Vol. 125, No. 3 The American Naturalist March 1985

NEIGHBORHOOD MODELS OF PLANT POPULATION DYNAMICS. I. SINGLE-SPECIES MODELS OF ANNUALS

STEPHEN W. PACALA AND J. A. SILANDER, JR.

Ecology Section, Biological Sciences Group, University of Connecticut, Storrs, Connecticut 06268

Submitted September 30, 1983; Accepted July 31, 1984

The absence of a general theory of plant population dynamics remains a critical gap in the field of plant population biology today. This is in contrast with animal population biology where a population dynamic theory is well developed and integrated into the field. Two attributes of plants are commonly cited as obstacles to the development of population dynamic models. First, plants are sessile and tend to interact primarily with nearby individuals. Thus the survivorship and fecundity of a plant are likely to be affected more by local population density than by the average density of the population. In this paper we deal exclusively with nonvegetatively reproducing species and so there is no ambiguity associated with the word "individual" (Harper 1977). The second is plastic growth such that the sizes or fecundities of adults may vary by several orders of magnitude. Population dynamic models that explicitly account for these two qualities of plants include both the spatial distribution of individuals and the effects of local population density on individual survivorship and fecundity. Such models are termed neighborhood models (Antonovics and Levin 1980). Although the development of a neighborhood population dynamic theory has been repeatedly called for in the ecological literature (Palmblad 1968; Werner 1976; Antonovics and Levin 1980; Weiner and Conte 1981), published models of plant population dynamics have excluded either plastic growth or the fact that plants interact primarily with nearby plants or both (DeAngelis et al. 1979; Watkinson 1980; MacDonald and Watkinson 1981; Weiner and Conte 1981; Tilman 1982). Schaffer and Leigh (1976) claim that the analysis of neighborhood models involves intractable mathematics associated with nonlinear diffusion equations in two spatial dimensions. They thus conclude that there may never be an adequate population dynamic theory for plants.

The purpose of this paper is to present a tractable formulation for neighborhood models of plant population dynamic processes. We specifically describe models for single-species populations of annuals lacking seed dormancy. Our approach, however, can be extended to include such complexities as seed dormancy, multispecies populations, and age- or size-structured populations. We have developed two kinds of models: analytically tractable models that are valid when seed

Am. Nat. 1985. Vol. 125, pp. 385–411.

dispersal is sufficiently large, and computer simulation models that are more general. These models are constructed from submodels of the survivorship, fecundity and dispersal of individual plants, and so provide descriptions of population-level processes in terms of the biology of individuals. Moreover, we have designed the models so that empirical tests are both possible and practical. All parameters and functional forms in a model may be estimated from experimental data collected during a single year. An empirically calibrated model may then be tested directly, by comparing the model's predictions with the results of a population dynamic perturbation experiment.

This paper is divided into five sections. In the first section, we briefly describe the submodels of individual plants from which we construct population dynamic models. In the second section, we present the computer models and, in the third, we derive and examine the analytical models. We also illustrate how these models may be used to address specific issues in plant ecology such as the relation between the shapes of a yield versus sowing-density curves and the dynamical behavior of plant populations. Finally, in the fourth and fifth sections, we describe how the models may be empirically tested and discuss how studies that combine neighborhood modeling with descriptive and experimental work can contribute to our understanding of the ecology of plants.

PREDICTORS FOR INDIVIDUAL PLANTS

Each of our population dynamic models is based on three submodels: a fecundity predictor, a survivorship predictor, and a dispersal predictor. To describe the first two predictors, we must first define the concept of an ecological neighborhood. A neighborhood may be defined generally as the area about a plant circumscribing all other individuals that interact with the plant. We approximate a plant's ecological neighborhood here as a circle with the plant at its center. Other plants within the circle are called neighbors (or neighboring plants) of the center plant.

We discuss two kinds of fecundity predictors. Seedling fecundity predictors (abbreviated SFP) predict the future seed set of a seedling as a function of the number and spatial arrangement of neighboring seedlings. Adult fecundity predictors (abbreviated AFP) give the seed set of an adult plant as a function of the number and spatial arrangement of neighboring adults. A population dynamic model contains a single fecundity predictor, either an AFP or an SFP. Survivorship predictors give the probability that an individual seedling survives to adulthood as a function of the number and spatial distribution of neighboring seedlings. Dispersal predictors predict the dispersal pattern of a plant's seedling progeny and the survivorship of plants from seed to seedling.

Given a survivorship, fecundity, and dispersal predictor, we can predict the fate of any individual plant through its life cycle. Beginning with a seed, we can predict whether or not the seed germinates and where it germinates with the dispersal predictor. We can predict whether or not a seedling survives to adulthood with the survivorship predictor. Finally, we can determine how many seeds an adult plant produces with the fecundity predictor.

Survivorship, fecundity, and dispersal predictors have appeared in the ecological literature (Mack and Harper 1977; Weiner 1982; Watkinson et al. 1983; and others reviewed in Harper 1977 and Silvertown 1982) and are defined empirically, as least-squares fits to experimental data. Before we discuss the computer models in detail, we briefly describe the experiments and statistical methods necessary to develop predictors, give some examples of predictors, and explain why there are two kinds of fecundity predictors. For a more complete treatment of this subject, see Silander and Pacala (1985).

Seedling Fecundity Predictors

To produce an SFP, the following data are collected: (1) the x- and y-grid coordinates on an experimental plot for each seedling at the beginning of the season and each adult at the end of the season, and (2) the number of seeds produced by each adult. One then calculates a neighborhood circle around each seedling and an index of crowding for each neighborhood. This index may be as simple as the number of neighboring seedlings or may include such complexities as distance from the center seedling to each neighbor, angular dispersion of neighbors, initial seedling size and/or germination date.

An SFP is a function that predicts the future seed set of a seedling from a crowding index for that seedling's neighborhood. For example, in figure 1 we plot adult seed set versus number of seedling neighbors. Each point represents a single *Arabidapsis thaliana* plant grown from broadcast seed in greenhouse flats during 1983. The line in the figure is a nonlinear least-squares fit (Marquardt algorithm) of a fecundity predictor to these data. Here, the predictor is $M/(1 + cn^T)$, where n is the number of neighboring seedlings, and M, T, and c are estimated constants. The parameter M may be interpreted as the number of seeds produced by a plant with no neighbors; c and T are decay constants.

In figure 1 the neighborhood radius is 4 cm. This value was chosen because it produced an SFP with a smaller residual variance than larger (6, 7, 8, 9, 10) or smaller (0.5, 1, 2, 3) radii. In general, the neighborhood radius used in the statistical analysis is chosen so as to minimize residual variance.

The SFP in figure 1 accounts for 77% of the variation in seed set. The unexplained variation in an SFP regression summarizes both density-independent factors that affect the fecundity of an individual and density-dependent factors not accounted for by the predictor.

Adult Fecundity Predictors

The only difference between AFPs and SFPs is that the crowding index in the former summarizes the number and spatial arrangement of adult neighbors rather than the number and arrangement of seedling neighbors. Thus, the only data required to produce an AFP are the x- and y-coordinates of all adult plants and the number of seeds produced by each plant. Figure 2 illustrates an AFP for *Arabidopsis thaliana* that accounts for 80% of the variation in seed set. This predictor is $M/(1 + cn^T)$, where n is the number of adult neighbors, and M and c

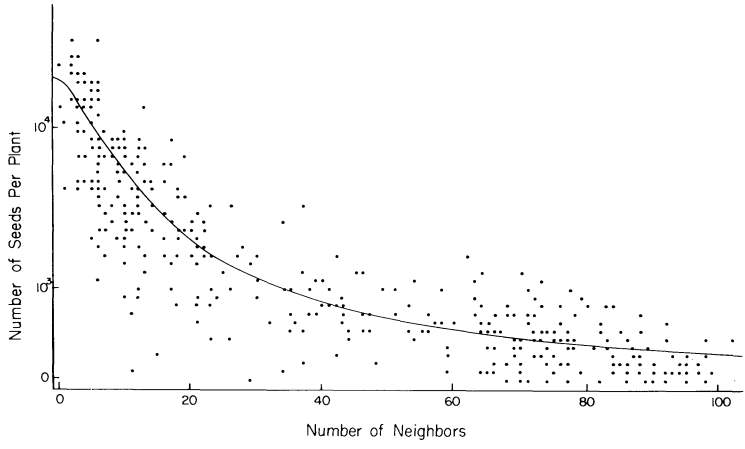

FIG. 1.—SFP for *Arabidopsis thaliana*.

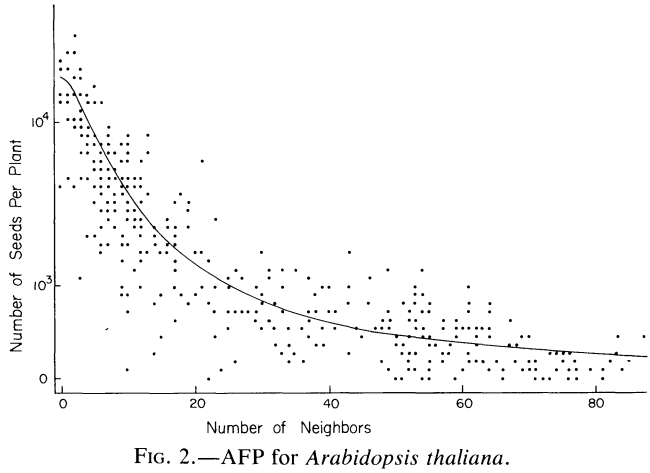

FIG. 2.—AFP for *Arabidopsis thaliana*.

are as before. Mack and Harper (1977) developed AFPs that accounted for up to 69% of the variation in a study of four species of dune annuals. Weiner (1982) developed AFPs for two species of alpine annuals that accounted for 82% and 86% of the variation in seed set. For examples of AFPs that include the distance to each neighbor and the spatial distribution of neighbors, see Silander and Pacala (1985) or Mack and Harper (1977).

