

## DISPERSAL AND NEIGHBORHOOD EFFECTS IN AN ANNUAL PLANT COMPETITION MODEL

JACOB WEINER\*

*Department of Biology, University of Oregon, Eugene, OR 97403 (U.S.A.)*

PAUL T. CONTE\*\*

*Department of Computer Science, University of Oregon, Eugene, OR 97403 (U.S.A.)*

(Accepted for publication 2 September 1980)

### ABSTRACT

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

A spatial simulation model of annual plant interference which employs dispersal and neighborhood effects is developed and implemented with a computer program. The following hypotheses are observed to be consistent with the behavior of the model:

(1) Dispersal rates are extremely important in determining the rate at which a species can colonize or eliminate an inferior competitor from an area.

(2) Dispersal rates and local competition result in spatial patterns in plant populations which retard or prevent competitive elimination under conditions where it would be expected from non-spatial models. If interspecific competition is more intense than intraspecific competition, a mosaic of patches each dominated by one species will develop, but these patches may be in equilibrium.

The inclusion of space in a plant competition model, even in a crude way, results in behavior which is significantly different from that of non-spatial models.

### INTRODUCTION

Darwin, perhaps the greatest ecologist, had a continuous preoccupation with numbers of organisms (Harper, 1967). Ecology has since focused on the factors determining the abundance and distributions of organisms. Types of interaction referred to as 'competition' have been considered by many

---

\* Present address: Department of Biology, Swarthmore College, Swarthmore, PA 19081, U.S.A.

\*\* Present address: Computing Center, University of Oregon, Eugene, OR 97403, U.S.A.

ecologists to be the most significant biotic factors affecting organisms' distribution, population size and structure, and evolution (Krebs, 1977). Competition has been the subject of much experimental and theoretical investigation during this century. Hypotheses concerning the ability of competing species to coexist in space and time have occupied a central place in these investigations.

Models can be useful in exploring hypotheses. Although models cannot test hypotheses in the same sense that empirical studies do, they can be employed as logical tests. As such, models demonstrate the logical correlates and implications of a hypothesis and are capable of disproving hypotheses. Modeling studies are often a good first step in developing and testing a hypothesis, answering the question "Is this possible and reasonable?"

Attempts to model competition in animal populations have been much more successful than similar attempts with plants (Harper, 1967; Schaffer and Leigh, 1976; Solbrig, 1976). There are two fundamental reasons for this. Because of the high degree of plasticity of plants (Bradshaw, 1967) and vegetative reproduction, number of individuals is not as good a measure of plant populations as it is of animal populations. Also, the immobility of plants, except in the seed stage, makes it impossible, in the view of many workers, to describe plant populations adequately without including their spatial pattern in the description (Mack and Harper, 1977). Experimentally, over a wide range of density conditions, growth and reproduction vary greatly as the spatial pattern is varied (Sakai, 1957; Harper, 1961, 1965). Density is not very useful in predicting the behavior of plant populations under experimental conditions unless the spatial pattern of the plants is a controlled variable. Whereas theoretical animal competition models have described the population in terms of density over time and the effect of density in changing the growth rate of the population, a plant competition model might do better to analyze the effect that neighbors have on the reproduction of individuals. But, if a model of this process is to be useful, it will have to incorporate many generations.

A computer-based simulation model which views annual plant populations as aggregated neighborhoods has been developed. Seed production of each species within an aggregate is a function of the number and species of each individual's neighbors. These seeds are then distributed in two-dimensional space. The seeds then compete with each other for survival in a similar fashion. The two-dimensional environment is homogeneous except for heterogeneity in the spatial pattern of the populations, which is both a cause and an effect of dispersal and the interaction of individuals.

The objective here is to explore the following hypotheses, which may be helpful in explaining plant diversity in nature:

(1) Dispersal rates will have a marked effect on the rate with which a species can colonize an area or eliminate an inferior competitor from an area.

(2) Dispersal rates and local competition may generate spatial patterns in plants which can retard or prevent competitive elimination under conditions where it would be expected from non-spatial models. This may occur because localized competition and dispersal prevent a species with an overall advantage in numbers from increasing its numbers through time, because groups may acquire territories from which they resist displacement (Levin, 1974), or because the heterogeneous dispersion of individuals increases the effect of intraspecific encounters. Spatial patterning arising from dispersal and competition acts as a buffer against competitive elimination. The specific hypothesis here is that, contrary to the behavior of non-spatial models, stable coexistence of two competing species can occur when interspecific competition is more intense than intraspecific competition, if the competition is local and seed dispersal is biased towards its source. Species may acquire territories from which the other species are excluded, but these sets of patches can be in equilibrium.

## THE MODEL

### *Assumptions*

The model incorporates:

- (1) A three-stage life cycle:
  - (a) adults (seeds surviving to adulthood);
  - (b) seeds to be dispersed from adults;
  - (c) seeds dispersed in space.
- (2) Local neighborhood competition which affects the performance of individuals.

Mortality occurs between stages c and a, and plasticity and/or mortality occurs between stages a and b. Reasonable assumptions or guesses are made about the quantitative expression of these factors from what is known of these phenomena. The model is designed to be as general as possible so that it can be easily adapted as more becomes known about the quantification of competition and dispersal.

Such a model, which is an attempt to focus on certain aspects of nature, must of necessity make simplifying assumptions which should be made explicit. The assumptions of this model are:

- (1) The environment is spatially and temporally homogeneous except for heterogeneity due to the populations themselves. Only competition, random

variation, and an individual's potential determine what it will do. Competition alone is being considered. This is a simplification, but one which is often necessary for the study of competition and one which may hold true in certain situations.

