OF AN ISOLATED PLANT

An isolated plant requires an increasing area of resources to grow. In this model, the ecological neighbourhood area expands logistically

$$q_t = \frac{q_{\max}}{1 + k e^{-Rt}} \quad (14)$$

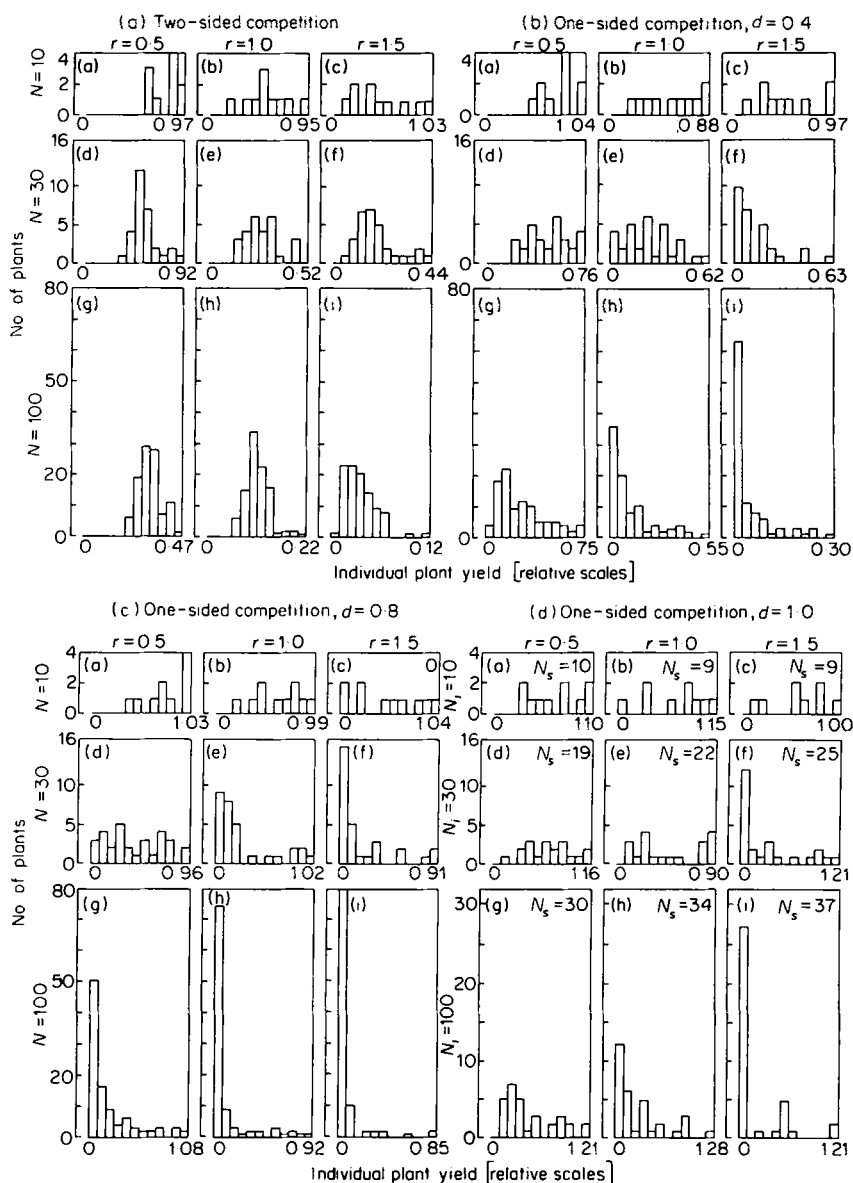


FIG. 3. The effects of density and competition type on the distribution of individual plant yield in simulated monocultures in habitats of 10 units in area. Density N is indicated as the total number of plants; final density N_f is also given when it does not equal initial density N_i . The parameter $w_m = 1$, $q = 1$ with a variance of 0.1 and r is as shown. Competition is (a) two-sided or one-sided where (b) $d = 0.4$, (c) $d = 0.8$ or (d) $d = 1.0$. Each distribution is scaled to the yield of the largest plant, which is indicated on the figure. See text for details.

