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A MODEL OF COMPETITION FOR SPACE[1]

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Abstract. A simple model of competition among individuals for space is defined and analyzed. Each individual is assumed to occupy a certain area and grow at a specified rate. When two individuals attempt to occupy the same area, one or the other dies. An analytic approximation for the model is developed and tested against computer simulations. The implications of the model for the self-thinning of even-aged stands, for the generation of overdispersed spatial patterns, and for the generation of bimodal size distributions are discussed.

Key words: competition; crowding; growth; models; monocultures; plant; self-thinning; simulations; spatial.

INTRODUCTION

Competition for space among many plants and sessile animals occurs through direct interactions among immediate neighbors. Many plants shade their neighboring plants and deprive them of light. Some barnacles pry off adjacent individuals, and some algae driven by wave action sweep an area clear of competitors. In this paper, we introduce a simple model of competition for space and explore some of its properties. We consider here competition only among members of the same species and of the same age, but our approach can be taken to model competition among individuals of different ages and members of different species as well.

Models of competition for space are intrinsically difficult because the intensity of interactions among individuals depends on their locations, and the interactions themselves modify the distributions of those locations. Similar problems do not arise in the more common Lotka-Volterra competition models because those models assume in effect that every individual encounters every other in the population. In other models of competition for space, there are two general approaches. The first, as exemplified by the studies of Mitchell (1975) and Ek and Monserud (1979), are simulation studies that take full account of the complexity of the interactions. Those particular models are of forests, but a similar approach can be taken to other systems (e.g., Maguire and Porter 1977). The second approach is analytic (e.g., Gates 1978, Gates and Wescott 1978). These models contain assumptions that in some way or another get around the problem that competition can change the character of the spatial distribution of the competing individuals; the assumptions thereby lead to analytically tractable models. For example, the model of Aikman and Watkinson (1980) assumes that the reduction in growth rate of each plant is proportional to some overall index of crowding. The extent of crowding, then, can be determined from the

growth rate of the population, which leads to a single equation for the density. That assumption is equivalent to those made in Lotka-Volterra models, in which total population size determines the effect of competition on each individual. A different approach, but one which also leads to a tractable model, is that of Armstrong (1974), who assumed that plants grow until they overlap. Growth stops at points of overlap. This assumption has the effect of not disturbing the initial random distribution of plants, and thus allows complete analysis of the model. In Armstrong's model, however, no death occurs and every individual that is initially present will persist. Only plant size is affected by the presence of other individuals.

In this paper, we take a third approach and develop an approximation that does take account of the change in distribution due to mortality caused by competition. Our model is not an exact analysis, but our simulations show that it provides a good approximation in many cases, and it may provide another approach to modeling competition among neighboring individuals. We use this approach only in the simplest context, that of competition among individuals of a single species and of the same age. We anticipate that our approach could be used for more than one age-class or more than one species, although the accuracy of the approximation would have to be checked in different contexts.

THE MODEL

Our approach is similar to that of Maguire and Porter (1977). Consider a two-dimensional plane surface that is uniform from the point of view of the organisms competing for it. Mathematically, we require that it be homogeneous and isotropic. For the analytic theory, we assume an infinite plane, but in the computer simulations the regions were finite squares. We are not concerned with the edge or boundary effects and have designed the simulations to make those effects as small as possible. Assume that each individual starts as a point and grows into a circle of increasing radius according to a specified growth law, $R(t)$, which gives the radius measured in arbitrary units at time t after its "birth." For now, we do not have to specify the growth

law, but we require that $R(t)$ be monotonically increasing with t.

An individual grows until it touches another individual. At the instant they touch, one or the other dies and disappears. In our model death and decay are assumed to occur immediately, but all that is actually needed is that one of the individuals no longer interact with any others. The rule for deciding which individual survives must be specified separately. Because individuals are the same size at any time, we assume that each has an equal chance of surviving. For populations with individuals of different size, there are other possible rules, which we will discuss later.

Assume that at some time, $t = 0$, points are randomly distributed on the infinite plane with a density D, the number of points per unit area. This assumption leads to a Poisson process in space, with the consequence that the number of points in any area A is a random variable that has a Poisson distribution with mean AD (Pielou 1977). Throughout, we refer to this distribution of points as a random distribution and use the fact that the location of every point is statistically independent of the locations of every other point.