(2) These theoretical populations are composed solely of annuals which grow, produce seeds, and die in one season (generation). Harper (1965) has pointed out that this makes annuals very suitable for the study of plant competition. It also makes them very suitable for modeling.

(3) The annual's growth is in synchrony. Seeds compete with seeds and adults compete with adults.

(4) The effect of an individual on another can be quantified.

(5) The effect of neighbors is negative, i.e. competitive, and the more neighbors an individual has, the more severe the effect of competition. But, as the number of neighbors increases, the effect of the addition of another individual decreases. The probability of survival and the extent of reproduction approach 0 asymptotically as the number of neighbors increases. Hence, as the population density goes up, the total seed output of an area rises but eventually levels off. This is a well-known plant density response (Harper, 1961).

(6) The nearer a neighbor is, the greater its effect.

(7) There is genetic uniformity or random variation of genotypes around a mean. Thus, evolution is not occurring at a rate fast enough to change the characteristics of each species within the periods modeled. All significant genotypic variation is interspecific. This is a risky assumption (Antonovics, 1976) but one which is necessary in the modeling of many ecological phenomena.

(8) Seed dispersal behavior is a property of each species and the pattern is not skewed. In actuality seed dispersal usually occurs in a somewhat asymmetric fashion, but there is no reason to believe that this would significantly affect the model. The degree of kurtosis of each species' dispersal pattern is under the modeler's control.

(9) There is no seed dormancy. Each seed attempts germination in the following season.

(10) The field exists isolated in space with seeds leaving the field, no seeds entering and a standard edge effect for adult competition.

### *Model description*

Attempts have been made to assess the effect of competition on individuals in terms of their neighbors (Mack and Harper, 1977; Weiner, 1978, 1981). The concept of a neighborhood has emerged as a convenient way of aggregating distances to neighbors. Thus, instead of a distance to each

neighbor, one has an average distance to all neighbors within each neighborhood. In addition to number and distance of neighbors, factors which might be used in describing the neighbor conditions experienced by an individual include their species, size, and angular dispersion. The job of the plant population modeler, using this approach, is to decide which of these factors are most important and useful and to find a mathematical expression which quantifies the relationship between these factors and the individual's growth or reproductive output. If one is studying annuals, the reproductive output is simply the seed production

$$R = f(R_{\max}, W)$$

where  $R$  is the seed production,  $R_{\max}$  is the production in the absence of competition, and  $W$  is the total effect of competition. Considering simultaneously growing annuals, and the number and species of neighbors within concentric neighborhoods of fixed size around an individual, the following equation is advanced (Weiner, 1978):

$$R = R_{\max} / 1 + \sum_{i=1}^p D_i \sum_{k=1}^s C_k N_{ik}$$

where  $R$  is the reproductive output of an individual (number or weight of seeds produced);  $R_{\max}$  is the reproductive output under the same abiotic conditions in the absence of neighbors;  $D_i$  is the effect of the  $i^{\text{th}}$  neighborhood;  $C_k$  is the effect of the  $k^{\text{th}}$  species;  $N_{ik}$  is the number of individuals of species  $k$  in neighborhood  $i$ ;  $p$  is the number of neighborhoods; and  $s$  is the number of species.

The different effects of species on each other and on themselves are expressed with competition coefficients, parallel to those of Lotka's (1925) and Volterra's (1926) competition equations except that the effect of competition is to reduce the reproduction of an individual rather than to reduce the growth rate of the population as a whole. In the simplest case, with one neighborhood and one species of neighbor this is essentially the reciprocal-yield relationship which has been most successfully used in predicting yield from density in monoculture (Kira et al., 1953; Holliday, 1960).

In the model, plants compete with plants in the above fashion and produce seeds which are dispersed through space from their point of origin. In the situation of simultaneously growing annuals, these seeds compete with their neighboring seeds similarly. Some seeds survive to adulthood and the process begins again. A version of the model with some degree of spatial aggregation can be implemented by a computer program. Aggregation is necessary to make the simulation tractable, for if neighborhoods were to be constructed and searched and seed dispersal patterns generated for each individual, modeling a population of any size would require computational

facilities usually reserved for air defence systems, not ecological modeling. By aggregating the model for logistic reasons, the notion of a truly individual view of interference and dispersal is compromised. Individuals are replaced by spatial aggregates of individuals each of which, if totally isolated, is similar to a non-spatial model. These aggregates are connected in space by dispersal and nearby adult interference effects. Hence, the spatially aggregated model is intermediate to non-spatial and individually oriented spatial models. As such, it is similar to other ecological models with spatial heterogeneity (e.g. Levin, 1974) with the exception that space and life history are viewed in a way which is more appropriate for plants.

In the computer simulation, two-dimensional space is divided into cells which can be thought of as hexagons. Each cell is surrounded by six equidistant cells. Cells represent aggregated locations; thus the cell itself is the immediate neighborhood of each plant or seed in that cell. The six equidistant cells comprise the next neighborhood. Thus, all individuals within a cell are considered to be the same distance from one another. In considering competition from nearby cells and dispersal, each individual is considered to be located in the center of the cell it occupies. The parameters' values determine how many individuals can occupy a cell. When cell populations are low (fewer than five adults per cell) the model's cells most closely approximate individual-centered neighborhoods.

