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MODELS OF THE DEVELOPMENT OF SPATIAL PATTERN OF AN EVEN-AGED PLANT POPULATION OVER TIME

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ABSTRACT

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The development of spatial patterns of a single even-aged population in a homogeneous area was studied by means of simulation and analytical models. The simulation model was designed to reflect ecological reality as much as possible, simultaneously keeping a reasonable level of simplicity. Results of simulations were supported by analysis of a simplified and more mathematically tractable model. It was shown that the main factor causing the decrease of aggregation intensity or tendency to regularity in the course of population development is the competition among neighbouring individuals. Random patterns may be a result of changes of initial aggregated pattern caused by competition among neighbours. Hence, an observed random pattern is not evidence for the independence of individuals.

INTRODUCTION

Spatial pattern (distribution of individuals in space) is an important characteristic of populations of sedentary organisms. The study of changes of type and intensity of spatial pattern plays an important role in contemporary quantitative ecology (Greig-Smith, 1979). A number of questions connected with this problem remain unanswered, however.

Kent and Dress (1979, 1980) presented models of development of spatial patterns of natural even-aged forest stands over time. Under their modelling assumptions they have shown that both random and aggregated spatial patterns are preserved over time and a regular (lattice) spatial pattern tends to change into a random spatial pattern. These conclusions are given for a single generation of trees; no new individuals are permitted to arise during the time of development. A homogeneous area is considered.

There is, however, a lot of field data indicating that even-aged population of trees, shrubs and herbs tend to decrease the intensity of aggregation in the

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course of self-thinning, being initially distributed in clumps (Kershaw, 1963, 1973; Greig-Smith, 1964, 1979; Williams, et al., 1978) or tend to nearly regular distribution (Laessle, 1965; Moore and Bhadresa, 1978; Phillips and MacMahon, 1981; Prach, 1981; Tagawa, 1965). For example, Tagawa (1965) writes: "The following possibility was pointed out that the trees of overstory showed a trend of making regular distribution, when they were of nearly the same age and made densely closed canopy...". Ford (1975) found that regular pattern is maintained in uniformly planted trees of *Picea sitchensis*. It is impossible to explain the data of all the above quoted authors using models of Kent and Dress (1979, 1980). We suppose that a very important factor influencing the formation of spatial pattern of an even-aged population in a homogeneous area during its development is the mortality of particular individuals influenced by competitive action of their neighbours (cf. Laessle, 1965; Keister, 1972; Whipple, 1980; Symonides, 1983). The influence of neighbours is completely omitted from the models of Kent and Dress (1979, 1980). We propose simulation and analytical models of the spatial pattern development, both of which take into account the influence of neighbours. The simulation model was designed to reflect ecological reality as much as possible while keeping a reasonable level of simplicity. Results of simulations were supported by analysis of a simplified and more mathematically tractable model. The objectives of the modelling effort were (1) to evaluate the extent to which the spatial pattern formation may be affected by competition among neighbours, and (2) to evaluate the possibility of spatial pattern intensity as a measure of population organization.

THE SIMULATION MODEL

The model is based on the following assumptions: the simulated plot (a quadrat) contains a population of n individuals. Each individual is considered separately; ith individual ($i = 1, 2, \ldots, n$) is described by its height (d_i) and by the radius of the circular plot which it occupies ($r_i = kd_i$, $k =$ constant). The area of this plot is $S_i = \pi r_i^2$. Each individual 'roots' in a fixed point within the plot (coordinates x_i, y_i).

The growth of each individual is described by a 'logistic-like' equation with an added expression of competition from neighbours. The difference equation is used with an appropriate time step (in the case of trees usually 1 year):

$$d_i(t+1) = d_i(t)\left[1 + a\left(1 - \frac{d_i(t)}{D}\right) \mathrm{RED}_i(t)\right] \tag{1}$$

where a is the length–growth rate and D is the maximum possible height of individual. The term RED_i expresses the competitive influence of neighbours and is computed in the following manner:

$$\mathrm{RED}_i = \max\left(0, \frac{QS_i - \sum_{j \neq i} \mathrm{OVER}_{ij} \frac{d_j}{d_i}}{QS_i}\right) \tag{2}$$

where Q is a parameter expressing the intensity of neighbours' influence on growth (the higher the value of Q, the weaker the influence), and OVER_{ij} is an area of overlap of ith and jth individuals (computed as the overlap of two circles). The area of overlap is weighted by the ratio of heights of influencing and influenced individuals. An individual is more influenced by its taller neighbours and less by the lower ones. Similarly, the probability of survival to the next point is computed. The survival or death of each individual is then decided by the Monte Carlo method, as it is usual in similar models (Shugart, 1984). For comparison, the version with constant value of survival probability (i.e. independent of neighbours' competition: random dying) was executed.