TABLE 2

Edge effects in simulated plant populations. Mean yield per plant \bar{w} is given for plants in the outer regions of simulated populations growing in an open square habitat with sides 5 units long, depending upon the degree of one-sidedness, d , of the competition between plants. The other parameter values are: $w_m = 1$, $q = 1$ with a variance of 0.1, and $r = 1$. See text for details

	$d = 0.2$		$d = 0.4$		$d = 0.8$	
	\bar{w}	n	\bar{w}	n	\bar{w}	n
Total population	0.10	250	0.13	250	0.13	250
Outer 0.5 units	0.13	83	0.16	95	0.18	87
Outer 0.1 units	0.19	25	0.22	19	0.24	21

where q_t is the ecological neighbourhood area at time t , q_{\max} is the maximum ecological neighbourhood area, R is the intrinsic initial growth rate and k is a defined parameter. The yield of an isolated plant is assumed to be directly proportional to q_t at all times. The plant is assumed to grow in height between time intervals, thus allowing yield to increase for each unit of area. Height and weight were allometrically related

$$h_t = uw_{mt}^v \quad (15)$$

where u and v are allometric parameters. In nature, height and weight increase concomitantly. However, the model operates in discrete time units, and therefore the weight of a plant at time t is assumed to depend upon its height at time $t-1$ as well as upon the ecological neighbourhood area at time t

$$w_{mt} = c \cdot q_t \cdot h_{t-1} \quad (16)$$

i.e. provided that the time increments are small, isolated plants behave like cylinders of density c expanding in height and basal area.

INTERFERENCE

The interference subroutines operate in the same way as in the static model. The priority for resources in one-sided competition is however given to the tallest plant, which is not necessarily the one with the largest ecological neighbourhood area. At time $t-1$

$$h_{t-1} = uw_{t-1}^v \quad (17)$$

and at time t ,

$$w_t = w_{m_i}(z_i/q_i)^r \quad (18)$$

where z_i is calculated according to the values of h_{i-1} of all nearby plants. This algorithm mimics competition for light in the canopy; the tallest plant gains a disproportionate share of the resources. The resulting growth of individual plants thus mimics observations made by Cannell, Rothery & Ford (1984), in that tall plants suppress the growth of shorter neighbours, but not vice-versa. This model may also be analogous to competition between root systems.

MORTALITY

The value of w_i for a given plant does not necessarily keep increasing; a small plant is often overtopped by more and more neighbours until eventually $w_t < w_{t-1}$. A routine is used whereby a plant of any size is allowed to experience a constant period of continuous negative growth before its death and removal from the population. This model is used despite its simplicity because it emphasizes the importance of increasing competitive pressure from nearby plants in self-thinning.

THE FULL MODEL

In plant populations, the processes of growth, interference and mortality occur concomitantly. For the model, it is however more convenient to deal with discrete time units. For the following simulations, 20 such units were allowed for, computing time being a limiting factor. An isolated plant grew from 0.001 to 10 000 units of weight during this period using the selected growth parameters. These were chosen to allow appreciable self-thinning within the number of time periods available; except where otherwise stated, the parameter values were $d = 0.4$, $c = 1$, $v = 0.3333$, $k = 8$, q_{\max} expanded from 0.01 to 1000 square units, $r = 1$ and $R = 0.3$. The habitat area was 10 000 square units, and was surrounded by guard plants.

Variations in intrinsic growth rate were not allowed for, so that all plants had identical ecological neighbourhood areas in even-aged stands. However, ecological neighbourhood area could be varied within a stand by using a normally-distributed range of emergence times: the mean emergence time was set at two time units, and the variance at 0.5 time units. Again, data are presented from one simulation run for each combination of parameter values.