There are two reasons why we consider two different types of fecundity predictors. First, both AFPs and SFPs have appeared in the literature and both seem to work. Second, the relative accuracy of SFPs and AFPs may depend on the time course of mortality. For example, if seedling mortality is heavy and adult mortality is light, then AFPs may provide better statistical fits than SFPs. However, if the reverse is true, then SFPs may prove more accurate than AFPs. In our study

of *A. thaliana,* mortality was less than 25% and AFPs are only slightly more accurate than SFPs.

Survivorship Predictors

We define a survivorship predictor as a function that predicts the probability that a seedling survives to adulthood, from an index of crowding for that seedling's neighborhood. Thus a survivorship predictor may be obtained from the same data set used to produce an SFP. After an index of crowding is calculated for each seedling's neighborhood, the data are arranged into a discrete number of classes. Each class represents a different mean level of crowding. The data are then graphed, with the mean index of crowding for each class on the horizontal axis, and the fraction of plants in each class that survives to adulthood on the vertical axis (see Watkinson et al. 1983). A survivorship predictor is obtained by fitting a function to these data statistically.

An example of a survivorship predictor is Be^{-an}, where B and a are estimated constants and n is the number of seedling neighbors. The parameter B may be interpreted as the probability of survival for a seedling with no neighbors; the parameter a is simply a decay constant. The neighborhood radius for a survivorship predictor, like the radius for a fecundity predictor, is chosen so as to minimize the residual variance. A plant species may have different radii for its survivorship.and fecundity predictors.

Dispersal Predictors

A dispersal predictor predicts the number and spatial location of seedlings produced by a mother plant, given the location and seed set of the mother plant. A dispersal predictor is obtained as a statistical fit to a data set, which contains the locations and seed sets of several parental plants together with the number and locations of each plant's seedling progeny. Simple dispersal predictors consist of two parts: an estimate of survivorship from seed to seedling (germination success) and a probability density function for the distance between a seedling and its mother (a dispersal function). Additional complexities may be included if warranted. For example, suppose that smaller seeds are produced by competitively stressed plants. In this case, the germination success of seeds produced by a plant might depend on an index of crowding for the plant, or on the number of seeds produced by the plant. We could also account for nonrandom clumping of seedlings that results from the existence of safe sites for germination or from the aggregation of seeds in depressions in the soil. Finally, we could include nonuniform directionality of seedfall resulting from wind or slope.

To obtain a data set for dispersal predictors, one must be able to identify the maternal seedling progeny of individual plants. There are a variety of ways to accomplish this and we offer three techniques here. First, one could remove seeds, before they fall, from all plants in an area, except for the seeds of a single individual. Second, one could grow single plants of one species against a background of a second species. Third, it is possible to chemically label plants with

unique radionuclides or rare earth elements. This tag is incorporated into seeds and can be detected in germinating seedlings (R. Primack, personal communication).

COMPUTER MODELS

Consider a population of seedlings growing on a rectangular plot. A neighborhood computer model stores the x- and y-coordinates of these seedlings, calculates a survivorship-predictor neighborhood circle around each seedling, and uses the survivorship predictor to determine whether or not each seedling survives. The computer then calculates fecundity predictor neighborhoods around each surviving plant and uses the fecundity predictor to determine the number of seeds produced by each adult. If the model contains an AFP, then only living plants are counted as neighbors. However, if the model includes an SFP, then all plants (alive or dead) are counted as neighbors. Finally, we use the dispersal predictor to determine where each seed germinates and so obtain the spatial distribution of seedlings in the second generation. By repeating the above algorithm, we can proceed to the third generation and so on.

In addition to the three predictors we must also specify boundary conditions in a neighborhood computer model. Boundary conditions describe the fate of a seed that disperses out of a plot. In all examples described in this paper, boundaries are absorbing: seeds that leave the plot are "lost." The effect of absorbing boundaries is to decrease the population size within the plot, especially near the plot's borders. To reduce boundary effects, we typically focus on the population dynamics of the center portion of a modeled plot. This also reduces the "edge effect" caused by plants that are located within a neighborhood radius of the plot's edge. Edge plants, with incomplete neighborhoods, tend to have fewer neighbors and thus tend to have higher survivorship and fecundity.

One way to mimic the dynamics of a portion of a large continuous plot is to make boundaries reflecting: seeds that hit the edge of the plot ricochet back into the plot. Reflecting boundaries require a suspension of one's biological intuition and do not eliminate edge effect. Nonetheless, in examples that we have considered, the dynamics of small plants with reflecting boundaries are very similar to the dynamics of small subplots that are embedded in large plots with absorbing boundaries. Computer runs for small plots are relatively inexpensive, and so reflecting boundaries provide a way to lessen the cost of exploring a model.

As Weiner and Conte (1981) have pointed out, one important technical problem has prevented the development of neighborhood computer models. Specifically, if the population of seedlings is large and any standard sorting algorithm is used, then a prohibitive amount of computer time is required to identify each plant's neighbors. Because population densities of seedlings are often 1000 per m^2 or higher, a model of even a 10 m^2 plot could contain over 10,000 plants. The model would have to sort these 10,000 items every generation. We have developed a sorting algorithm that is very fast because of the data structure used to store each plant's location: a two-dimensional array of linked lists (see Appendix A). With this algorithm, the computer time required by our model increases only linearly

with the area of the modeled plot. Below we present specific examples of neighborhood computer models. Some of these runs involved population sizes averaging over 10,000 for 20 generations, and yet required only 3 min of computer time (IBM 3081).

To illustrate neighborhood computer models, we offer two groups of examples which differ markedly in their dynamical behaviors. All of these examples share the following attributes. (a) Plots are square and measure $33\frac{1}{3}\,r$ on a side, where r is the neighborhood radius of the fecundity predictor. (b) Boundaries are absorbing. (c) We report population densities only for the $13\frac{1}{3}\,r \times 13\frac{1}{3}\,r$ subplot at the center of the $33\frac{1}{3}\,r \times 33\frac{1}{3}\,r$ plot. The 10 r wide buffer zone effectively insulated this subplot from boundary and edge effects, because we observed no significant changes in the results when we increased the width of the buffer region to $13\frac{1}{3}\,r$ or decreased it to $6\frac{2}{3}\,r$. (d) Each example was initiated with a random scatter of 200 adult plants. (e) All runs were iterated for 25 generations. (f) All fecundity predictors are AFPs. (g) The dispersal predictor is as follows: The distance between a seedling and its mother is an exponential random variable with the mean equal to $\frac{4}{3}\,r$. Thus, on average, progeny will decrease exponentially in abundance with increasing distance from their mother. Also, germination success is 100% and progeny are equally likely to disperse in any direction. (h) Survivorship is density independent and so the survivorship predictor is a constant. To save computer time, we actually disperse only those seeds which survive to become adults. In other words, before seeds are dispersed, we multiply the number of seeds produced by each plant by the survivorship and round the resulting quantity to the nearest integer.

The above list specifies all aspects of each example except for the forms of the AFP and the values of the survivorship.

Group 1

In these examples, the fecundity predictor is $M/(1 + cn)$. Again, M and c are constants and n is the number of neighbors. This hyperbolic decay is a special case of the predictor in figure 2, and implies that the potential seed set of a plant (M) is divided among the plant and its neighbors. We present results for three runs with M equal to 10, 30, and 50. In all runs, the parameter c equals 0.9 and the survivorship equals 0.6.

The population densities produced by each run are graphed in figure 3 (dashed lines). Densities are expressed as numbers of adult plants per neighborhood area. Notice that, in all three runs, density increases rapidly to a relatively steady state. The stochastic fluctuations in figure 3 are the result of the randomness of dispersal in the model.

Group 2

Here, the fecundity predictor is Qe^{-vn}, where Q and v are constants. The parameter Q may be interpreted as the number of seeds produced by a plant with no neighbors; v is a decay constant. This exponential form decays more rapidly

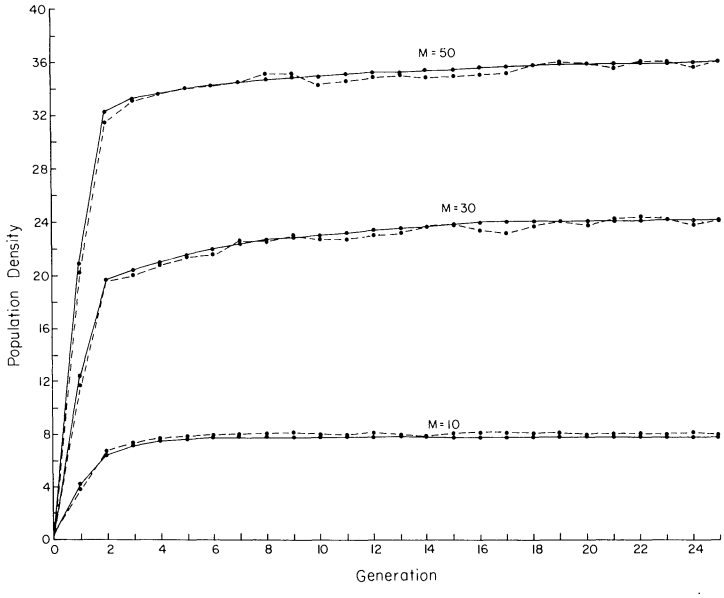

FIG. 3.—Results from the computer model runs in group 1 (dashed lines) and numerical solutions of analytical model (15) (solid lines). The parameters for both the analytical and computer model trajectories are: survivorship = 0.6, probability of germination = 1, $c = 0.9$, $M = 10$, 30, and 50. The mean dispersal distance in the computer runs is $\frac{4}{3}r$.

with increasing n than the hyperbolic form in group 1. It implies that each neighbor reduces the potential seed set of a plant by a constant fraction. Figure 4 contains the results of three runs with Q equal to 10, 20, and 100; v equal to 0.2; and the survivorship equal to 0.2. Notice that when Q is 10 and 20, the population density of adult plants again increases rapidly to a relatively steady state. When Q is 100, however, population density changes in a very erratic manner and shows no tendency to settle into a steady state.