As soon as individuals start to grow and interact according to our rules, they will no longer be randomly distributed. Counting only survivors and identifying the location of each survivor by the location of its center of growth, no individual can have another within a distance $2R(t)$, twice the radius of each individual. Furthermore, the distribution of survivors greater than $2R(t)$ apart may depend on the locations of others. The interactions leading to mortality can generate positive or negative correlations between the locations of the survivors. The extent and sign of the correlations is shown in the simulation results. We first proceed to develop an analytic approximation to this model by assuming that there is no correlation between the locations of survivors, given the restriction that they are at least $2R(t)$ apart at time t. We call this a *truncated random distribution*, which is a special case of the class of spatial distributions described by Pielou (1960).

Let $F(R)$ be the probability that a randomly chosen individual survives to be of radius R. Since we have assumed that the growth law $R(t)$ is known and increases monotonically with t, the function $F[R(t)]$ can be immediately interpreted as the probability that an individual survives to time t. To construct a differential equation for $F(R)$, we compute the additional mortality during some short time interval during which each individual grows from radius R to a radius $R + \Delta R$. If we define $M(R)\Delta R$ to be the probability that an individual of radius R dies during the time it would have grown to radius $R + \Delta R$, then we can write

$$F(R + \Delta R) = F(R)[1 - M(R)\Delta R]. \qquad (1)$$

To compute $M(R)\Delta R$ we multiply the probability that an individual touches another during the time it takes to grow from size R to size $R + \Delta R$ by its prob-
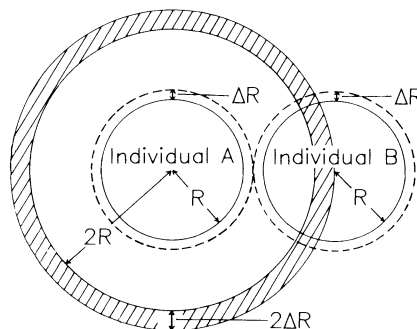

Fig. 1. As individual A, represented by the left circle, grows from radius R to radius $R + \Delta R$, it will collide with any neighbor—for example, individual B—whose center is inside the hatched annulus with inner radius $2R$ and outer radius $2R + 2\Delta R$.

ability of dying if it touches (which is one-half in this case). As shown in Fig. 1, the probability that an individual touches another during the time interval is the probability that there is another individual in the hatched annulus centered at the center of growth with radii $2R$ and $2R + 2\Delta R$. From our assumption of a truncated random distribution, that probability is just the area of the annulus ($\approx 8R(t)\Delta R$ when ΔR is small) multiplied by the initial density D, multiplied by the probability $F(R)$ that the individual in the annulus has also survived to time t. This is where we need the assumption of the truncated random distribution of survivors. Without that assumption, we cannot compute the density of survivors in the annulus. The density of survivors in the annulus could depend on the numbers and location of individuals that the individual of interest encountered before it reached size R. We show with the simulation results that our approximation is very good but not exact.

With our approximation, we obtain

$$M(R)\Delta R = (4RD\Delta R)F(R), \qquad (2)$$

which, together with Eq. 1, leads to the differential equation for $F(t)$ in the limit as ΔR goes to zero:

$$\frac{dF(R)}{dR} = -4\pi RDF^2(R). \qquad (3)$$

Our model is completely deterministic, so $F(R)$ must be interpreted as the average for an infinite plane.