Seeds compete with seeds only within their immediate neighborhood (i.e. cell) and the probability of an individual of species  $j$  surviving to adulthood  $R_j$  is a function of two values:

(1)  $W_j$  is the total effect of the number and species of its competitors

$$W_j = \sum_{k=1}^s C_{jk} N_k - C_{jj} \quad (1)$$

where  $W_j$  is the total effect of competition;  $C_{jk}$  is the effect of a seed of species  $k$  on a seed of species  $j$ ;  $N_k$  is the number of seeds of species  $k$  in the cell; and  $s$  is the number of species present. The  $C_{jj}$  term is subtracted so that the plant will not be competing with itself.

(2)  $K_j$  is the probability of a seed of species  $j$  surviving in the absence of any competition. The relationship is hyperbolic

$$R_j = \frac{K_j}{1 + W_j} \quad (2)$$

Within a cell, the expected number of seeds of species  $j$  [ $N(\text{seeds})_j$ ] that survive to the adult stage [ $N(\text{adults})_j$ ] is simply the probability that a single seed of species  $j$  will survive multiplied by the population of seeds of species  $j$  in that cell

$$N(\text{seeds})_j \times R_j = N(\text{adults})_j$$

The number of seeds which survive to adulthood in a cell can be treated as a mean value, around which there is random normal variation.

Adults compete in a similar fashion except that competition from cells around the individual's cell can also be considered. The equation for the total effect of competition by adults is

$$W_j = \sum_{i=1}^p D_i \sum_{k=1}^s C_{jk} N_{ik} - D_i C_{jj}$$

where  $W_j$ ,  $C_{jk}$ ,  $N_{ik}$  and  $s$  are adult equivalents to the same values in eq. 1,  $D_i$  is the effect of neighborhood  $i$  and  $p$  is the number of neighborhoods. The more distant a neighborhood, the smaller the effect of an individual within it. The number of neighborhoods considered and their relative effects are correlates of the degree of localization of adult interference effects, and are under the modeler's control. In implementing the simulations, neighborhoods have been limited to the immediate cell and its ring of six contiguous cells.

The number of seeds produced by an adult is determined in the same fashion as the probability of a seed's surviving (eq. 2), with  $R_j$  = the number of seeds produced by an adult and  $K_j$  = the maximum seed production of an individual of species  $j$ . Total production of seeds of species  $j$  is equal to the number of seeds produced by an individual of species  $j$  in that cell times the population of species  $j$  in the cell

$$N(\text{adults})_j \times R_j = N(\text{seeds produced})_j$$

Seeds of each species produced within a cell are dispersed through the two-dimensional space into the neighborhoods and beyond in proportions that are a characteristic of and therefore constant for each species. Dispersal is determined on the basis of what fraction of seeds falls into the immediate cell, into the first ring of cells, and beyond. The number of seeds entering a cell from another cell can also be treated as a mean value around which there is random normal variation. Seeds dispersed beyond the two neighborhoods occur in higher frequency toward the cell of origin. These seeds land in cells and the cycle starts for the next generation. The model is summarized in Fig. 1.

This spatial model differs most significantly from non-spatial models such as the Lotka–Volterra equations in that:

- (1) Competition is local and viewed from the individual level. The effect of neighbors is to reduce an individual's probability of survival and reproductive output. Effects on the population occur through this mechanism.
- (2) Dispersal is included.
- (3) Several elements can be treated stochastically rather than deterministically. The number of seeds of each species entering a cell from each source