The examples in figures 3 and 4 were chosen because they illustrate both the chief value and the chief shortcomings of neighborhood computer models. The chief value of these models is that they provide a way to determine the population dynamic consequences of specific fecundity, survivorship, and dispersal predictors. Because all three predictors may be obtained empirically, it should be possible to obtain population dynamic models for real monocultures of annuals growing in either the field or greenhouse. Moreover, computer models may be readily modified to include the inevitable complexities encountered in an empirical study. There are, however, two chief shortcomings of neighborhood computer models. First, it is difficult to explore a computer model fully to determine its complete repertoire of dynamical behavior. Thus, the model illustrated in figure 3 appears to be "well-behaved" for all values of M but we cannot be certain of this. Second, the predictions of a computer model may be difficult to understand in intuitive terms. For example, why does the model illustrated in figure 4

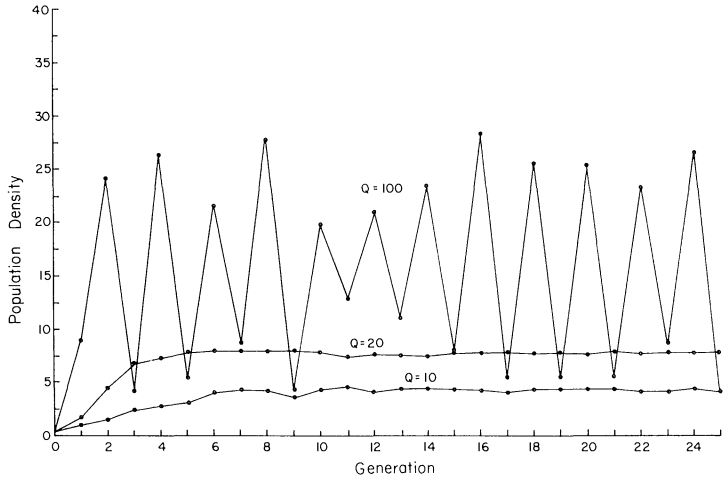

FIG. 4.—Results from the computer model runs in group 2. Parameter values are: survivorship = 0.2, probability of germination = 1, $\nu = 0.2$, $Q = 10$, 20, and 100. Mean dispersal distance is $\frac{4}{3}\,r$.

produce a smooth trajectory if $Q = 10$ or $Q = 20$ and a highly erratic trajectory if $Q = 100$? To obviate the shortcomings of neighborhood computer models, we now explore an analytically tractable formulation.

ANALYTICAL MODELS

We have developed analytically tractable analogues of neighborhood computer models for cases in which the dispersal predictor has two characteristics. First, the location of each seedling is governed by the dispersal function: $L(d_{\mathbf{uv}})$. Here $L(d_{\mathbf{uv}})$ is the probability density function for the vector-valued location of a seedling **u**, given the location of the seedling's mother **v**. Notice that this probability density is a function solely of the distance, $d_{\mathbf{uv}}$, between a seedling and its mother. Second, the probability of germination is constant.

Dispersal predictors that possess these two characteristics include a wide variety of biologically reasonable forms. For example, see the computer models that produced figures 3 and 4. The above characteristics, however, exclude some important cases. For example, if seeds aggregate in depressions in the soil, then the probability density for the location of a seedling will not be a function solely of the distance between the seedling and its mother. Rather, the locations of seedlings will depend, in part, on the locations of soil depressions. Also, if there are safe sites for germination, then the probability of germination will depend on spatial location. Although it is possible to modify the methods described below to include complexities such as safe sites and nonuniform soil topography, we focus first on the simple case.

Consider an infinite plane on which seedlings are growing. The spatial pattern of these seedlings will in general depend on the number and spatial distribution of

their parents, the number of seeds produced by each parent, the germination success, and the nature of seed dispersal. Because dispersal has a random component, the spatial pattern of seedlings is governed by a stochastic process. In Appendix B, we show that this stochastic process becomes a Poisson process in the limit as the mean dispersal distance (the mean distance between a seedling and its mother) becomes large. More specifically, we demonstrate the following in Appendix B: If the locations of seedlings in generation t are governed by a Poisson process and dispersal is sufficiently large, then the locations of seedlings in generation $t + 1$ are governed by a stochastic process that is approximately Poisson. The parameter of the Poisson process is simply the average population density of seeds on the plane. If S_t is the average population density of seeds in generation t, and g is the probability of germination, then the average density of seedlings is gS_t.

The spatial pattern of seedlings produced by a Poisson process with parameter gS_t may be characterized as follows. (1) The number of seedlings in a spatial region of area, A, is Poisson distributed, with parameter: AgS_t. Thus, the probability that a region of area A will contain n seedlings is $(e^{-\lambda}\lambda^n)/(n!)$, $\lambda = AgS_t$. (2) Statement (1) is true no matter what the shape of the spatial region is, what the value of A is, or where the region is located on the plane. In other words, the spatial pattern of seedlings is the random spatial pattern (as opposed to a clumped or overdispersed pattern) discussed by Pielou (1969) and many others. The intuitive reason why the spatial pattern of seedlings is random when dispersal is large, is simply that, with large dispersal seedlings become randomly mixed over large areas. Thus, the spatial pattern of seedlings depends more on the randomness infused by large dispersal than on the spatial location and fecundity of each parent plant. For further discussion of Poisson processes, see Feller (1968, 1971) or Karlin and Taylor (1975, 1981).

In all of our analytical neighborhood models, we assume that the locations of seedlings are governed by a Poisson process. The spatial distribution of seedlings in a computer model will be exactly random only in the limit as dispersal becomes infinite. We now demonstrate through an example, however, that a random spatial pattern may be a good approximation for cases in which dispersal distances are biologically reasonable.

Our example involves the neighborhood computer model that produced figure 3. Figure 5 contains results from 11 runs of this model, each with a different value for the mean dispersal distance. Each run consisted of 15 generations and, in every generation, we calculated the following clumping index for the center $13\frac{1}{3}\ r \times 13\frac{1}{3}\ r$ portion of the modeled plot:

$$\text{clumping index} = \frac{\text{variance of the number of neighbors per seedling}}{\text{mean number of neighbors per seedling}}.$$

The expected value of this index is one if the spatial distribution of seedlings is random. Each point in figure 5 is a mean clumping index for a run, calculated by averaging the clumping-index values from generations 10 to 15. We wait until generation 10 to calculate the clumping index to reduce its dependence on the initial spatial distribution. Notice that the average clumping index rapidly ap-

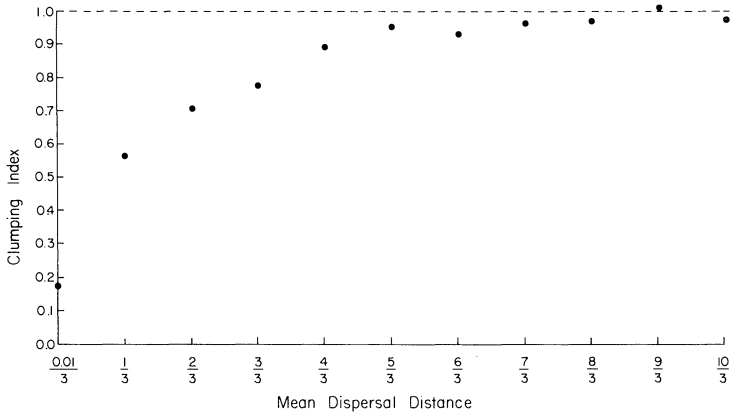

FIG. 5.—Mean clumping-index values for seedlings in computer model runs. The functional forms for the predictors are the same as in the examples in group 1. Parameter values are: $M = 10$, $c = 0.9$, survivorship $= 0.6$, $g = 1$. The mean dispersal distances on the horizontal axis are given in units of r, where r is the neighborhood radius for the fecundity predictor.

proaches one as the mean dispersal distance is increased. Thus, the stochastic process which governs the locations of seedlings is approximately Poisson for all dispersal distances in the figure greater than the neighborhood radius. A detailed investigation of conditions that result in randomly distributed seedlings is beyond the scope of this paper. Such a study would be a fruitful area for further work, especially if part of a more general study of the dependence of spatial pattern on the forms of dispersal, survivorship, and fecundity predictors.

Analytically tractable neighborhood models have the following form:

$$\begin{aligned} S_{t+1} &= gS_t\, Z(S_t)\, F(S_t) \\ \begin{bmatrix}\text{Yield}\end{bmatrix} &= \begin{bmatrix}\text{Seedling}\\ \text{density}\end{bmatrix} \begin{bmatrix}\text{Average}\\ \text{survivorship}\end{bmatrix} \begin{bmatrix}\text{Average}\\ \text{fecundity}\end{bmatrix}. \end{aligned} \tag{1}$$

To derive specific models of the form (1), we must derive functional forms for average survivorship, $Z(S_t)$, and average fecundity, $F(S_t)$.

Suppose that the average population density of seedlings on an infinite plane is gS_t. The locations of seedlings are assumed to be governed by a Poisson process. Suppose that we select a seed at random and draw a neighborhood circle of radius r around it. We can use the properties of Poisson spatial processes to predict, in a statistical sense, the number and spatial arrangement of other seedlings in the neighborhood. For example, the probability that there are n neighbors is given simply by the Poisson distribution: $(e^{-\lambda}\lambda^n)/(n!)$, $\lambda = gS_t\pi r^2$ (see the definition of the Poisson process given above). The locations of neighbors are independent random vectors. Each random vector is uniformly distributed over the neighborhood circle (see Hoel et al. 1971).