SIMULATION RESULTS

The assumptions of the dynamic model were very simplistic, and yet the simulated populations resembled actual plant populations quite closely in their behaviour.

The relationship between mean plant weight and surviving plant density in a simulation of randomly-dispersed, even-aged identical plants (Fig. 4(a))

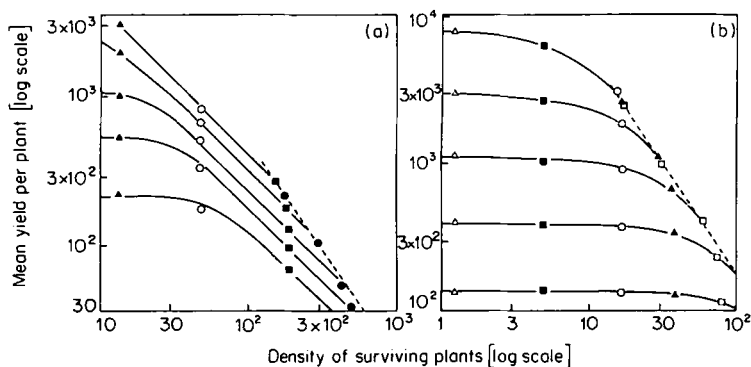


FIG. 4. Mean yield per plant as a changing function of time in simulated monocultures. Details of the model and parameter values are given in the text. Individual plants can withstand (a) 3 time units and (b) 0 time units of negative relative growth. The lines show the relationship between mean yield and density (scaled as the number of surviving plants within the habitat) at two time unit intervals from time = 12 units, giving the best fits of equation (1). The dashed line is the thinning line, of gradient $-3/2$. In each diagram, each symbol represents a single simulated population.

was qualitatively very similar to that found for *Fagopyrum esculentum* Moench by Yoda *et al.* (1963). At each time interval, the mean yield-density function provided an excellent fit to the data. These curves were, however, truncated by a straight line representing the $-3/2$ power law: no combinations of yield and density occurred beyond this line. A given stand approached the thinning line asymptotically, and during thinning the yield of individual stands increased whilst the density of surviving plants decreased. Note that this simulation assumed that plants with a continuous negative growth rate remained in the population for three time units before death occurred.

The position of the thinning line relative to the mean yield-density curves depended upon the period of negative growth which could be sustained by the plants. If this period was very brief, the mean yield-density curves were truncated by a thinning line at a density of approximately a^{-1} (Fig. 4(b)).

This simulation is similar to published data from populations of *Lolium perenne* L. (Kays & Harper, 1974).

The gradient of the thinning line was strongly influenced by the allometric parameter v relating shoot height and weight. A gradient of $-3/2$ was obtained only when v equalled 0.33. Values of 0.2 and 0.4 gave rise to thinning gradients of -1.26 and -1.70 which are well within the range of values observed in nature (White, 1980). The intercepts of the thinning lines were greatly increased given high values of v (Fig. 5(a)), as biomass per unit area was accumulated more quickly by the growing plants. The thinning