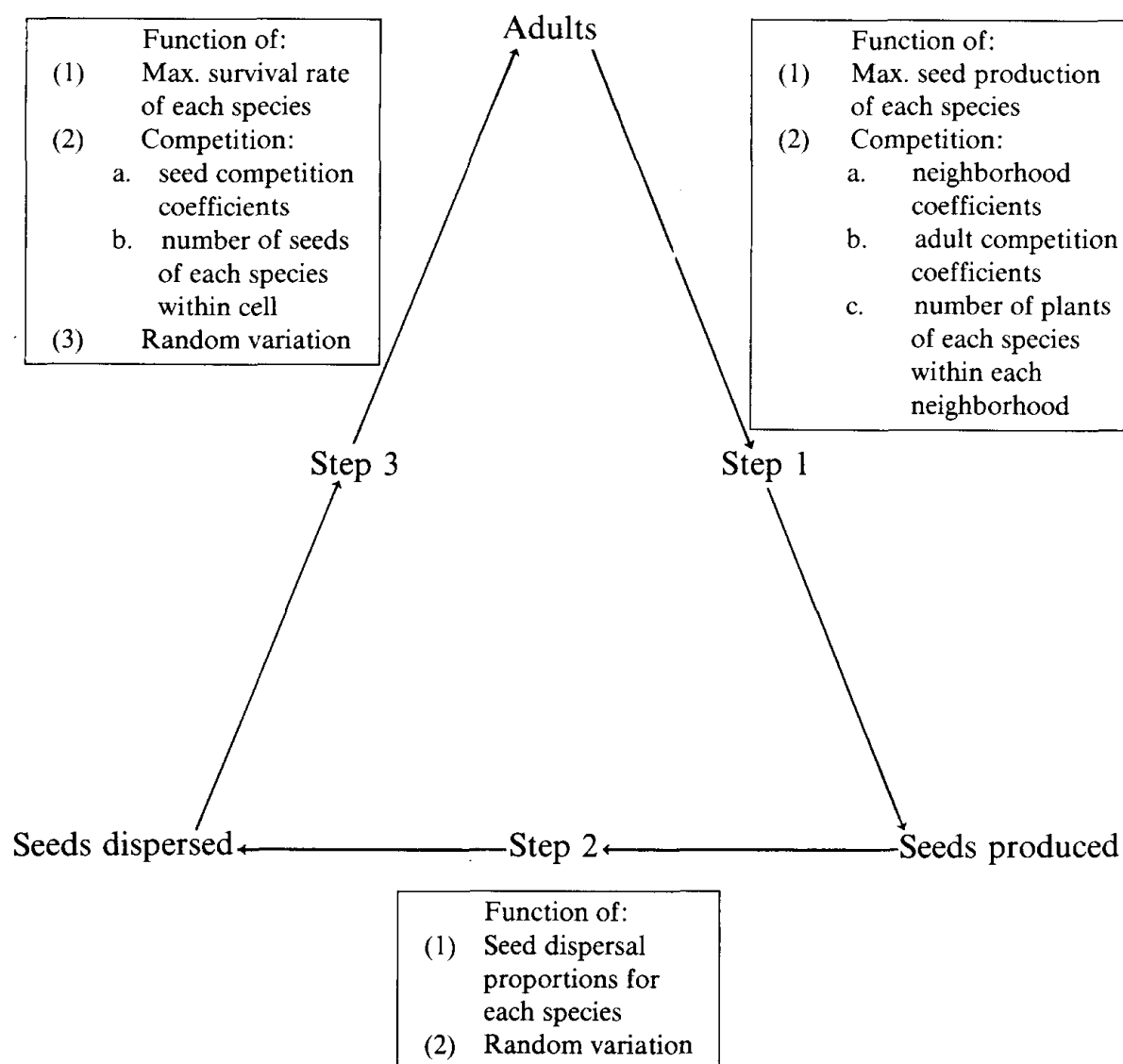


Fig. 1. Summary of simulation model.

and the number of seeds of each species which survive within each cell are treated as mean values, around which there is random normal variation.

A computer program was written in ALGOL to implement the model.

## RESULTS AND DISCUSSION

### *Effect of dispersal rates on population growth and competitive elimination*

#### *Dispersal and one species population growth*

The first hypothesis is that the dispersal rate affects the rate of population growth from a few individuals to the carrying capacity of an area. This hypothesis, which has been made implicitly by several workers (e.g. Gadgil,



1971; Harper, 1977), is that the more dispersal is localized, the slower the growth rate of the population will be. In our model, maximum number of adults which can survive within a cell in monoculture can be calculated as a limit

$$R_j = N \frac{K_j}{1 + C(N-1)} = \frac{K_j}{1/N + C - C/N} \quad \text{as } N \rightarrow \infty, R_j \rightarrow K_j/C$$

Starting with one individual and without changing other parameters, three dispersal rates were simulated. In the first run [Example 1, run a (Fig. 2)], 65% of the seeds produced by an individual fall into the first neighborhood (immediate cell), 35% into the second neighborhood, and none are dispersed beyond the second neighborhood. Run b is different in that the percentage of seeds distributed to the second neighborhood is decreased by 5% and this number is dispersed 'long distance', i.e. beyond the second neighborhood. In run c, 60% of the propagules enter the first neighborhood, 30% enter the second, and 10% go farther.

The results demonstrate that with increased values for long distance dispersal the population growth rate is increased (Fig. 2). Without long-distance dispersal population growth occurs within a cell and contiguous cells as propagules are dispersed. The presence of long-distance dispersal in run b provides for the dispersal of ten seeds from the original parent to cells beyond the first two neighborhoods. Of these, one survives to adulthood and this represents a new center for population growth. When the number of propagules dispersed beyond the neighborhoods is increased to 10%, two distant seeds survive. The ability to get propagules to uncolonized areas is limiting population growth in runs a and b.

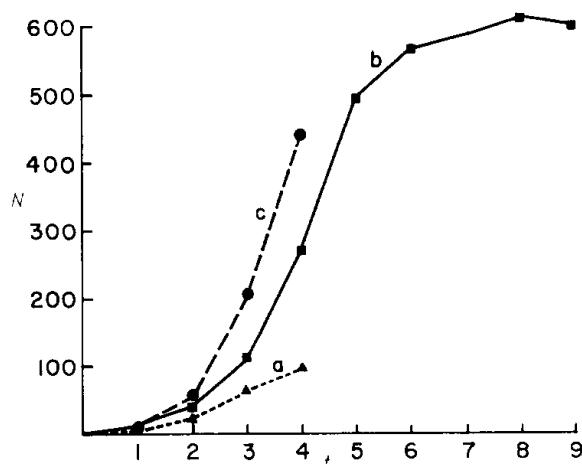


Fig. 2. (Example 1) Population growth from one individual in a large field demonstrating effects of long range dispersal. Population size as a function of time.

Thus, the presence or absence of long-distance dispersal is extremely important in determining the population growth rate. Without long-distance dispersal, even if relatively rare, equilibrium is postponed. The overall population growth behavior (Fig. 2) conforms to logistic growth (Pearl and Reed, 1920) but the steepness of the sigmoid curve is determined by dispersal rates as well as fecundity.

### *Competitive advantage and dispersal*

Similar results are observed with respect to the role of dispersal on the rate with which a superior competitor eliminated an inferior one. When long-distance dispersal does not occur, the length of time required for elimination is greatly increased. In one series of runs, when 20% of the seeds of both species were dispersed beyond the second neighborhood, the time required for competitive elimination was reduced by 80% over identical runs without long-range dispersal.

While dispersal rates do not seem to affect the ability of one species to eliminate the other when there is a clear competitive advantage, the rate of elimination is affected. Changes in the fraction of seeds distributed to surrounding cells and beyond change the number of generations required for elimination.