We use the above information about the neighborhood configurations of seedlings together with a fecundity and survivorship predictor to derive expressions for average survivorship and fecundity. For example, suppose that the survivor-

ship predictor, $z(n)$, is a function solely of n, the number of neighbors. Because we consider an infinite population (positive density on an infinite plane), the fraction of seedlings that have n neighbors is equal to the probability that a randomly chosen seedling has n neighbors

$$\frac{e^{-\lambda}\lambda^n}{n!},$$

where $\lambda = gS_t\pi r_s^2$ and r_s is the neighborhood radius for the survivorship predictor. To simplify the notation we set the spatial scale so that πr_s^2 equals one. Thus, the average survivorship of seedlings is

$$\begin{aligned} Z(S_t) &= \sum_{n=0}^{\infty} \frac{e^{-S_tg}(S_tg)^n}{n!} z(n) \\ &= \sum_{n=0}^{\infty} \begin{bmatrix}\text{Fraction of seedlings}\\ \text{with } n \text{ neighbors}\end{bmatrix} \begin{bmatrix}\text{Probability of survival for}\\ \text{a seedling with } n \text{ neighbors}\end{bmatrix}. \end{aligned} \tag{2}$$

Suppose that the fecundity predictor is also a function solely of the number of neighbors. If this predictor is an SFP, then we can use (2) to obtain an expression for average fecundity. In the most simple case, the fecundity and survivorship predictor neighborhoods are equal in size. Then

$$\begin{aligned} F(S_t) &= \sum_{n=0}^{\infty} \frac{e^{-S_tg}(S_tg)^n z(n)}{n!\, Z(S_t)} f_s(n) \\ &= \sum_{n=0}^{\infty} \begin{bmatrix}\text{Fraction of adult}\\ \text{plants that had } n\\ \text{neighbors as seedlings}\end{bmatrix} \begin{bmatrix}\text{Number of seeds produced}\\ \text{by an adult that had}\\ n \text{ seedling neighbors}\end{bmatrix} \end{aligned} \tag{3}$$

where $f_s(n)$ is the SFP. With $Z(S_t)$ and $F(S_t)$ given by (2) and (3), the model (1) may be written

$$S_{t+1} = gS_t \sum_{n=0}^{\infty} \frac{e^{-S_tg}(S_tg)^n}{n!} z(n)f_s(n). \tag{4}$$

In Appendix C1, we present expressions for $F(S_t)$ for the two remaining cases: $r_f > r_s$ and $r_f < r_s$, where r_f is the neighborhood radius for the fecundity predictor.

Suppose that the fecundity predictor is the AFP: $f_a(n)$. If the survivorship predictor is also density dependent, then the derivation of $F(S_t)$ involves intractable mathematics. We can, however, derive an expression for average fecundity if survivorship is density independent. For example, suppose that the survivorship predictor is the constant P. We set the spatial scale so that the area of the AFP neighborhood equals one. Then, the fraction of adult plants that have n adult neighbors is

$$\begin{aligned} &\sum_{m=n}^{\infty} \left[\frac{e^{-S_tg}(S_tg)^m}{m!}\right] \left[\binom{m}{n} (P)^n (1-P)^{m-n}\right] \\ &\sum_{m=n}^{\infty} \begin{bmatrix}\text{Fraction of adults that}\\ \text{had } m \text{ seedling neighbors}\end{bmatrix} \begin{bmatrix}\text{Probability that } n \text{ of these}\\ \text{neighbors survived to adulthood}\end{bmatrix}. \end{aligned} \tag{5}$$

The above expression reduces to the Poisson distribution: $\frac{e^{-PS_tg}(PS_tg)^n}{n!}$ (see the end of Appendix B where analogous algebra is presented), and so the average fecundity of plants is

$$F(S_t) = \sum_{n=0}^{\infty} \frac{e^{-PS_tg}(PS_tg)^n}{n!} f_a(n). \tag{6}$$

With $F(S_t)$ given by (6) and $Z(S_t)$ equal to P, the model (1) becomes

$$S_{t+1} = PgS_t \sum_{n=0}^{\infty} \frac{e^{-PS_tg}(PS_tg)^n}{n!} f_a(n). \tag{7}$$

Thus far, we have considered simple fecundity and survivorship predictors in which the independent variable is the number of neighbors. It is also possible to derive $Z(S_t)$ and $F(S_t)$ for cases involving more complicated predictors. For example, in Appendix C2 we derive $F(S_t)$ for an AFP that includes the distance to neighbors.

The general model (1) gives yield (S_{t+1}) as a function of sowing density (S_t). The dynamical behavior of a model population of annuals is determined by the shape of the yield versus sowing density function (abbreviated YD function) defined in (1). In what follows, we first derive results that relate the shape of the YD function defined by a model to the model's dynamical behavior. We then analyze three specific examples of (1) in detail. In each of these examples, survivorship is density independent and the fecundity predictor is an AFP. The models in the first two examples are analytical analogues of the neighborhood computer models whose output is illustrated in figures 3 and 4. We use results derived for the analytical examples to explain the computer model output in these figures. Finally, we show that the dynamics of the analytical examples are qualitatively and quantitatively similar to the dynamics of the corresponding computer examples.

Analysis and Results for the General Model (1)

Equilibria of the model (1) satisfy:

$$1 = g\,F(S_t)\,Z(S_t) \tag{8}$$

and the conditions for the local stability of an equilibrium are

$$\begin{aligned} 1 &< \Psi(\hat{S}); \text{ unstable; trajectories nonoscillatory} \\ 0 &< \Psi(\hat{S}) < 1; \text{ stable; trajectories nonoscillatory} \\ -1 &< \Psi(\hat{S}) < 0; \text{ stable; trajectories oscillatory} \\ \Psi(\hat{S}) &< -1; \text{ unstable; trajectories oscillatory} \end{aligned} \tag{9}$$

where $\Psi(S_t) = gF(S_t)Z(S_t) + gS_t \frac{d[F(S_t)Z(S_t)]}{dS_t}$, and $\hat{S}$ is the equilibrium density. Equation (8) states that population dynamic equilibria correspond to the places where the YD function (1) intersects the 45° line: $S_{t+1} = S_t$. Conditions (9) show that local stability is determined by the slope of the YD function at equilibrium.

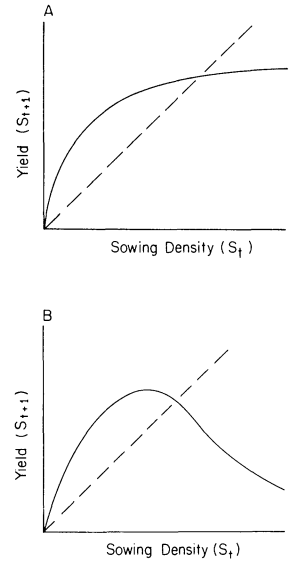

FIG. 6.—*A*, asymptotic yield vs. density function; *B*, humped yield vs. density function.

Yield versus density relations have been the subject of considerable empirical inquiry. Published YD relations typically fall into one of two categories: asymptotic as shown in figure 6*A*, or humped as shown in figure 6*B* (Myerscough and Marshall 1973; Harper 1977; Silvertown 1982). To define these two forms more precisely, the slope of an asymptotic YD relation is positive, monotone decreasing and equal to zero in the limit as S_t tends to infinity. The slope of humped forms is positive and monotone decreasing for small values of S_t, equal to zero for a single value of S_t, and negative for large values of S_t. Asymptotic YD relations are commonly referred to as the constant yield law (Harper 1977).

Two results are obvious consequences of equation (8) and conditions (9). *Result I:* Suppose that a model of the form (1) defines an asymptotic YD relation. By equation (8), the model has a unique positive equilibrium which exists if $\Psi(0) > 1$. By conditions (9), this equilibrium is always locally stable. In fact, it is straightforward to prove that the equilibrium is also globally stable. *Result II:* Suppose that (1) defines a humped YD relation. As in Result I, this model has a unique positive equilibrium which exists if $\Psi(0) > 1$ (see eq. [8]). The local stability of this equilibrium will depend on the precise shape of the YD relation. Below, we show that, in some cases, equilibria may be stable or unstable and trajectories may be oscillatory or nonoscillatory. Moreover, humped YD relations can result in chaotic population dynamics.

Example 1

This example is the analytical analogue of the computer example that produced the trajectories in figure 4. Thus, the survivorship predictor is a constant, P, and

the AFP is Qe^{-vn}. With these specifications the model (7) becomes

$$\begin{aligned} S_{t+1} &= PS_t g \sum_{n=0}^{\infty} \frac{e^{-PS_t g}(PS_t g)^n}{n!} Qe^{-vn} \\ &= QPgS_t e^{-PS_t g} \sum_{n=0}^{\infty} \frac{(PS_t g e^{-v})^n}{n!} \\ &= QPgS_t \exp[-PS_t g(1 - e^{-v})]. \end{aligned} \tag{10}$$

The model (10) is mathematically equivalent to the extensively studied exponential form of the logistic equation (see May and Oster 1976), and yet accounts for such complexities as plastic plant growth, the spatial distribution of individuals, and the fact that plants interact primarily with nearby plants. The unique positive equilibrium of (10) is $\hat{S} = \ln(QPg)/[Pg(1 - e^{-v})]$. This equilibrium exists if $PQg > 1$ and $v > 0$. Because the YD relation defined by (10) is humped, the model may exhibit a wide variety of dynamical behaviors:

$$\begin{aligned} &0 < \ln(PQg) < 1; \text{ internal equilibrium is stable; trajectories nonoscillatory} \\ &1 < \ln(PQg) < 2; \text{ internal equilibrium is stable; trajectories oscillatory} \\ &2 < \ln(PQg); \text{ internal equilibrium is unstable; trajectories oscillatory.} \end{aligned} \tag{11}$$

The dynamics when $\ln(PQg) > 2$ have also been categorized as part of a study of the exponential logistic equation. Sustained oscillations occur for all values of $\ln(PQg)$ greater than 2, and dynamics appear chaotic if $\ln(PQg)$ is greater than 2.6924. . . (May and Oster 1976).

The above results explain why the computer model analogous to (10) produced a highly erratic trajectory when $\ln(PQg) = 2.996$, and relatively well-behaved trajectories when $\ln(PQg) = 0.693$ or $\ln(PQg) = 1.386$ (see fig. 4). This result is predicted by the stability conditions for the analytical model because (10) has chaotic dynamics if $\ln(PQg) = 2.996$, and a stable positive equilibrium if $\ln(PQg) = 0.693$ or $\ln(PQg) = 1.386$.