To avoid a possible edge effect, the simulated plot was considered to be bounded by identical plots on each edge.

At the beginning of simulation, the initial height and location of each individual were generated. The initial heights were generated as random numbers with normal distribution $N(\mu, \sigma^2)$ with given μ and σ. Coordinates were generated according to the desired type of spatial pattern. The regular pattern was represented by the square lattice. Coordinates of individuals exhibiting random patterns were generated as independent random numbers with uniform distribution.

A flexible generator of aggregated (contagious, clumped) pattern was developed. The probability of appearance of an individual was considered to vary within the plot. The continuous function of coordinates $Z(x, y)$ was constructed for reducing the probability of appearance of an individual. Coordinates x and y were then generated as in the case of the random pattern; however, the individual was 'accepted' with the probability $Z(x, y)$, i.e. if the additional random number ($u \in \langle 0, 1 \rangle$; uniform distribution) was smaller than the value of $Z(x, y)$. Obviously, the character of the spatial pattern is determined by the function $Z(x, y)$. In our model it was constructed in the following way. First, q random points were generated within the plot (coordinates X_i, Y_i, $i = 1, 2, \ldots, q$). Then:

$$Z(x, y) = \min\left(1, \sum_{i=1}^{q} \exp\left[-\left((x - X_i)^2 + (y - Y_i)^2\right)/s^2\right]\right) \tag{3}$$