If all offspring were so highly dispersed as to be random in space the model's behavior would essentially be that of one big cell, all individuals having an equal probability of interacting with one another. Random dispersal has been shown to have a homogenizing effect on population heterogeneity (Levin, 1976). Heterogeneity originating from restricted dispersal and local competition changes this, such that competitive elimination is retarded. Competitive elimination may be a very slow process. Until recently, theoreticians have been concerned primarily with the maintenance of diversity under equilibrium conditions. An emphasis on disequilibrium is developing among researchers (e.g. Connell, 1978; Huston, 1979). If competitive elimination is a very slow process, higher diversity than would occur under equilibrium conditions may be the rule. Forces which tend to retard elimination, i.e. lengthen the time required to reach equilibrium, should increase diversity (Huston, 1979) and may be as important as those forces which act at equilibrium, since this state may rarely be achieved. Dispersal in plant populations may have an important role in retarding competitive elimination and, thus, increasing diversity.

### *Interspecific and intraspecific competition*

According to the now classical competition models of Lotka (1925) and Volterra (1926), if intraspecific competition is greater than interspecific

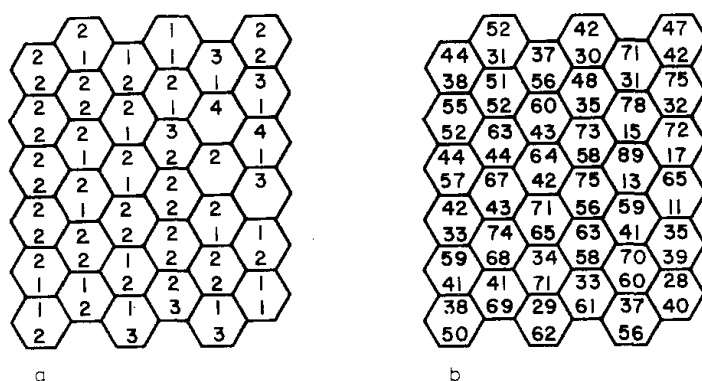


Fig. 3. Example 2a: (a) fifth generation adults after starting with five randomly placed individuals of each species. Intraspecific competition is more intense than interspecific competition within each cell, the number of individuals of species 1 is above the number of individuals of species 2; (b) sixth generation seeds.

competition, equilibrium coexistence of the two species should occur, but if interspecific competition is more intense an unstable equilibrium is the outcome, resulting in elimination of one of the two species. Cases of both types, greater interspecific competition and greater intraspecific competition, have been documented in plant competition experiments (Harper, 1977).

The effect of relative intra- and interspecific competition values on the spatial patterning of populations is illustrated in Example 2. When intraspecific competition is more intense (Example 2a) plants will tend to produce more seeds and seeds will be more likely to survive when in the presence of other species than when amongst their own type. Thus, five generations after starting with five randomly-placed adults of each species, cohabitation of almost every cell in the field has occurred (Fig. 3a). Seeds produced by and distributed from these adults are also well mixed interspecifically (Fig. 3b). Occupation of every cell in the field by adults of both species occurred in the next generation and equilibrium coexistence occurs as in the Lotka–Volterra models (Fig. 4).

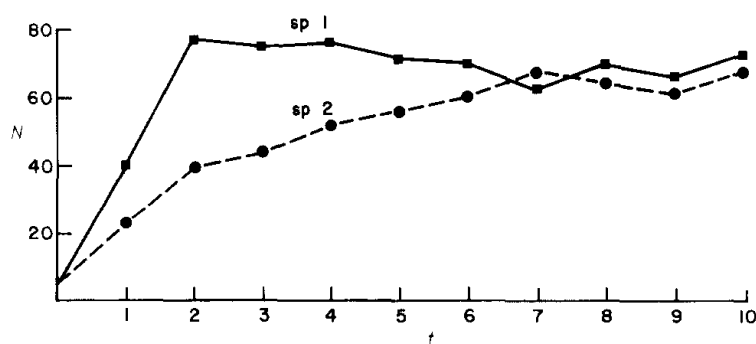


Fig. 4. Example 2a. Intraspecific competition is greater than interspecific competition. Population size as a function of time.

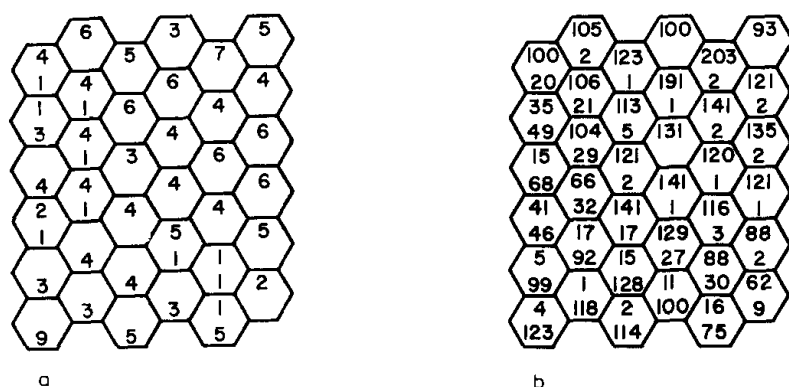


Fig. 5. Example 2b: (a) fifth generation adults. Interspecific competition is more intense than intraspecific competition. (Initial conditions are the same as in Example 2a.); (b) sixth-generation seeds.

When interspecific competition is more intense (Example 2b) groups tend to occupy somewhat exclusive territories which may overlap (Fig. 5a). In such a case seeds produced and distributed from individuals of different species are found cohabiting cells in general, but they occur in highly biased mixtures reflecting the territories occupied by their parents (Fig. 5b). The degree of cell cohabitation by adults of both species for Examples 2a and 2b is illustrated in Fig. 6. In the latter case there is a tendency for total population sizes to diverge, resulting in elimination of one of the species (Fig. 7). This is the unstable equilibrium behavior predicted from the Lotka-Volterra equations and with which the hypothesis is concerned.