To further compare the model (10) with the analogous computer model, we first transform (10) so that the dynamical variable is the population density of adults. If $X_t = PgS_t$, then

$$X_{t+1} = QPgX_t \exp[-X_t(1 - e^{-v})]. \tag{12}$$

In figure 7, we plot numerical solutions of the model (12) for the parameter values: $P = 0.2$, $g = 1$, $v = 0.2$, $Q = 10$, 20, and 100. These are the same values used to produce the computer model trajectories in figure 4. Notice the striking correspondence between the predictions of the analytical and computer models in figures 4 and 7.

Example 2

Here, the AFP is $M/(1 + cn)$ and survivorship is again constant. With these predictors, the analytical model is

$$S_{t+1} = PS_t g \sum_{n=0}^{\infty} \frac{e^{-PS_t g}(PS_t g)^n}{n!} \frac{M}{1 + cn}. \tag{13}$$

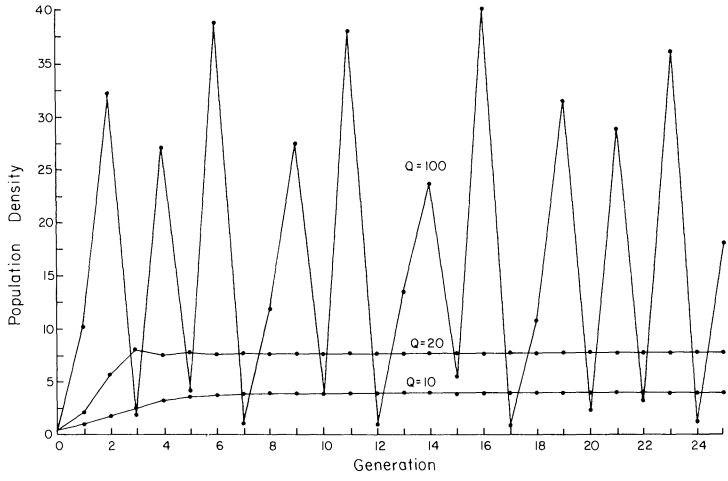

FIG. 7.—Numerical solutions of analytical model (12). The parameter values are: $P = 0.2$, $g = 1$, $v = 0.2$, $Q = 10$, 20, and 100.

The above example is the analytical analogue of the computer model that produced the trajectories in figure 3. The model (13) is not as tractable as (10). However, if $c = 1$, then (13) can be expressed in a much more simple form

$$S_{t+1} = M \sum_{n=0}^{\infty} \frac{e^{-PS_tg}(PS_tg)^{n+1}}{(n+1)!} = M(1 - e^{-PS_tg}). \tag{14}$$

This equation defines an asymptotic YD relation. Thus, (14) has a single stable positive equilibrium, if $M > 1$ (see Result I).

To treat cases other than $c = 1$, we first transform (13), so that the dynamical variable is the density of adult plants. If X_t is the population density of adults ($X_t = PgS_t$), then

$$X_{t+1} = MPgX_t \sum_{n=0}^{\infty} \frac{e^{-X_t}X_t^n}{n!} \frac{1}{1+cn}. \tag{15}$$

The slope of the YD function (15) is

$$\Psi(X_t) = MPg \sum_{n=0}^{\infty} \frac{e^{-X_t}X_t^n}{n!} \frac{[n+1-X_t]}{1+cn}.$$

The sign of the above quantity does not depend on P, g, or M, and so we need only plot (15) for a range of values of c, to determine if this YD relation is monotone. In figure 8, we see that (15) gives the constant yield law for values of c less than or equal to one. We thus conjecture that the model has a single positive equilibrium if $PgM > 1$, and that this equilibrium is locally stable if $c \leq 1$. In contrast, if $c > 1$, then the model may have oscillatory dynamics. For example, in figure 9, we plot a

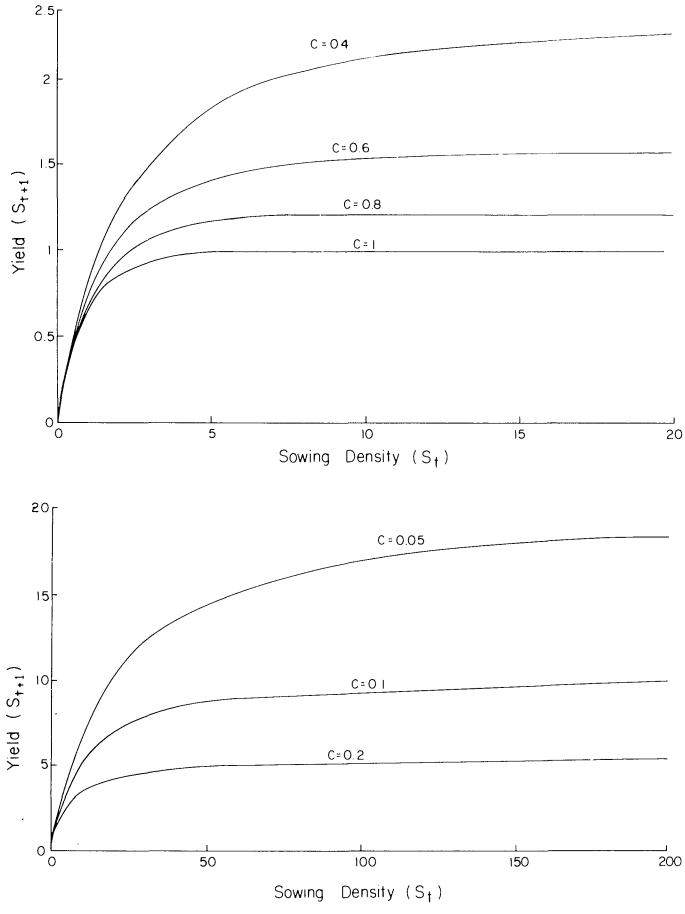

FIG. 8.—Yield vs. sowing-density functions defined by model (15). Parameter values are: $M = 1$, $P = 1$, $g = 1$, $c = 0.05, 0.1, 0.2, 0.4, 0.6, 0.8$, and 1.

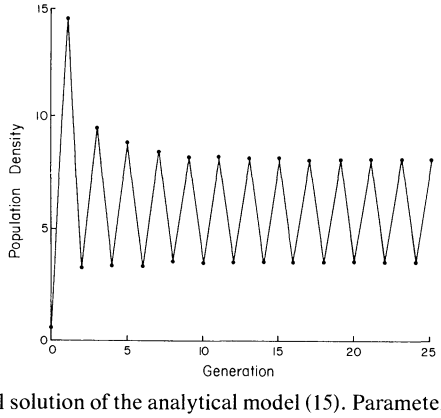

FIG. 9.—A numerical solution of the analytical model (15). Parameter values are: $M = 50$, $c = 15$, $P = 0.9$, and $g = 1$.

numerical solution of (15) for the following parameter values: $g = 1$, $c = 15$, $M = 50$, and $P = 0.9$. Notice that oscillations are persistent.

To compare the model (15) with the analogous computer model, we first set P, M, c, and g at the same values used for the computer runs in figure 3 ($P = 0.6$, $g = 1$, $c = 0.9$, $M = 10$, 30, and 50), and then obtain numerical solutions of (15). These trajectories are also graphed in figure 3 (solid lines). As before, there is striking quantitative agreement between the predictions of the analogous computer and analytical models. The reason for this agreement is that, in the computer examples, dispersal is larger than the neighborhood radius (see fig. 5). Thus, the stochastic process that governs the spatial pattern of seedlings in the computer model is closely approximated by a Poisson process.

Example 3

Because fecundity predictors tend to be concave (see figs. 1, 2), they may be approximately linear for plants with crowded neighborhoods. Thus, an appropriate AFP, for plants growing at high mean density, might be $\gamma - \mu n$, where γ and μ are constants. With this AFP, the model (7) becomes

$$\begin{aligned} S_{t+1} &= PS_t g \sum_{n=0}^{\infty} \frac{e^{-PS_t g}(PS_t g)^n}{n!} (\gamma - \mu n) \\ &= Pg\gamma S_t - \mu(PS_t g)^2. \end{aligned} \tag{16}$$

The above model is mathematically equivalent to the discrete-time logistic equation, and yet accounts for the sedentary nature and plastic growth of plants. Here, the constant $(Pg\gamma - 1)$ is the intrinsic rate of increase and $(Pg\gamma - 1)/(\mu P^2 g^2)$ is the carrying capacity. Notice that these quantities are expressed in terms of measurable properties of individual plants. Because the analysis of the discrete-time logistic is well known, we will not analyze (16), other than to point out that the model defines a humped YD relation.

EMPIRICAL CALIBRATION AND MODEL TESTING

There are two steps to an empirical test of a neighborhood model. First, the model must be calibrated for an experimental species. Because all functional forms and parameters in a neighborhood model are contained in the survivorship, fecundity, and dispersal predictors, empirical calibration reduces to producing these three predictors for an experimental species. Thus, all functional forms and parameter values may be estimated from data obtained in simple experiments lasting a single year (see the section on predictors at the beginning of this paper or Silander and Pacala [1985]). The predictions of an empirically calibrated model are then tested with a population dynamic experiment. Population densities are first perturbed in several monoculture plots. These plots are then censused annually, to determine how well the model predicts the actual dynamics that follow a perturbation. Ideally, empirical calibration would be repeated in every year of the population dynamic experiment. This would allow one to assess year-to-year

changes in the three predictors. Temporal variation may be included in a neighborhood model by simply altering the predictors in the model from generation to generation.

DISCUSSION

We describe general and testable population dynamic models for monocultures of annual plants. These models explicitly include plastic plant performance, the spatial distribution of individuals, and the fact that plants interact primarily with nearby plants. We discuss both analytical models that are valid when dispersal is sufficiently large and computer models that are more general. The computer models are designed to determine the population dynamic consequences of specific fecundity, survivorship, and dispersal predictors. It is relatively straightforward to include the many complexities associated with plant performance, interplant interactions, and plant dispersal in computer models. The more simple analytical models are used to explain the predictions of corresponding computer models. In some cases, the quantitative predictions of analytical models are virtually identical to those of their computer model counterparts (see figs. 3, 4, 7). Finally, because our neighborhood models are based on predictors for individual plants, these models provide explanations for population-level phenomena in terms of the biology of individuals.