Eq. 3, with the appropriate initial condition $F(0) = 1$, has the solution

$$F(R) = \frac{1}{1 + 2\pi R^2 D}. \qquad (4)$$

The probability that a plant survives to size R is shown in Fig. 2 as the curve labeled "analytic approximation."
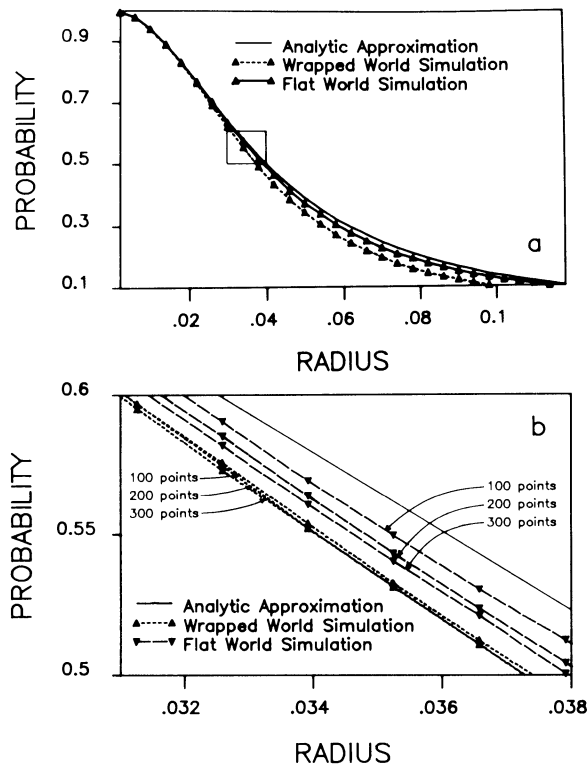
FIG. 2. The probability of survival $F(R)$ as a function of the radius of an individual. (a) 100 individuals were randomly placed in the unit square and allowed to grow until only 10% of the individuals remained. (b) More detail is shown of the curves in the boxed region at center left in a. It shows how the results change when the area in which plants grow is increased while the initial density of individuals is kept constant.

There are two important features to this solution. First, $F(R)$ is entirely independent of the growth curve $R(t)$. The growth curve is required to relate size and age (or the equivalent, time since growth started). Second, $F(R)$ in Eq. 4 is essentially parameter free. The only parameter is D, the initial density, and Eq. 4 is a function of the product $\pi R^2 D$, which is the ratio of the area of each individual of radius R to an area initially containing an average of one individual. If the units of length are chosen so D is one, then $F(R)$ depends only on R.

The fact that Eq. 4 is parameter free greatly simplified the problem of simulating this model. It was unnecessary to explore large regions of parameter space. Instead we could concentrate on a few simulations that checked the predicted form of $F(R)$ and the underlying assumption of the truncated random distribution of points.

In the simulations, we had to model a finite region of the plane. We modeled a square region and allowed two possibilities for individuals at the edges. For the *flat world* model, there were assumed to be no individuals beyond the edges of the square, so that indi-

viduals near the edge experienced less competition. For the *wrapped world* model, individuals that grew over the edge wrapped around to the opposite side of the square. Thus, the space was a direct product of a circle with itself. Although this geometry is sometimes called a "torus," that label is not strictly correct because the space we modeled had no curvature, as would a torus.

We simulated the process of growth and competition by initially choosing coordinates from a pseudorandom number generator. We then allowed each individual to grow until the first pair touched. The survivor was chosen by generating another random number, and the growth continued until a second pair touched. The process continued until only a few individuals were left. This entire process was repeated many times and the results, described below, were calculated as the average over the replicates. For each case, we specified the number of points (which determined the density D), the number of replicates, and the choice of a wrapped or flat world.

RESULTS

The first question is whether the approximate survival function given by Eq. 4 is an adequate description of the simulation results. As shown in Fig. 2, this approximation is quite good. The difference between the approximation and the simulations becomes noticeable when $\approx 20\%$ of the individuals have died. When only half of the individuals remain, the curve generated by the wrapped world simulation is $\approx 6\%$ lower than the analytic approximation, and the curve for the flat world is $\approx 2\%$ lower than the approximation.

The second question is whether the accuracy of Eq. 4 is due to the accuracy of the critical underlying assumption, that of a truncated random distribution. We can test that assumption independently by computing distances to nearest neighbors. We compared the distribution of distances to nearest neighbors in the simulations with the distances obtained from a simulation of the process of distributing discs randomly on a plane, subject to the constraint that the centers not be within $2R$ of one another. There is apparently no analytic solution for the distance to nearest neighbors for the case of randomly distributed discs (Simberloff 1979), so a simulation was necessary to estimate the expected distribution.