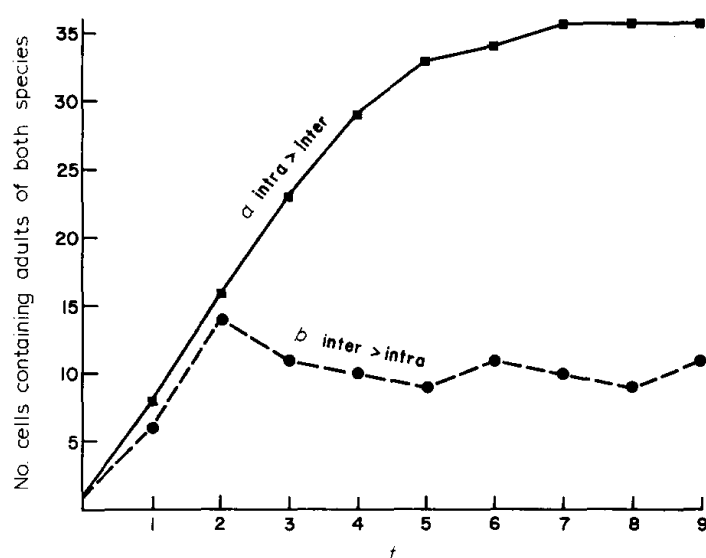


Fig. 6. Examples 2a and 2b. Number of cells containing adults of both species as a function of time.

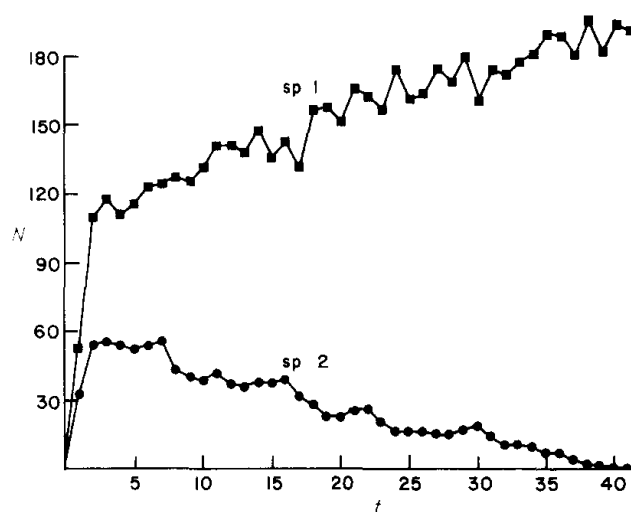


Fig. 7. Example 2b. Interspecific competition is greater than intraspecific competition. Population size as a function of time.

In the spatial model, it is observed that this instability occurs only when there is a high degree of mixing through dispersal. Seed dispersal proportions in Example 2b which result in instability are 60% to the first neighborhood, 30% to the second and 10% beyond for both species. When there is no long distance component of seed dispersal, such as in Example 2c where the dispersal proportions are 60% to the first neighborhood, 40% to the second, and none beyond, elimination does not occur (Fig. 8).

Further investigation of this result was undertaken. In Example 3 elimination occurs when interspecific seed competition values are higher than intraspecific values and seeds are widely dispersed (Fig. 9). A change in the initial advantage (Example 3b) results in elimination of the other species

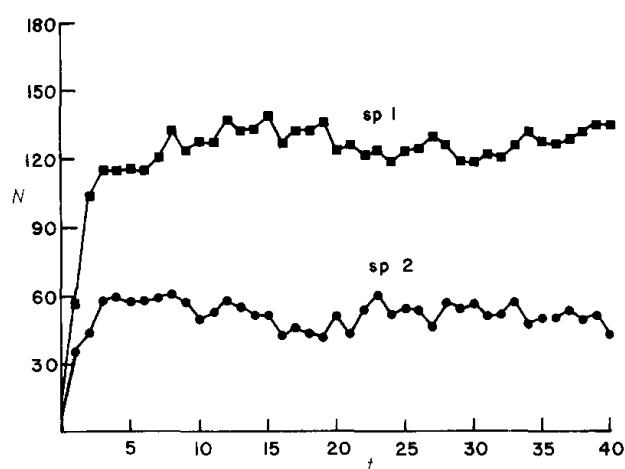


Fig. 8. Example 2c. Interspecific competition is greater than intraspecific competition and no long distance dispersal. Population size as a function of time.

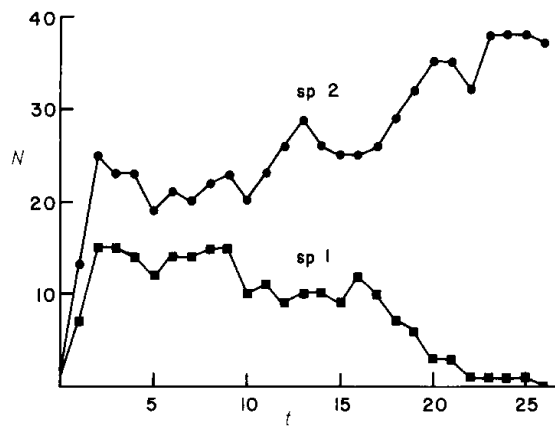


Fig. 9 (left). Example 3, run a. Unstable equilibrium, interspecific competition is greater than intraspecific, species 2 has initial advantage, seeds highly dispersed.