In this paper, we focus primarily on the exposition of our modeling approach. Neighborhood models can be used to address a wide variety of issues in plant ecology. For example, we have presented results that relate the shapes of yield versus sowing-density functions to the dynamical behavior of plant populations. We now offer two possible avenues for future theoretical work. First, many empirical studies have demonstrated that both density-dependent survivorship and density-dependent fecundity may influence plant population dynamics (reviewed in Harper 1977). To study the conditions that determine the relative importance of these factors in regulating plant populations, one could study a series of models with different density-dependent survivorship and fecundity predictors. Second, plant dispersal clearly influences the spatial distribution of plants. Under some conditions, short dispersal results in a clumped distribution of seedlings (Bartlett 1960), because offspring tend to be aggregated around their mother's location. A clumped distribution of seedlings is also expected if seeds aggregate in depressions in the soil. In contrast, if plants are overdispersed because of competition, and each plant produces from one to a very few seeds, then short dispersal may result in an overdispersed distribution of seedlings. Because the fecundities and survivorships of individuals depend on their spatial distribution, dispersal may influence the dynamics of a plant population. To examine the effects of dispersal on population dynamics, one could compare the predictions of several computer models with the same fecundity and survivorship predictors, but with different dispersal predictors.

Neighborhood models should also prove useful in empirical studies of plant population dynamic processes. An empirically calibrated and tested model would provide explanations for the abundances and dynamics of single-species popula-

tions. These explanations would be given in terms of the empirically calibrated survivorship, fecundity, and dispersal predictors. Moreover, because our population dynamic models are based on predictors for individual plants, the models should prove useful in empirical studies of the individual ecology of plants. For example, plant autecologists commonly measure the physiological responses of plants to light, water and nutrient regimes. To determine the population dynamic consequences of these physiological responses, one could grow populations of plants under different environmental conditions and obtain survivorship, fecundity and dispersal predictors for the plants in each population. One could also compare such attributes of plant species as growth form, phenology, and habitat preference, with the dispersal, survivorship and fecundity of each species. New relationships might thus be discovered among population dynamics, the nature of interplant interactions, and the physiology and natural history of a species.

The models described in this paper can serve as a foundation on which to develop a general plant population dynamic theory. We are currently working in four areas to extend neighborhood theory. First, we are building seed dormancy into the models. Second, we are developing age- and size-structured population dynamic models for perennial plants. Our perennial models contain neighborhood predictors that give the size and seed set of a plant at the end of a growing season, as functions of conditions at the beginning of the growing season. These conditions include the size and age of the plant, and the number, size, and spatial distribution of neighbors (see Waller 1981). Third, we are working to model explicitly spatial heterogeneity in physical conditions that affect fecundity and survivorship. Fourth, we are building multispecies neighborhood models.

Finally, neighborhood population dynamic models may serve as the basis for a theory of the evolutionary ecology of plants. In an evolutionary model, different genotypes would have different fecundity, survivorship, and dispersal predictors. The purpose of an evolutionary model would be to determine how these attributes of individual plants evolve, and, in so doing, to study the evolution of plant population dynamic processes.

SUMMARY

We present tractable formulations for neighborhood models of annual plant population dynamic processes. These models are constructed from submodels, termed predictors, of individual plants. Fecundity and survivorship predictors give the fecundity and survivorship of an individual as a function of local population density. Dispersal predictors predict the dispersal pattern of a plant's maternal progeny and the survivorship of plants from seed to seedlings.

We develop both computer models and analytically tractable models. Our computer models are designed to determine the population dynamic consequences of specific fecundity, survivorship and dispersal predictors. The analytical models are valid when dispersal is sufficiently large, and are used to explain the predictions of analogous computer models. We show through examples that the predictions of corresponding computer and analytical models may be virtually identical.

Empirical tests of these models are practical because all model parameters and functional forms can be estimated with data obtained in a single year. We describe the experiments and statistical methods used to test a neighborhood model.

Finally, we describe how neighborhood models can be used to address specific issues in plant ecology and discuss possible extensions of neighborhood theory.

ACKNOWLEDGMENTS

We are indebted to N. Chiariello, K. Holsinger, and J. Roughgarden for invaluable discussion and bibliographic information. We thank T. Killeen and B. Johnson for technical advice, R. Primack for provocative discussions, and E. DeCarli and L. E. K. Pacala for typing the manuscript.

APPENDIX A

If the x- and y-coordinates of plants in a neighborhood computer model are stored in a simple array, then the computer must compare the locations of all possible pairs of plants to determine which plants are in each plant's neighborhood. It is prohibitively time consuming to calculate distances between all possible pairs of plants if the number of plants is large. To circumvent this problem, we store the locations of plants in a more complex data structure: a two-dimensional array of linked lists.

Consider a two-dimensional array, $g(i, j)$, in which i and j each range from zero to N. Thus, $g(a, b)$ is the entry in the ath row and bth column of a table with $(N + 1)^2$ entries. Now consider a two-dimensional array of linked lists: $G(i, j)$, $i = (0, 1, 2, \ldots, N)$, $j = (0, 1, 2, \ldots, N)$. $G(i, j)$ is also a table with $N + 1$ rows and $N + 1$ columns. However, each "position" in the table is now more complicated. Specifically, each position is occupied by a linked list, a data structure which may be thought of as a table with a variable number of rows. Each "row" of a linked list is called a node. Thus, the linked list $G(a, b)$ is located in the ath row and bth column of a two-dimensional table, and the data structure $G(i, j)$, $i = (0, 1, 2, \ldots, N)$, $j = (0, 1, 2, \ldots, N)$, contains $(N + 1)^2$ separate linked lists.

Suppose that we wish to store the coordinates of a plant, x and y, in this data structure. We first truncate the values of the coordinates: $Tx = \text{trunc}(x)$, $Ty = \text{trunc}(y)$. We then store the values of x and y in a node of the linked list: $G(Tx, Ty)$. Each node of a linked list contains the x- and y-coordinates for a different plant. The data structure $G(i, j)$ may be thought of as a grid framework on the modeled plot. For example, the grid square (linked list) $G(1, 2)$ contains all plants with an x-coordinate greater than or equal to one and less than two, and a y-coordinate greater than or equal to two and less than three.

To identify all neighbors of a plant located at the position, (x, y), we first calculate a neighborhood circle around (x, y). All plants in all grid squares (linked lists) wholly within this circle are neighbors of the plant. To locate the remaining neighbors, we must calculate the distance between (x, y) and each plant in grid squares that lie partly within the neighborhood circle. All plants in grid squares outside the neighborhood circle are not neighbors of the plant at (x, y). For a more concrete example, suppose that the plant is located at $x = 50.5$, $y = 50.5$, and that the neighborhood radius is one. This plant will be located in the linked list $G(50, 50)$. The only grid square wholly within the neighborhood circle is $G(50, 50)$, and so all plants in $G(50, 50)$ are neighbors of the plant at $x = 50.5$ and $y = 50.5$. The grid squares $G(51, 50)$, $G(50, 51)$, $G(51, 51)$, $G(50, 49)$, $G(49, 50)$, and $G(49, 49)$ lie partly within the neighborhood, and so we must retrieve the locations of potential neighbors in these six linked lists and calculate the distance between each potential neighbor and the point (50.5, 50.5). Finally, all grid squares $G(i, j)$ such that $i < 49$, $i > 51$, $j > 51$, or $j < 49$ will contain no neighbors of the plant at $x = 50.5$, $y = 50.5$. Recall that if locations were stored in a simple array, then the computer would have to calculate distances between the plant at (50.5, 50.5) and all other plants on the modeled plot.

The amount of computer time required to locate the neighbors will depend on the number of linked lists, $(N + 1)^2$, into which the plot is divided. For example, if $N = 0$, then all plants are stored in a single linked list. In this case, the computer must calculate distances between all possible pairs of plants. If $(N + 1)^2$ is large relative to the number of plants, then the computer will waste time in checking the many empty grid squares. Thus, a program will be most efficient for some intermediate value of N. The optimal value or values of N will depend on the number and spatial distribution of plants in the model. In the examples that we have considered, a good value of N is very roughly $\sqrt{2S}$, where S is the average number of plants in the run.

Finally, one other advantage of storing the locations of plants in a two-dimensional array of linked lists is that this data structure allows a very efficient use of computer memory. With over 10,000 plants in some runs, memory may be in short supply.

APPENDIX B

We assume that seedlings of the first generation are distributed over an infinite plane and that the locations of these seedlings are governed by a Poisson process. The seedlings then interact via a survivorship and fecundity predictor and set seed. In this appendix, we demonstrate that if dispersal is sufficiently large, then the locations of seedlings in the second generation are governed approximately by a Poisson process. Below, unless otherwise specified, the word seedling refers to first-generation plants.

The following argument is valid for population dynamic models that contain either an AFP or an SFP. However, a simpler argument would suffice for models containing an SFP.

We start by dividing the infinite plane into grid squares. The i–jth grid square is labeled R_{ij}, and each grid square measures V units on a side. We set the spatial scale so that i and j are the coordinates for the point at the center of R_{ij}. Inside each grid square is a smaller grid square labeled R'_{ij}. The border of R'_{ij} is r_s units from the border of R_{ij}, where r_s is the neighborhood radius for the survivorship predictor. Inside R'_{ij} is a still smaller grid square labeled R''_{ij}. The border of R''_{ij} is r_f units from the border of R'_{ij}, where r_f is the neighborhood radius for the fecundity predictor. The regions R_{ij}, R'_{ij}, R''_{ij}, R_{ij+1}, R'_{ij+1}, and R''_{ij+1} are illustrated in figure B1.