The parameters q and s are user-determined and correspond to the number

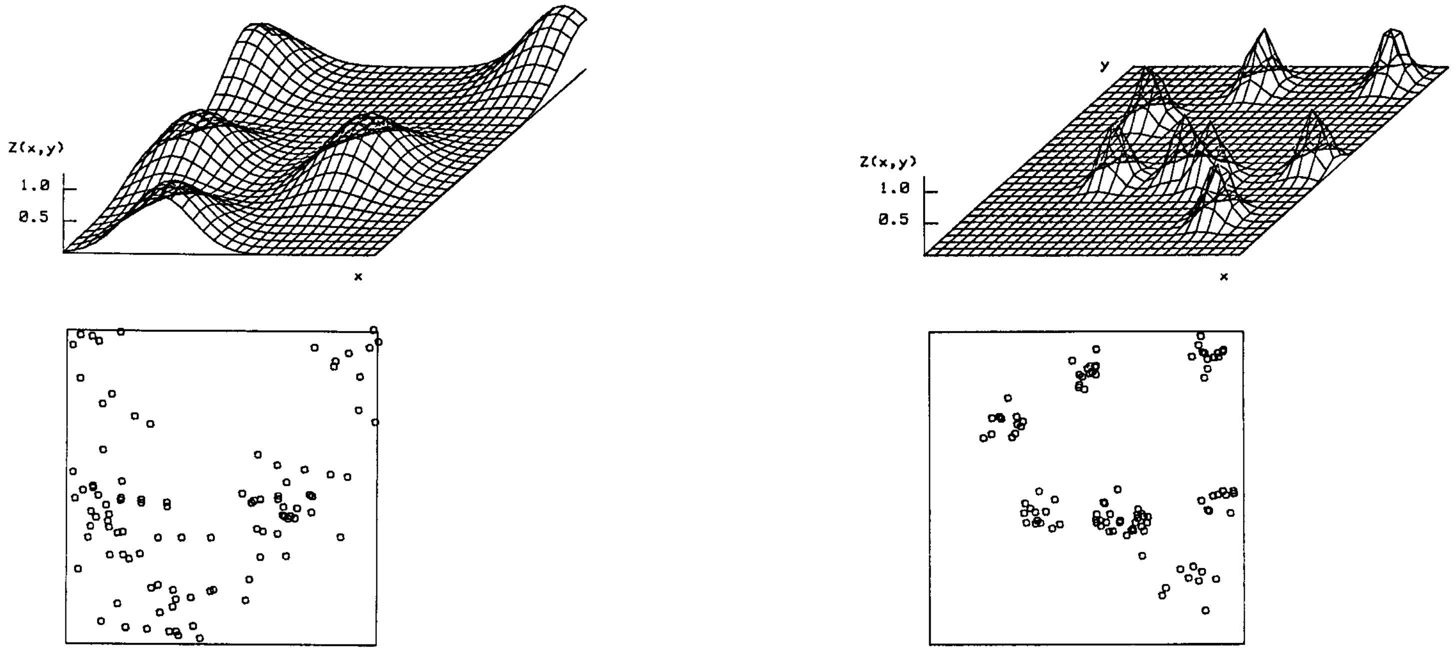

Fig. 1. Generation of aggregated spatial pattern. Above: The function $Z(x, y)$. Below: Corresponding realization of spatial pattern. Parameters used—Left: $q = 5$, $s = 0.15$; right: $q = 8$, $s = 0.05$. For further explanation see the main text.

of clusters and their dimension respectively. Examples of different functions $Z(x, y)$ and corresponding realizations of spatial pattern are in Fig. 1. This method seems to be more convenient for our purposes than a similar method of Matérn (1971) or methods of Diggle (1979). Moreover, in further simulation experiments, the use of such a function allows the expression of influence of the plot heterogeneity on the processes in a population (i.e. on the model parameters). If desired, the function $Z(x, y)$ may be constructed to allow the generation of spatial pattern with more than one scale of aggregation.

At the beginning of simulation and then after regular time intervals selected characteristics of the population were computed (density, average height, characteristics of spatial pattern). As a characteristic of spatial pattern, the indices of Clark and Evans (1954) and of Hopkins (1954) were used. (For discussion on their use see Pielou, 1977.)

The index R of Clark and Evans (1954) is defined:

$$R = \bar{v}\, 2\sqrt{\rho} \tag{4}$$

where $\bar{v}$ is the observed mean distance between neighbouring individuals, and ρ is the density; $R = 2$ in the case of completely regular (square lattice) pattern, $R = 1$ in the case of random pattern and decreases down to zero with increase of aggregation. The index of Hopkins (1954) is defined:

$$A = \frac{\sum a_1}{\sum a_2} \tag{5}$$

where a_1 are squares of a random point-to-plant distance, and a_2 squares of a random plant-to-neighbour distance. The same number of measurements of each kind is supposed; $A > 1$ indicates aggregated pattern, $A = 1$ random, $A < 1$ some degree of regularity. Characteristics of spatial pattern were computed also separately for individuals taller and shorter than average.

It should be noted that there are different measures of spatial pattern intensity behaving differently under self-thinning conditions. For measures based on counts of individuals in quadrats, the behaviour of characteristics of a population subjected to random dying was derived analytically (e.g. Pielou, 1977). For distance methods this seems to be impossible (in a general case). However, even among them are differences in behaviour. Consequently, under certain conditions, different measures may characterize changes in the course of self-thinning even contradictorily. Hence, it is necessary to relate conclusions on the changes of spatial pattern to the index used.

The model was executed for initial aggregated random and regular patterns with the probability of dying both with and without dependence on