The results are shown in Fig. 3, with the dashed curve in each part being the expected distribution, and the solid curve being the distances found in the simulation of the competitive model. Fig. 3a shows that the initial distribution does not differ significantly from that expected ($P = .73$; $N = 1000$; Kolmogorov-Smirnov Test). For larger values of R (Fig. 3c), there is a slight but statistically significant difference between the approximate and actual distributions ($P = .022$; $N = 1000$). There are fewer nearest neighbors than expected for distances slightly larger than $2R$ and more than expected for larger distances. Although the simulation
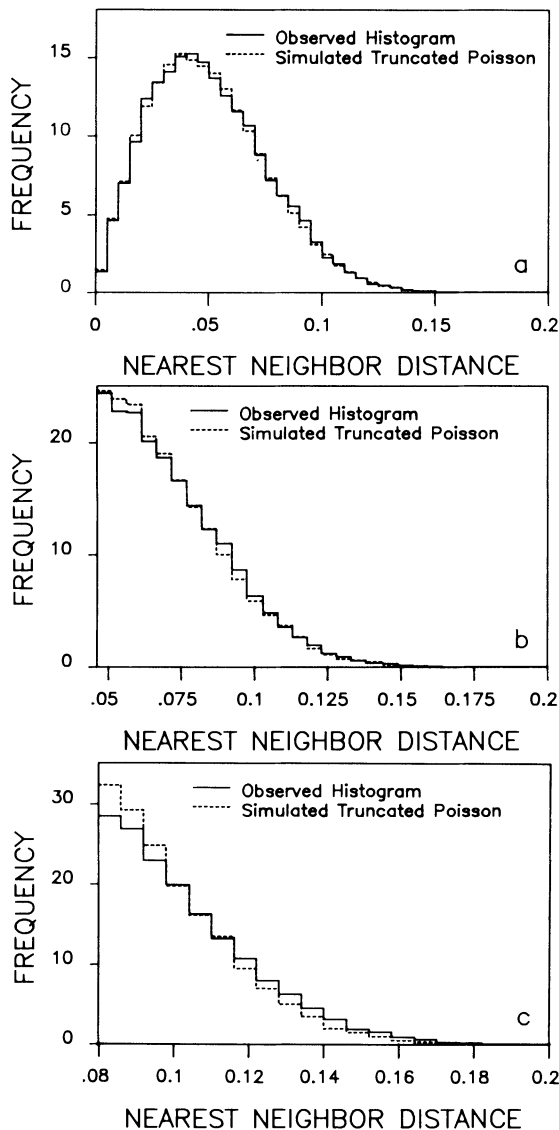
FIG. 3.   A comparison of the truncated Poisson distribu-
tion (– – –) with the distribution of nearest neighbor distances
produced by the model (——). The truncated Poisson distri-
bution was calculated by placing points randomly onto the
unit square (wrapped world) such that no two points were
closer than the radius of an individual. Histograms were cal-
culated at three times: (a) time = 0; 100% of plants alive;
50 000 samples. (b) time = 0.0230; 75% of plants alive; 37 500
samples. (c) time = 0.0399; 50% of plants alive; 25 000 sam-
ples. A comparison of the solid and dashed curves gave P
values of (a) .73, (b) .32, (c) .022 (Kolmogorov-Smirnov Test,
$N = 1000$, Hollander and Wolfe 1973:219).

results show that the assumption of a truncated random
distribution is not exactly valid, it is approximately so.

DISCUSSION

Overdispersed spatial patterns

Our model of interactions generates an overdis-
persed distribution of points in space. As a measure of

the extent of overdispersion we used the ratio of the
observed nearest neighbor distance to the nearest
neighbor distance expected under the assumption of a
random distribution. This ratio is 1 for a random dis-
tribution. Fig. 4a shows the increase in this ratio with
time.

If the individuals are initially underdispersed (that
is, clumped to some degree) then the interactions we
assume tend to reduce quickly the degree of underdis-
persion. To illustrate this, we assumed a random dis-
tribution of points that were centers of clumps of in-
dividuals, with the locations of each individual within
the clump being generated from a circular bivariate
normal distribution with a specified variance. Fig. 4b
shows the change in the extent of clumping, as mea-
sured by the ratio of observed to expected nearest
neighbor distance, for one example.