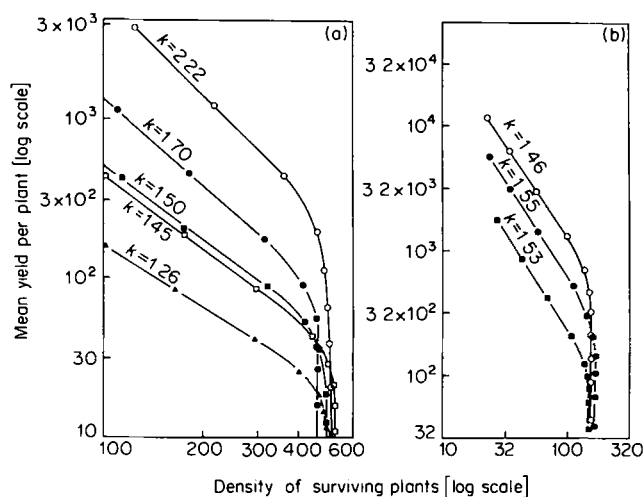


FIG. 5. The influence of varying parameters on the thinning slopes of simulated populations. (a) The effects of changing the height-weight allometric constant v on the time course of populations of approximately 500 plants, each of which can sustain 4 time units of negative relative growth (other parameters are given in the text). $v = 0.2$ (\blacktriangle), 0.3 (\square), 0.3333 (\blacksquare), 0.4 (\bullet) and 0.5 (\circ). (b) The effects of changing the efficiency of resource utilization of individual plants, r , on the time courses of populations of approximately 150 plants; $r = 0.7$ (\circ), $r = 1.0$ (\bullet) and $r = 1.3$ (\blacksquare). See text for other parameter values; density is scaled as in Fig. 4. The gradients, k , of the thinning lines are indicated.

line was also affected by the value of r , which determines the efficiency of resource utilization of individual plants. Stands with a high r thinned more quickly than those with lower values, and the gradient of the thinning line increased slightly with the value of r (Fig. 5(b)). Plants with high values of r use resources with relatively greater efficiency at low densities; therefore the increased rate of thinning reflects the poor growth of the smallest, least efficient plants whilst the increased thinning gradient reflects the increasing efficiency of the stand as a whole as more and more smaller plants die.

The distribution of plant weights altered quite dramatically with time (Fig. 6). The initial distribution was a consequence of the relative emergence times of the plants. In the example shown in Figure 6, there were two major pulses of emergence, giving rise to a bimodal distribution of individual plant yield (Fig. 6(a)) which persisted for some time (Fig. 6(b)). As more

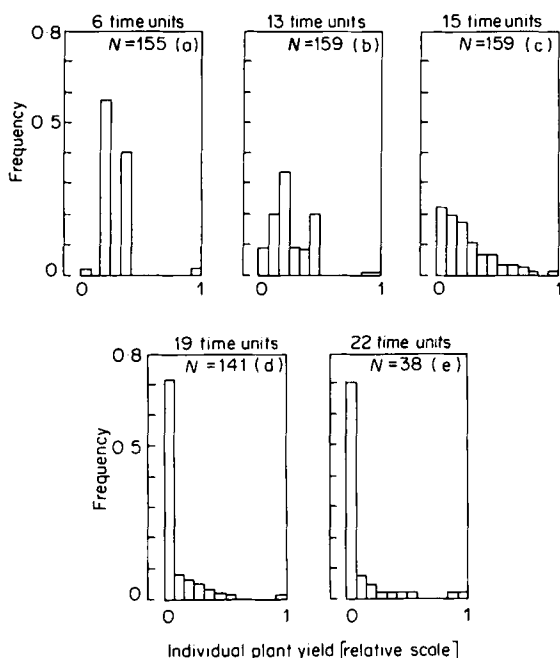


FIG. 6. The changing frequency distribution of individual plant yield with time in a simulated plant population. There were 159 seedlings, each of which could withstand 3 time units of continuous negative relative growth. The mean emergence time was set at 2 time units, with a variance of 0.5 units. See text for other parameters and further details.

plants were subjected to interference from their growing neighbours, the distribution became asymmetrical, with many small plants and only a few large ones (Fig. 6(c) and (d)). The smallest plants died during self-thinning, but the asymmetry was maintained by other plants becoming increasingly suppressed (Fig. 6(e)). The position of a plant in the size distribution depended upon its emergence time, its relative growth rate and the competitive pressure from its neighbours. The development of these simulated distributions is qualitatively similar to those observed in plant populations (e.g. Obeid *et al.*, 1967; Ford, 1975).

Discussion

The simulation models presented in this paper are the first to describe so many features of the behaviour of plant monocultures simultaneously. The models may therefore be used to predict the behaviour of plant populations after perturbations, and may prove useful in the management of monocultures. Probably the greatest value of these models is to aid our understanding of the processes of interference, with particular regard to the basis of the mean yield-density response and self-thinning.