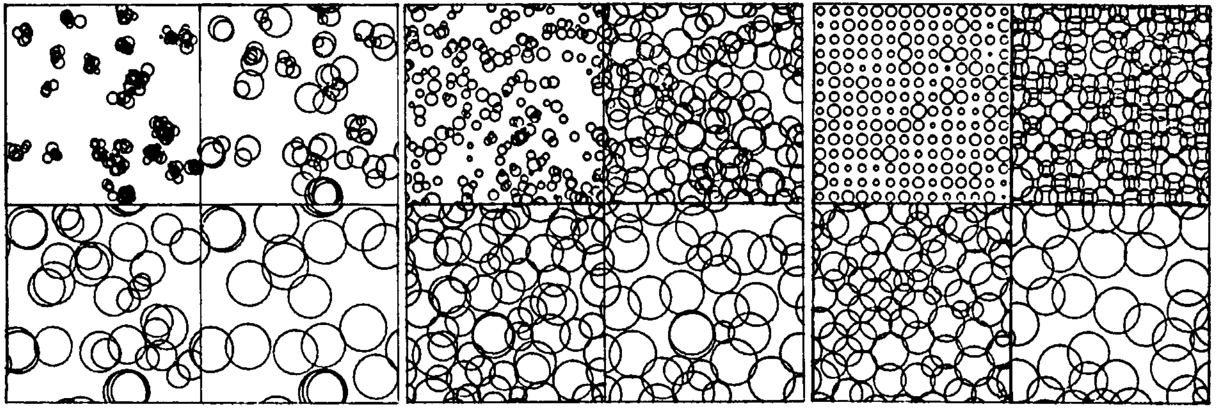

Fig. 2. Development of the simulated plots with initial aggregated (left), random (middle) and regular pattern (right). The particular runs differ in the type of initial pattern only. In each case, the state of the plot in times 0 (above left), 5 (above right), 10 (below left) and 20 (below right) is shown.

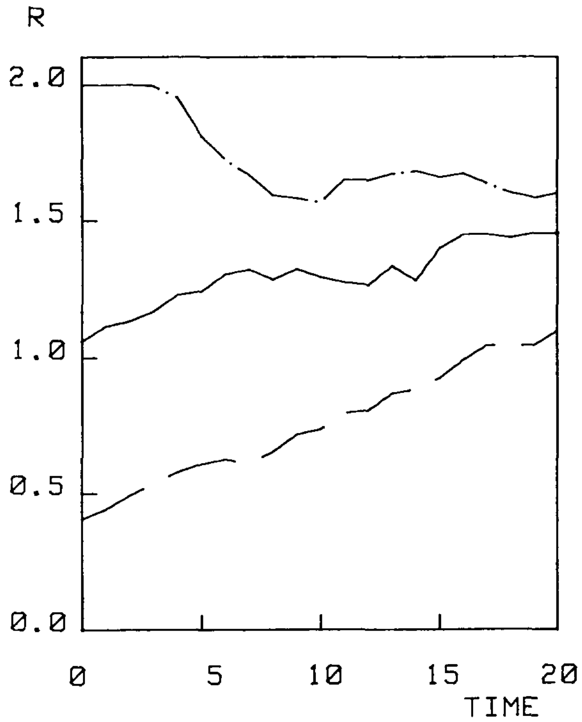

Fig. 3. Changes of the *R* statistics over time in simulated populations with initial aggregated (- - - - - -), random (———) and regular (· — · — ·) spatial pattern. Corresponds to plots in Fig. 2.

neighbours. In the case of random dying, both the *R* and *A* value approach (remain) 1 regardless of the initial type of pattern. In the case of dependence on neighbours, the *R* value increases with time, except in the case of initial lattice pattern. These conclusions hold for a wide range of types of initial aggregated pattern. Typical cases are shown in Fig. 2, corresponding courses of *R* values in Fig. 3. The changes of *A* values correspond to those of *R* values. Note that starting with aggregated pattern, the *R* value reaches the values indicating random pattern after some time.

Considering other characteristics of population development, we found differences in the rate of self-thinning among particular cases (most rapid in the case of aggregated pattern, see Fig. 4). Considering taller and lower individuals separately, the taller ones were usually spaced more evenly than the lower ones.