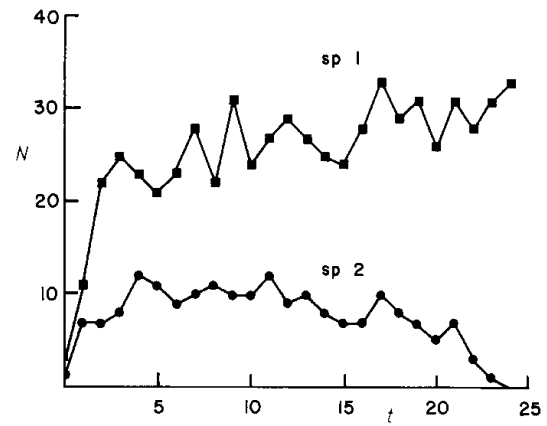


Fig. 10 (right). Example 3, run b. Parameters are the same as in run a except species 1 has initial advantage.

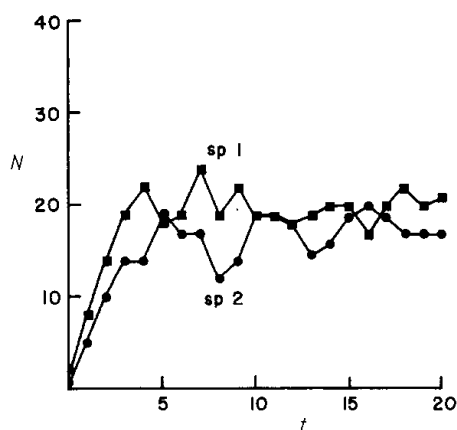


Fig. 11 (left). Example 3, run c. 'Unstable equilibrium', parameters are the same as in run b except seeds not highly dispersed.

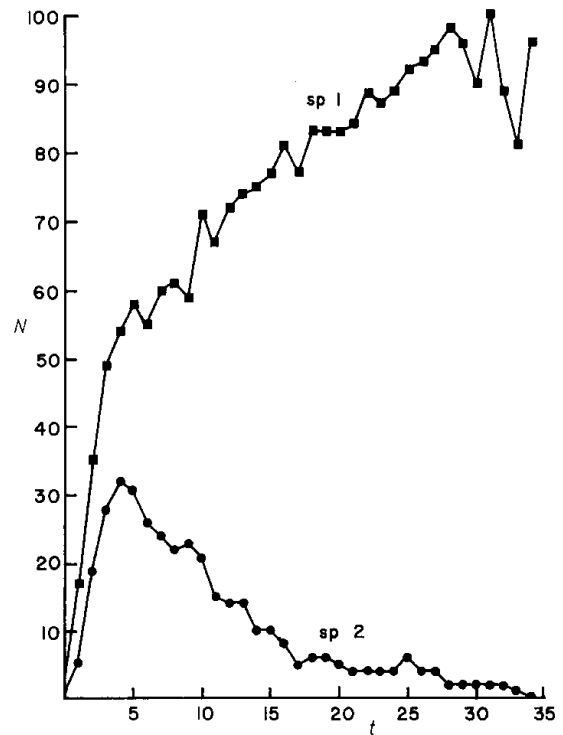


Fig. 12 (right). Example 4a. 'Unstable equilibrium' with long-range dispersal. Population size as a function of time.

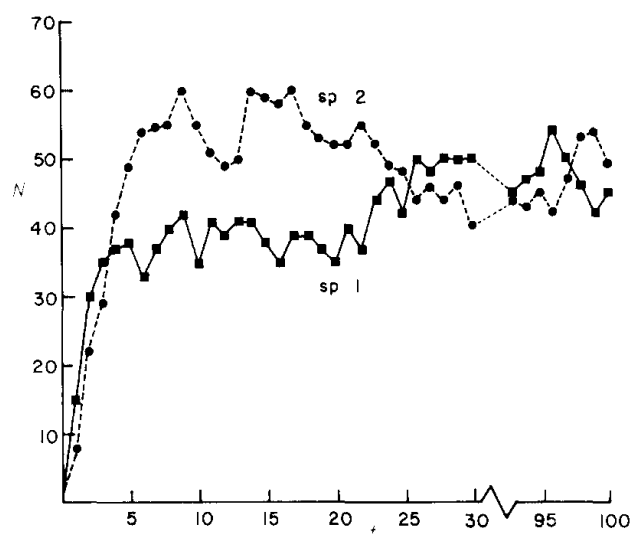


Fig. 13. Example 4b. 'Unstable equilibrium' without long-range dispersal.

(Fig. 10), demonstrating that unstable equilibrium behavior is, in fact, what is occurring. However, when long-distance dispersal is reduced (Example 3c), no tendency towards elimination is observed (Fig. 11). A third case is presented in Example 4. Here, both adults and seed interspecific competition values are 50% higher than their intraspecific counterparts. Initialization is with three randomly placed adults of species 1 and one of species 2. Again, when long-distance dispersal is present (Example 4a) elimination occurs (Fig. 12) but without it (Example 4b) the equilibrium is stabilized and equilibrium coexistence occurs (Fig. 13). This result has been retested under a wide variety of conditions including variations in initial conditions, neighborhood effects, and carrying capacities. When the competition values are symmetrical and neither species is inherently superior, unstable equilibrium behavior always depends upon significant long distance dispersal in this model. This is because the model treats competition and, to a lesser extent, dispersal as local phenomena.