YIELD-DENSITY RESPONSE

Most models describing the mean yield-density function have resulted from fitting data to empirical equations (Bleasdale & Nelder, 1960; Holliday, 1960; Willey & Heath, 1969). Reciprocal models, such as equation (1) used in this paper, have additionally been derived from theoretical principles. The initial such derivation, proposed by Shinozaki & Kira (1956), assumed that plants grew in a logistic manner, and that the effectiveness of resource utilization remained constant. Barnes (1977) derived other mean yield models from various other assumptions of plant growth. His derived models assume that a constant total yield is reached at high density irrespective of time, and yet this is only possible if the efficiency of resource utilization by individual plants, r equals one and if the plants do not grow in height. The simulation models in this paper show that r must be allowed to vary in order to account for populations where the efficiency of resource utilization of the whole population, b , does not equal one. Such variations might reflect changes in the shape of plants that occur with both time and density: for example, greater stand height at high densities might lead to $b < 1$, and lodging would lead to $b > 1$.

The parameters of the mean yield model may be related to those from the model for individual plant yield. Given two-sided competition, with the mean yield of isolated plants and the mean ecological neighbourhood area both fixed at q , the simulated populations approximately follow the model

$$\bar{w} = q(1 + qN)^{-r}. \quad (13)$$

It can therefore be seen from equation (1)

$$\bar{w} = \bar{w}_m(1 + aN)^{-b} \quad (1)$$

that the parameter \bar{w}_m estimates the mean yield of isolated plants, a estimates the mean ecological neighbourhood area and b estimates r (Fig. 2).

With one-sided competition however, b was a poor estimator of r (Table 1). Both parameters refer to the effectiveness with which resources are taken

up from the ecological neighbourhood area (see above; Watkinson, 1980), but r applies to the individual plant whereas b is estimated from the behaviour of the population. From equation (1), at high densities

$$\bar{w} \propto (aN)^{-b}. \quad (19)$$

The value of N^{-1} gives the mean zone of influence, \bar{z} , for individual plants. Therefore

$$\bar{w} \propto (\bar{z}/a)^b \quad (20)$$

and since a estimates the ecological neighbourhood area of the plants, then

$$\bar{w} \propto \left(\frac{1}{N} \sum_{i=1}^N \frac{z_i}{q_i} \right)^b. \quad (21)$$

In contrast, the simulation model assumes that

$$\bar{w} \propto \frac{1}{N} \sum_{i=1}^N \left(\frac{z_i}{q_i} \right)^r \quad (22)$$

(from equation (8)). Equations (21) and (22) will only give the same value of \bar{w} if both b and r equal 1 or if the distribution of z_i/q_i is symmetrical about the mean value. In the simulations, this distribution was symmetrical at high densities only in the case of two-sided competition, assuming a normal distribution of ecological neighbourhood areas (Fig. 3(ah) shows the distribution of individual plant yield, which is the same as that of z_i/q_i since r equals one). As one-sided competition gave rise to populations with asymmetric size distributions at high densities (Fig. 3(bh) and (ch)), the estimate of b using equation (1) cannot equal r under one-sided competition except when r equals one.

The distribution of z_i/q_i can affect mean yield per plant and hence the estimates of a and, in particular, b using equation (1) (Fig. 2; Table 1). The parameter b therefore does much more than simply estimate the utilization efficiency of individual plants. It is also influenced by the structure of the size hierarchy of the population, as generated by the age-structure of the population and the degree of one-sided competition. Two populations differing only in age-structure would give different values of b provided that $r \neq 1$.

SELF-THINNING

A major feature of the dynamic model is that realistic self-thinning resulted. The assumptions of this model are therefore discussed in more detail here because there is still debate over the mechanism of this process.

In the simulations, the amount of biomass per unit of canopy volume increased towards a maximum value at the start of self-thinning. After this point the increase in standing crop was almost entirely effected by an increase in stand height (Fig. 7). In Fig. 7 mean plant height is taken as the height of the canopy. If canopy height is defined as the height of the tallest plant, biomass per unit volume can increase substantially even during self-thinning, as observed by Lonsdale & Watkinson (1983), since spaces between the taller plants are still available for plant growth.