Self-thinning

The analytic result, Eq. 4, can be related to the geo-
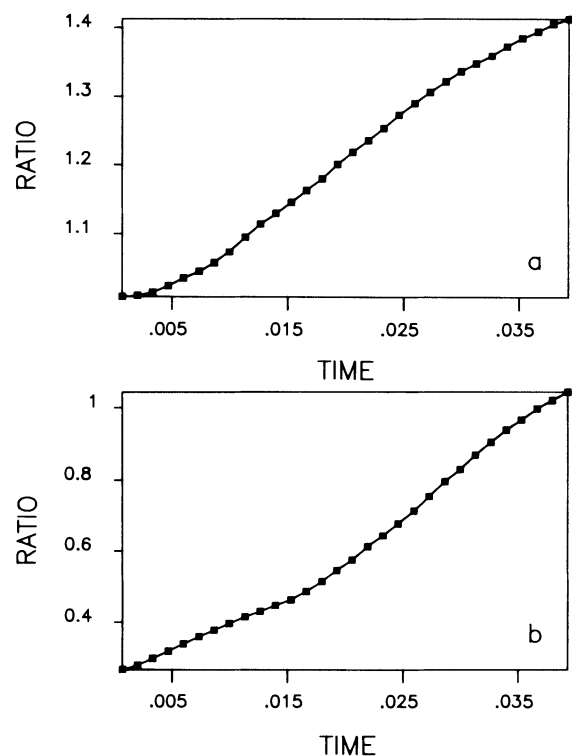metric theory of self-thinning in even-aged stands of

FIG. 4.   Graphs of the ratios of observed mean distance to
nearest neighbor, assuming randomly placed points, vs. time.
This ratio is > 1 for overdispersed points, < 1 for clumped
points, and = 1 for randomly placed points (Clark and Evans
1954). (a) 100 points were randomly placed on the unit square
and allowed to grow. (b) 100 points were initially arranged
in one of 10 clumps, each clump center being randomly placed
in the unit square. Within a clump, point locations were sam-
pled from a circular bivariate normal distribution with a stan-
dard deviation of 0.2. All simulations were done in the wrapped
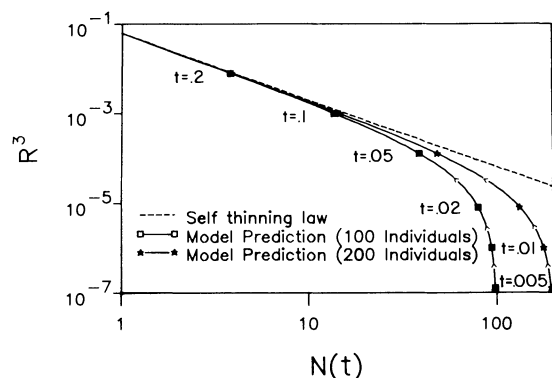world. Notice that the process of competition causes the ratio
to increase over time.

Fig. 5. A graph of R^3 vs. $N(t)$ for the model and the self-thinning law. Two curves are shown from the model: 100 individuals at a density of 100, and 200 individuals at a density of 200 plants per standard square in the wrapped world. As the population grows it traces out the curve in the direction of the arrows. Five times (values as indicated) are shown on each curve.

plants. Yoda et al. (1963) found that if the log of mean plant mass is plotted against the log of the density of survivors the values found from stands of different ages will fall on a line with a slope of $-3/2$. This is known as the self-thinning rule for plants and has been extensively documented in a variety of plant species (Harper 1977:Chapter 6). Yoda et al. (1963) explained this rule with a geometric theory that has been recently expanded by White (1981). Yoda et al. argued that plant mass is proportional to the volume, which is proportional to the cube of a measure of length L, if the shape of each plant does not change. If the plants are limited by space, the number that can be present in a finite area is inversely proportional to L^2. Therefore, the biomass per individual is proportional to the number in the plot raised to the $-3/2$ power.