Let Y''_{ij} be a random variable giving the yield (total no. of seeds produced) in the region R''_{ij}. Consider any two grid squares, R_{ij} and R_{ab}, $(i, j) \neq (a, b)$. By the properties of Poisson processes:

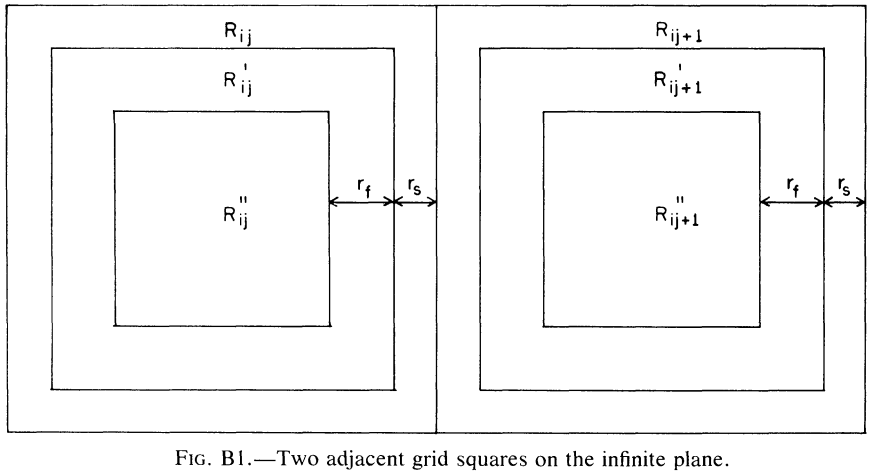

FIG. B1.—Two adjacent grid squares on the infinite plane.

The number and spatial locations of seedlings inside R_{ij} are independent of the number and spatial locations of seedlings inside R_{ab}. (B1)

Because the border of R'_{ij} is r_s units from the border of R_{ij}, the survivorships of seedlings inside R'_{ij} are not affected by seedlings outside of R_{ij}. Similarly, the fecundities of adults inside R''_{ij} are not affected by plants outside of R'_{ij}. Thus:

The yield in R''_{ij} is not affected by plants outside of R_{ij}. However, Y''_{ij} is affected by the number and spatial distribution of plants within R_{ij}. (B2)

From (B1) and (B2), we conclude that Y''_{ij} and Y''_{ab}, $a = (-\infty, \infty)$, $b = (-\infty, \infty)$, $i = (-\infty, \infty)$, $j = (-\infty, \infty)$, $(i, j) \neq (a, b)$, are independent random variables. It is straightforward to express the above intuitive argument in the form of a mathematical proof.

We now show that the Y''_{ij}, $i = (-\infty, \infty), j = (-\infty, \infty)$, are also identically distributed. Let (X'_k, U'_k) be the spatial coordinates of the kth seedling in the region R_{ij}. We define the "adjusted" location (X_k, U_k) of the kth seedling as: $X_k = X'_k - i$, $U_k = U'_k - j$. Let $g_{ij}(x_1, u_1, x_2, u_2, \ldots, x_m, u_m|m)$ be the probability density for the adjusted locations of seedlings in R_{ij}, given that there are m seedlings in R_{ij}. Further, let $f_{ij}(m)$ be the probability density for the number of seedlings in R_{ij} (the Poisson density). Finally let

$$q_{ij}(m, x_1, u_1, \ldots, x_m, u_m) = f_{ij}(m)g_{ij}(x_1, u_1, \ldots, x_m, u_m|m).$$

By the properties of the Poisson spatial process

$$q_{ij}(m, x_1, u_1, \ldots, x_m, u_m) = q_{ab}(m, x_1, u_1, \ldots, x_m, u_m) \tag{B3}$$

for any two areas, R_{ij} and R_{ab}.

We define the conditional density of Y''_{ij}, given the number and adjusted spatial locations of seedlings inside R_{ij}, as $c_{ij}(y|m, x_1, u_1, \ldots, x_m, u_m)$. Because the same functions are used for the survivorship and fecundity predictors in each grid square

$$c_{ij}(y|m, x_1, u_1, \ldots, x_m, u_m) = c_{ab}(y|m, x_1, u_1, \ldots, x_m, u_m), \tag{B4}$$

for any two areas $(i, j) \neq (a, b)$. The consequence of (B3) and (B4) is that the Y''_{ij}, $i = (-\infty, \infty), j = (-\infty, \infty)$, are identically distributed random variables.

Let Γ_{ij} be the region between the borders of R_{ij} and R''_{ij}. The area of Γ_{ij} is labeled A_Γ, and is equal to $4[V(r_f + r_s) - (r_f + r_s)^2]$. Also, suppose that $A_{R''}$ is the area of R''_{ij}. This area is equal to $(V - 2r_s - 2r_f)^2$ and so

$$\lim_{V\to\infty} \frac{A_\Gamma}{A_{R''}} = 0. \tag{B5}$$

Equation (B5) states that, if V is large, then R''_{ij} occupies most of the area within R_{ij}. Because yield is typically proportional to area, we expect that, when V is large, most of the yield of R_{ij} will be produced within R''_{ij}. It is, in fact, straightforward to prove the following: Suppose that, for any $V > 2r_s + 2r_f$, there is a positive probability that $Y''_{ij} > 0$. Further suppose that the fecundity of plants has a finite upper bound. Then

$$\lim_{\substack{V\to\infty \\ \alpha\to\infty}} \frac{\sum_{i=-\alpha}^{\alpha} \sum_{j=-\alpha}^{\alpha} Y^{\Gamma}_{ij}}{\sum_{i=-\alpha}^{\alpha} \sum_{j=-\alpha}^{\alpha} Y''_{ij}} = 0 \tag{B6}$$

where Y^{Γ}_{ij} is the yield of the region Γ_{ij}. Thus, if V is sufficiently large

$$\lim_{\alpha\to\infty} \frac{\sum_{i=-\alpha}^{\alpha} \sum_{j=-\alpha}^{\alpha} Y''_{ij}}{\sum_{i=-\alpha}^{\alpha} \sum_{j=-\alpha}^{\alpha} 1} \simeq \lim_{\alpha\to\infty} \frac{\sum_{i=-\alpha}^{\alpha} \sum_{j=-\alpha}^{\alpha} Y_{ij}}{\sum_{i=-\alpha}^{\alpha} \sum_{j=-\alpha}^{\alpha} 1} = S, \tag{B7}$$

where Y_{ij} is the yield of R_{ij}, and S is mean population density of seeds produced on the infinite plane. Because the Y''_{ij} are independent and identically distributed

$$E(Y''_{ij}) = \lim_{\alpha \to \infty} \frac{\sum_{i=-\alpha}^{\alpha} \sum_{j=-\alpha}^{\alpha} Y''_{ij}}{\sum_{i=-\alpha}^{\alpha} \sum_{j=-\alpha}^{\alpha} 1} \tag{B8}$$

where $E(Y''_{ij})$ is the expectation of Y''_{ij}.

In what follows, we assume that V is large, and use the approximation: $E(Y''_{ij}) \simeq S$.

With these preliminaries, we now derive a probability density for the number of seedlings that germinate in the second generation within a small region, τ, of area A_τ. To simplify the notation we first adjust the location of the origin and the grid framework so that the region, τ, contains the origin.

We assume that the dispersal function for a seedling $L(d_{\mathbf{uv}})$ depends only on the distance, $d_{\mathbf{uv}}$, between the mother's location vector, $\mathbf{v}$, and the seedling's location vector, $\mathbf{u}$. Thus the density function $L(d_{\mathbf{uv}})$ is symmetric: $L(d_{\mathbf{xy}}) = L(d_{\mathbf{yx}})$. One may also interpret $L(d_{\mathbf{uv}})$ as the dispersal function for the location of a seed immediately prior to germination.

The distance between any plant in R_{ij} and any point in τ may be written as $\sqrt{i^2 + j^2} + \epsilon$ (ϵ gives the difference between the actual distance and $\sqrt{i^2 + j^2}$). Now, suppose that the mean dispersal distance of seeds is $\bar{d}$, and that $\bar{d}$ is large relative to V and to the largest linear dimension (i.e., length) of τ. Under these conditions, and for many biologically reasonable dispersal functions, we may approximate $L(\sqrt{i^2 + j^2} + \epsilon)$ by $L(\sqrt{i^2 + j^2})$. For example, if the dispersal function is the exponential density

$$L(\sqrt{i^2 + j^2} + \epsilon) = \frac{1}{\theta \bar{d}} \exp\left[-\left(\frac{\sqrt{i^2 + j^2} + \epsilon}{\bar{d}}\right)\right] \tag{B9}$$

where θ is a normalizing constant, then

$$L(\sqrt{i^2 + j^2} + \epsilon) = L(\sqrt{i^2 + j^2}) - \frac{\epsilon}{\theta \bar{d}^2} \exp\left[-\left(\frac{\sqrt{i^2 + j^2}}{\bar{d}}\right)\right] + 0(\epsilon^2/\bar{d}^3).$$

Here, $0(\epsilon^2/\bar{d}^3)$ means terms of order $\epsilon^2/\bar{d}^3$. Thus, if $\bar{d} \gg \epsilon$

$$L(\sqrt{i^2 + j^2} + \epsilon) \simeq L(\sqrt{i^2 + j^2}). \tag{B10}$$

Let $H(y)$ be the probability density for Y''_{ij}. Using the approximation (B10), we write the probability that k seeds will disperse from R''_{ij} to τ as

$$\Phi(k) = \sum_{y=k}^{\infty} H(y) \binom{y}{k} \delta_{ij}^k (1 - \delta_{ij})^{y-k}$$

$$\delta_{ij} = \int_\tau L(\sqrt{i^2 + j^2})\, d\mathbf{u} = L(\sqrt{i^2 + j^2})\, A_\tau.$$

The probability generating function for the number of seeds that disperse from R''_{ij} to τ is

$$\phi(s) = \sum_{k=0}^{\infty} \sum_{y=k}^{\infty} H(y) \binom{y}{k} \delta_{ij}^k (1 - \delta_{ij})^{y-k} s^k$$

$$= \sum_{y=0}^{\infty} H(y) \sum_{k=0}^{y} \binom{y}{k} \delta_{ij}^k (1 - \delta_{ij})^{y-k} s^k$$

$$= \sum_{y=0}^{\infty} H(y)\,[1 + \delta_{ij}(s - 1)]^y$$

$$= h[1 + \delta_{ij}(s - 1)]$$

where $h(w)$, $w = 1 + \delta_{ij}(s - 1)$, is the generating function for Y''_{ij}.