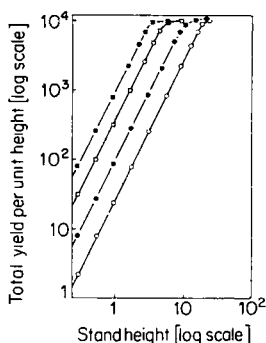


FIG. 7. The trajectories of biomass packing with time in simulated plant populations from four initial densities, 14 (\circ), 50 (\bullet), 190 (\square) and 500 (\blacksquare) plants within the habitat. Each plant can survive 3 time units of continuous negative relative growth; the other parameter values are given in the text. Biomass packing is defined as the total yield divided by the stand height, which is taken as the mean height of the plants.

The height h of a surviving plant was an allometric function of its weight w

$$h = uw^v \quad (17)$$

where u and v are allometric parameters. Assuming that mean plant height is a good estimate of the canopy height and that $b = 1$, the total yield $\bar{w}N$ of a thinning stand occupying a habitat of unit area is approximately

$$\bar{w}N \simeq \bar{h}P \quad (23)$$

where P is the biomass per unit of canopy volume. Therefore

$$\bar{w}N = u\bar{w}^vP \quad (24)$$

and

$$\bar{w}^{v-1} \simeq (uP)^{-1}N \quad (25)$$

and

$$\bar{w} \simeq (uP)^{v-1} \cdot N^{1/(v-1)}. \quad (26)$$

When $v = 1/3$, equation (26) simplifies to the $-3/2$ power law. When $v = 0.5$, the expected thinning line would have a gradient of -2 , and when $v = 0.2$ the gradient would be -1.25 . The simulations generated gradients of -1.5 , -2.22 and -1.24 respectively (Fig. 5(a)). Mean plant height is likely to be an underestimate of canopy height, which is determined by the larger plants. Nevertheless, equation (26) still applies (as does the rationale behind the interpretation of Fig. 7) provided that canopy height is proportional to mean plant height, in which case u must be multiplied by the proportionality constant.

The intercept of the thinning line (given by the term $(uP)^{v-1}$ in equation (26)) is determined by the parameters of the height-weight allometry and by the biomass density per unit of canopy volume. Together these parameters restrict the total biomass which can be accumulated by a stand within a given period of time. As the stand height increases, so does the total biomass per unit area—thus resulting in a thinning gradient exceeding one. At any moment, however, the same stand biomass may be achieved by populations at lower densities as is achieved by thinning populations, thus giving rise to the reciprocal relationship between mean yield per plant and density.

This approach is a generalization of the first explanation of the $-3/2$ power law proposed by Yoda *et al.* (1963), in which the allometric constant v was assumed to be $1/3$. This hypothesis was criticized by White (1981) as plants do not have the simple, unchanging geometric form apparently required for the assumption to be valid (but see Pickard, 1983). Furthermore, the allometric relationship does not explain why mortality should occur at all. In this simulation, mortality results from one-sided competition for limited resources, and operates according to fixed spatial relationships between plants of constant geometric form. The fact that self-thinning operates in seaweeds in the same way as in trees (Cousens & Hutchings, 1983) weakens the generality of this approach.