If dispersal and the effect of neighbors were to occur over relatively large distances without diminution, the model's behavior would approach that of one large cell, which is not unlike the behavior of non-spatial models. Under such circumstances, if interspecific competition is greater than intraspecific competition each group will suppress the other population more than it suppresses its own population. If one group gains an advantage from initial conditions or random events it will exert greater pressure on the other group than the other group exerts on it because of its advantage in overall numbers. In the spatial model this overall advantage is expressed through dispersal, since competition occurs at a local level. If, however, dispersal is also a local phenomenon, the overall population sizes may have no effect on

what occurs locally. A minority species will be able to maintain its local advantages. An overall advantage gained by one group through initial conditions or random events may be maintained, but it does not increase through time. Thus, whole populations do not have a significant effect on what happens locally, and local subpopulations may be in equilibrium. This leads to a patchwork of monocultures or highly-biased mixtures. The genesis and maintenance of such mosaics in nature are often attributed to abiotic heterogeneity, but the model's behavior suggests that such spatial heterogeneity of the populations themselves can arise and be maintained through local competition and dispersal when interspecific competition is more intense than intraspecific competition.

### *Seed-bath effect*

The importance of the dense seed shadow under a parent annual in the model and in nature suggests either that this type of dispersal is selectively advantageous in many circumstances or that it is unavoidable. An annual plant that produces many seeds most of which fall nearby has a very good chance that at least one of its offspring will replace it in the location in the next generation. Janzen (1970), in discussing tropical trees, has suggested that the disadvantage for a seedling in being near its parent is more significant in determining the plants' distribution than the seed-bath effect, although he attributes this to predation rather than competition. Thus, selection should maximize long-distance dispersal, presumably by wind or animals. For annuals for which predation is not as intense as it is for tropical trees the strategy of producing many small seeds, most of which fall nearby, may be conservative in keeping the likelihood of an offspring replacing its parent high, while maintaining some degree of high risk-high reward long-distance dispersal. This is, in a sense, similar to producing two types of propagule: one highly dispersed with a low probability of survival, and another with low dispersal and a high probability of survival. The second propagule strategy is mimicked by putting many low-probability propagules in an already proven site which is likely to have fewer propagules of other individuals. This may help explain why seed dispersal polymorphisms are relatively rare. Another implication is that if the parent's site is a better risk than other places, optimally dispersed seeds will not be maximally dispersed.

### ACKNOWLEDGEMENTS

The authors thank S.A. Cook, P. Frank and J.D. Udovic for helpful comments and criticisms. This research was supported, in part, by PHS-NIH Training Grant 5T32 GM 0 7257.



## REFERENCES

- Antonovics, J., 1976. The new ecological genetics. *Syst. Bot.*, 1: 233–245.
- Bradshaw, A.D., 1967. Evolutionary significance of phenotypic plasticity in plants. *Adv. Genet.*, 13: 115–155.
- Connell, J.H., 1978. Diversity in tropical rain forests and coral reefs. *Science*, 199: 1302–1310.
- Gadgil, 1971. Dispersal: population consequences and evolution. *Ecology*, 52: 253–261.
- Harper, J.L., 1961. Approaches to the study of plant competition. In: *Mechanisms in Biological Competition*. Proc. 11th Symp. Soc. Exp. Biol. Academic Press, New York, NY., pp. 1–39.
- Harper, J.L., 1965. The nature and consequences of interference amongst plants. In: *Genetics Today*. Proc. 11th Intern. Cong. Gen., Vol. 2, The Hague, The Netherlands, pp. 465–482.
- Harper, J.L., 1967. A Darwinian approach to plant ecology. *J. Ecol.*, 55: 247–270.
- Harper, J.L., 1977. *Population Biology of Plants*. Academic Press, London.
- Holliday, R., 1960. Plant population and crop yield. *Nature (London)*, 186: 22–24.
- Huston, M., 1979. A general hypothesis of species diversity. *Am. Nat.*, 113: 81–101.
- Janzen, D.H., 1970. Herbivores and the number of tree species in tropical rain forests. *Am. Nat.*, 104: 501–528.
- Kira, T., Ogawa, H. and Sakazaki, N., 1953. Intraspecific competition among higher plants. I. Competition–density–yield interrelationship in regularly dispersed populations. *J. Inst. Polytech. Osaka Univ., Ser. D.*, 4: 2–15.
- Krebs, C.J., 1977. *Ecology: The Experimental Analysis of Distribution and Abundance*. Harper and Row, New York, NY.
- Levin, S.A., 1974. Dispersion and population interactions. *Am. Nat.*, 108: 207–228.
- Levin, S.A., 1976. Population dynamic models in heterogeneous environments. *Annu. Rev. Ecol. Syst.*, 7: 287–310.
- Lotka, A.J., 1925. *Elements of Physical Biology*. Reprinted in 1956 by Dover, New York, NY.
- Mack, R.N. and Harper, J.L., 1977. Interference in dune annuals: spatial pattern and neighborhood effects. *J. Ecol.*, 65: 345–363.
- Pearl, R. and Reed, L.J., 1920. On the growth rate of the population of the United States since 1790 and its mathematical representation. *Proc. Nat. Acad. Sci. U.S.A.*, 6: 275–288.
- Sakai, K., 1957. Studies on competition in plants. VII. Effect on competition of a varying number of competing and non-competing individuals. *J. Genet.*, 55: 227–234.
- Schaffer, W.M. and Leigh, E.G., 1976. The prospective role of mathematical theory in plant ecology. *Syst. Bot.*, 1: 209–233.
- Solbrig, O.T., 1976. Plant population biology: an overview. *Syst. Bot.*, 1: 202–208.
- Volterra, V., 1926. Fluctuations in the abundance of a species considered mathematically. *Nature (London)*, 118: 558–560.
- Weiner, J., 1978. Studies on interference in annual plants. Ph.D. Thesis, Univ. Oregon, Eugene, OR.
- Weiner, J., 1981. A neighborhood model of annual plant interference (submitted for publication).