Because the Y''_{ij}, $i = (-\infty,\infty)$, $j = (-\infty,\infty)$, are independent and identically distributed, the generating function for the total number of seeds that disperse from the R''_{ij} to τ is simply the product of the generating functions for the numbers of seeds that disperse from each area R''_{ij}, $i = (-\infty,\infty)$, $j = (-\infty,\infty)$, to τ:

$$\psi(s) = \prod_{i=-\infty}^{\infty} \prod_{j=-\infty}^{\infty} h[1 + \delta_{ij}(s - 1)]$$

$$\log[\psi(s)] = \sum_{i=-\infty}^{\infty} \sum_{j=-\infty}^{\infty} \log\left\{\sum_{y=0}^{\infty} H(y)\,[1 + \delta_{ij}(s - 1)]^y\right\}. \tag{B11}$$

Recall that $\delta_{ij} = A_\tau L(\sqrt{i^2 + j^2})$. For many biologically reasonable dispersal functions, if the mean dispersal distance of seeds is large relative to A_τ, then the probability is small that any given seed will disperse into τ. For example, if $L(d_{uv})$ is given by (B9), then

$$\delta_{ij} = \frac{A_\tau}{\theta \bar{d}} \exp\left(\frac{-\sqrt{i^2 + j^2}}{\bar{d}}\right), \text{ and } \lim_{\frac{A_\tau}{\bar{d}} \to 0} \delta_{ij} = 0.$$

If δ_{ij}, $i = (-\infty,\infty)$, $j = (-\infty,\infty)$ is small, then

$$\log\left\{\sum_{y=0}^{\infty} H(y)\,[1 + \delta_{ij}(s - 1)]^y\right\} = \log\left\{\sum_{y=0}^{\infty} H(y)\,[1 + y\delta_{ij}(s - 1) + 0(\delta_{ij}^2)]\right\}$$

$$= \log[1 + E(Y''_{ij})\delta_{ij}(s - 1) + 0(\delta_{ij}^2)]$$

$$\simeq E(Y''_{ij})\delta_{ij}(s - 1).$$

Recall that $S \simeq E(Y''_{ij})$ (see [B7] and [B8]). Using this approximation, we rewrite (B11) as

$$\log[\psi(s)] \simeq \sum_{i=-\infty}^{\infty} \sum_{j=-\infty}^{\infty} [E(Y''_{ij})\delta_{ij}(s - 1)]$$

$$\simeq SA_\tau(s - 1) \sum_{i=-\infty}^{\infty} \sum_{j=-\infty}^{\infty} L(\sqrt{i^2 + j^2})$$

$$\simeq SA_\tau(s - 1)$$

$$\psi(s) \simeq e^{SA_\tau(s-1)}.$$

This is the probability generating function for a Poisson random variable. To summarize, if dispersal is sufficiently large, then the probability that there are k seeds in τ, immediately prior to germination, is approximately

$$\frac{e^{-SA_\tau}(SA_\tau)^k}{k!}.$$

We now use the probability of germination, g, together with the binomial density, to derive the probability that there are m second-generation seedlings in τ

$$\text{Probability that there are } m \text{ second-generation seedlings in } \tau = \sum_{k=m}^{\infty} \frac{e^{-SA_\tau}(SA_\tau)^k}{k!}\binom{k}{m} g^m (1-g)^{k-m}$$

$$= \frac{e^{-SA_\tau}(SA_\tau g)^m}{m!} \sum_{k=m}^{\infty} \frac{[SA_\tau(1-g)]^{k-m}}{(k-m)!}$$

$$= \frac{e^{-SA_\tau}(gSA_\tau)^m}{m!} e^{SA_\tau(1-g)}$$

$$= \frac{e^{-gSA_\tau}(gSA_\tau)^m}{m!}.$$

Thus, the probability that m seedlings germinate within τ during the second generation is given by the Poisson distribution with the mean equal to the average population density of seedlings on the plane.

APPENDIX C

1. Here, we derive average fecundity $[F(S_t)]$ for cases in which the survivorship predictor is $z(n)$ (n is the number of neighbors), the SFP is $f_s(n)$, and the radii of the fecundity and survivorship predictor neighborhoods (r_f and r_s) are not equal. We set the spatial scale such that $\pi r_s^2 = 1$. If $r_f > r_s$

$$F(S_t) = \sum_{n=0}^{\infty}\sum_{m=0}^{\infty}\left[\frac{e^{-S_tg}(S_tg)^m z(m)}{m!\, Z(S_t)}\right]\left(\frac{e^{-\lambda}\lambda^n}{n!}\right)[f_s(n+m)],$$

$$\lambda = S_tg(\pi r_f^2 - 1).$$

If $r_s > r_f$

$$F(S_t) = \sum_{m=0}^{\infty}\sum_{n=0}^{m}\left[\frac{e^{-S_tg}(S_tg)^m z(m)}{m!\, Z(S_t)}\right]\left[\binom{m}{n}(\pi r_f^2)^n(1-\pi r_f^2)^{m-n}\right][f_s(n)].$$

2. In this section, we derive average fecundity $[F(S_t)]$, for the case in which the survivorship predictor is a constant, P, and the AFP is $M/(1+cI)$. Here, I is $\Sigma_{i=1}^{n}[1-(d_i/r_f)^2]$; I is assumed to equal zero if n equals zero, d_i is the distance to the ith neighbor, r_f is the neighborhood radius of the AFP, and other symbols are as before (see Silander and Pacala [1985] for a discussion of this fecundity predictor). Recall that the locations of neighbors are independent random vectors and that the location of each neighbor is uniformly distributed over the neighborhood circle. Thus, the random variables d_i, $(d_1, d_2, \ldots, d_n)$, are independent and identically distributed, with density function: $D(x) = 2x/r_f^2$. Using this fact, it is straightforward to prove that the random variable, γ_i, defined as $\gamma_i = (d_i/r_f)^2$, is uniformly distributed over the interval (0, 1). Furthermore, the γ_i, $[i = (1, n)]$ are independent and identically distributed. Thus, if: $\Lambda = \Sigma_{i=1}^{n}\gamma_i$, then Λ is the sum of n independent

and uniformly distributed random variables. We know from Feller (1971) that the density function $U_n(z)$ of Λ is

$$U_n(z) = \frac{1}{(n-1)!} \sum_{a=0}^{n} (-1)^a \binom{n}{a} (z-a)_+^{n-1}, \quad n \geq 1.$$

Here, the notation, $(z-a)_+^{n-1}$, means $\dfrac{(z-a)^{n-1} + |(z-a)^{n-1}|}{2}$.

We can rewrite the fecundity predictor, $M/(1+cI)$, in terms of the variables Λ and n: $M/(1+cn-c\Lambda)$. Thus $F(S_t)$ is

$$F(S_t) = Me^{-PS_tg} + \sum_{b=1}^{\infty} \left[\frac{e^{-PS_tg}(PS_tg)^b}{b!} \int_0^b U_b(z) \frac{M}{1+cb-cz} dz \right].$$

LITERATURE CITED

Antonovics, J., and D. A. Levin. 1980. The ecological and genetic consequences of density-dependent regulation in plants. Annu. Rev. Ecol. Syst. 11:411–452.

Bartlett, M. S. 1960. Stochastic populations models. Methuen, New York.

DeAngelis, D. L., C. C. Travis, and W. M. Post. 1979. Persistence and stability of seed-dispersed species in a patchy environment. Theor. Popul. Biol. 16:107–125.

Feller, W. 1968. An introduction to probability theory and its applications. Vol. I. Wiley, New York.

———. 1971. An introduction to probability theory and its applications. Vol. II. Wiley, New York.

Harper, J. L. 1977. Population biology of plants. Academic Press, New York.

Hoel, P. G., C. D. Port, and C. J. Stone. 1971. Introduction to probability theory. Houghton Mifflin, Boston.

Karlin, S., and H. M. Taylor. 1975. A first course in stochastic processes. Academic Press, New York.

———. 1981. A second course in stochastic processes. Academic Press, New York.

MacDonald, N., and A. R. Watkinson. 1981. Models of an annual plant population with a seedbank. J. Theor. Biol. 93:643–653.

Mack, R. N., and J. L. Harper. 1977. Interference in dune annuals: spatial pattern and neighborhood effects. J. Ecol. 65:345–363.

May, R. M., and G. Oster. 1976. Bifurcations and dynamic complexity in simple ecological models. Am. Nat. 110:573–599.

Myerscough, P. J., and J. K. Marshall. 1973. Population dynamics *Arabidopsis thaliana* (L.) Heynh. strain 'estland' at different densities and nutrient levels. New Phytol. 72:597–617.

Palmblad, I. G. 1968. Competition in experimental populations of weeds with emphasis on the regulation of population size. Ecology 49:26–34.

Pielou, E. C. 1969. An introduction to mathematical ecology. Wiley, New York.

Schaffer, W. M., and E. G. Leigh. 1976. The prospective role of mathematical theory in plant ecology. Syst. Bot. 1:209–232.

Silander, J. A., and S. W. Pacala. 1985. Neighborhood predictors of plant performance. Oecologia (in press).

Silvertown, J. W. 1982. Introduction to plant population ecology. Longman, New York.

Tilman, D. 1982. Resource competition and community structure. Princeton University Press, Princeton, N.J.

Waller, D. M. 1981. Neighborhood competition in several violet populations. Oecologia 51:116–122.

Watkinson, A. R. 1980. Density-dependence in single-species populations of plants. J. Theor. Biol. 83:345–357.

Watkinson, A. R., W. M. Lonsdale, and L. G. Firbank. 1983. A neighborhood approach to self-thinning. Oecologia 56:381–384.

Weiner, J. 1982. A neighborhood model of annual-plant interference. Ecology 63:1237–1241.

Weiner, J., and P. T. Conte. 1981. Dispersal and neighborhood effects in an annual plant competition model. Ecol. Model. 13:131–147.

Werner, P. A. 1976. Ecology of plant populations in seasonal environments. Syst. Bot. 1:246–268.