It is surely no coincidence that the power law nevertheless appears to relate weight or volume to area. Charles-Edwards (1984a) has suggested that each growing point on a plant requires a minimum flux of assimilate in order to grow and survive. The individual leaf bud thus requires a sufficient supply of light, water and nutrients and its behaviour is otherwise largely independent of the plant to which it is attached. A canopy may therefore be regarded as an aggregate of buds, growing upwards by virtue of the accumulation of support tissue. Charles-Edwards (1984b) argues that such a canopy behaves as if all plants within it display the simple volume-area allometry assumed in the simulation even if the component plants do not. Plant suppression and death still occur, as plants with few buds with access to resources and space eventually die because of one-sided competi-

tion in the manner described by the simulation. Variations in gradient from $-3/2$ would be encountered whenever the weight-volume relationship is not linear (see Lonsdale & Watkinson, 1983) and whenever some section of the canopy is unavailable to the buds for structural reasons. A stand ultimately ceases to self-thin along a $-3/2$ gradient when resource, structural or physiological constraints prevent further growth in height: any further mortality results in self-thinning along a gradient of $-b$ provided that the survivors can grow to take advantage of the released resources (see Lonsdale & Watkinson, 1982).

Not all plant populations need behave in quite this way. For example, in stands of *Pinus radiata* D. Don., the suppressed plants need not die after their growth stops, and so these plants obey the $-3/2$ power law only if the suppressed plants are excluded from the analysis (West & Borough, 1983). It is likely that the suppressed plants are kept alive by a transfer of resources from the dominant plants via root grafts (West & Borough, 1983). Provided that the suppressed plants are below the canopy level of the dominants, they do not affect the volume available for new growth. The dominant plants therefore obey the $-3/2$ power law, as observed, losing individuals to the suppressed class. The transfer of resources to the suppressed plants may slow the rates of growth of the dominant plants, but would not affect their "thinning" gradient.

The remarkable constancy of thinning gradients and intercepts over many orders of plant size (White, 1980) suggests that the height-weight allometries and the biomass packing values are remarkably constant in plants. One would expect plants of different morphologies to give rise to different thinning lines, as is observed to some degree by Lonsdale & Watkinson (1983). The manipulation of these allometries would test this hypothesis of self-thinning; possible methods include the incorporation of heavy isotopes into growing plants and the comparison of the growth of climbing plants on different support structures.

SIZE HIERARCHY DEVELOPMENT

Size hierarchy development has already been investigated using simulation techniques similar to the ones used in this paper. The models of Diggle (1976) and Gates (1978) are particularly relevant. Both models were developed to describe the distribution of individual plant yield in a monoculture, with particular reference to the repeated occurrence of bimodality within even-aged stands reported by Ford (1975). Both workers found that it was necessary to assume one-sided competition if bimodality was to be simulated, and that the more typical asymmetric distributions were then

also easily generated. These models assumed that the dominant plant of any pair took up all the resources from the overlap region. Incomplete one-sided competition was introduced into the model of Ford & Diggle (1981), allowing it to mimic accurately the growth of stands of *Tagetes patula* L. One-sided competition need not occur in all plant monocultures, however, and may not be important among some populations of even-aged plants with similar growth rates (Turner & Rabinowitz, 1983) or when light is not the limiting factor.

The simulations of Aikman & Watkinson (1980) attempted to generate realistic self-thinning as well as the development of yield distribution. Many of the assumptions used in the model presented in this paper were also used by Aikman & Watkinson (1980), in particular the assumption that individual plant yield at any time is a function of area but that growth is better described as a function of weight. Their simulated populations failed to track along thinning lines realistically because the competition function took into account competitive ability relative to the mean and not competition between neighbouring plants. Mortality thus ceased when only plants of high competitive ability remained.

The simulation model given in this paper may also be used to relate the yields of individual plants to the spatial arrangements of their neighbours: details are given in Firbank (1984).

No model can ever give a perfect description of reality in ecology; successful simulation models merely proffer a series of hypotheses which are not rejected by comparison with observed phenomena. Nonetheless, it is encouraging that realistic simulations of plant population behaviour have resulted from very simple assumptions about plant growth. If such simple yet robust assumptions can be used to describe interference in plant monocultures, there would appear to be no reason why similar models cannot be developed to describe more complex ecological systems.

We thank Dr P. Ansley and Dr A. Bangham for assistance with technical aspects of the computing and Miss S. Mitchell for drawing the diagrams. This research was supported by a N.E.R.C. studentship to L.G.F.

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