In our model, assume that the volume of an individual is proportional to $R^3(t)$, where the constant of proportionality c depends on shape. If, in a bounded area, there are initially N_0 individuals, then at time t there are on average $N(t) = N_0 F(R)$ remaining. We can then solve for $R(t)$ as a function of $N(t)$ to obtain the expression for R^3:

$$R^3 = \{[N_0 - N(t)]/2\pi DN(t)\}^{3/2}. \qquad (5)$$

Eq. 5 defines a curve of R^3 as a function of $N(t)$, which is shown in Fig. 5. As t increases from 0, the population moves up the curve in the direction given by the arrows, with the rate of movement dependent on the growth law $R(t)$. When $N(t) \ll N_0$, Eq. 5 can be approximated by

$$R^3 \approx [N_0/2\pi DN(t)]^{3/2}, \qquad (6)$$

which is the self-thinning law. This is the dashed line in Fig. 5. Kays and Harper (1974; Fig. 4), in an experimental study of competition in *Lolium perenne*,

show results that are similar to those of Fig. 5, although that similarity does not imply similar mechanisms of competition.

Bimodal size distributions

We used a slightly more general version of our model to find whether it is possible to generate or maintain a bimodal distribution of sizes in the population. A bimodal distribution of sizes has been found in some experimental plant populations (Ford 1975, but see Rabinowitz 1979), and it is thought to be due to differences in growth rates caused partly by intrinsic differences and partly by the inhibition of smaller plants by larger ones. In our model we assigned different growth rates and then allowed different degrees of competitive advantage in the larger individuals; there was no inhibition of growth.

To model random growth rates, we assumed that for each individual the growth law was $R(t) = R_0 t$, where R_0 was chosen from a specified probability distribution. We used three different distributions for R_0. In the first, the Gaussian, each plant's growth rate was chosen at birth by sampling from a Gaussian or normal distribution with a specified mean and variance. In the second, the uniform, each growth rate was sampled from a uniform distribution. Finally, in the third, the bi-Gaussian, each growth rate was sampled from a bimodal distribution constructed from summing two identical Gaussian distributions with different means. Each plant's growth rate R_0, once chosen at birth, was fixed throughout its lifetime. For Gaussian and uniform growth rates, cases were examined in which each distribution had a mean of 5 and a coefficient of variation of 0, 0.5, 1, and 2. Any portion of the distribution extending into negative growth rates was truncated at zero, guaranteeing that no individual could have a neg-
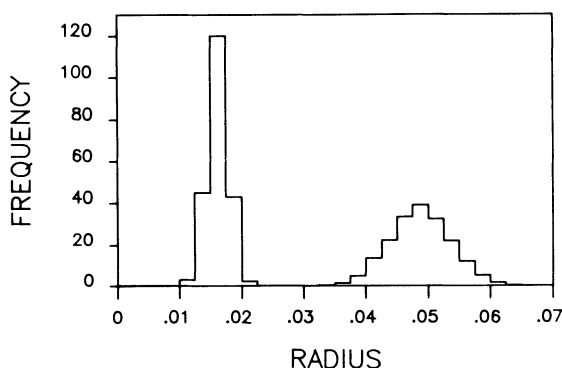

Fig. 6. A frequency distribution of plant size produced when growth rates were sampled from a bi-Gaussian distribution. Birth rates, fixed at birth, were sampled from a bi-Gaussian distribution, consisting of the sum of two normal distributions having means of 2 and 6 with a standard deviation of 0.1. This frequency distribution was calculated when 44% of the initial 100 plants had died. The simulation was carried out in the wrapped world.

ative birth rate. All simulations were done in the wrapped world geometry.

We also considered three models of competition. In the first, an individual had the same chance of surviving an encounter with another individual regardless of their relative sizes. In the second, an individual's chance of surviving an encounter was equal to the ratio of their radii, and in the third, the chance of surviving was equal to the ratio of their areas.

With a Gaussian or uniform distribution of growth rates, there was no tendency for a bimodal distribution of sizes to develop. The distributions were all unimodal. For the bi-Gaussian, which ensures a bimodal distribution of growth rates, there was an initial tendency to produce a bimodal distribution of sizes, and the competition did not tend to change the relative numbers in the different modes. An example is shown in Fig. 6. We conclude then that this mechanism of competition does not generate bimodal distributions, but also does not eliminate bimodality due to other causes.

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