This model was used to simulate the development of natural birch (*Betula pendula* Roth.) growths on clear cuttings. The model was calibrated using data of S. Vacek (Forestry Research Institute, VÚLHM, Opočno,

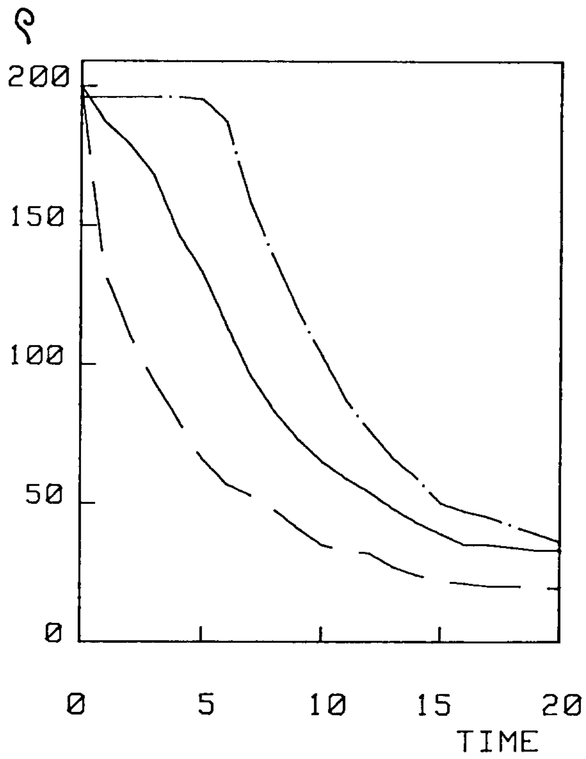

Fig. 4. Changes of density (ρ) over time in simulated populations with initial aggregated (- - - - - -), random (———) and regular (· — · — ·) spatial pattern.

Czechoslovakia, unpublished data, 1980) from East Bohemia (three plots of different age 8, 22 and 38 years). Data on growth and thinning only were used in the course of calibration; changes of spatial pattern of simulated and field population were compared afterwards. The comparison of the behaviour of simulated and field populations is displayed in Fig. 5.

ANALYTICAL MODEL

Let there be n living individuals in the beginning of the self-thinning procedure in an area of size A. Each of them 'roots' on a fixed point and occupies a circle with the centre in this point and radius growing with time to a fixed constant K. The growth rate of the radius and the constant K is the same for all individuals. If the areas occupied by two different individuals begin to overlap, one of them becomes extinct. (If this occurs among more individuals in the same instant, the order of dying is decided at random.) Then the self-thinning procedure may be divided into steps in each

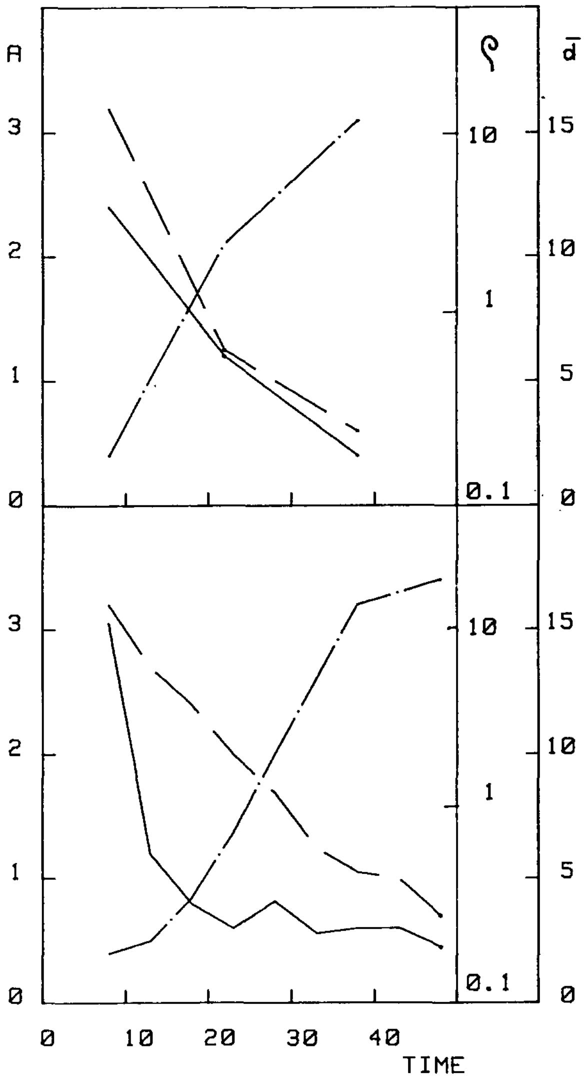

Fig. 5. Comparsion of behaviour of field (above) and simulated (below) birch population. —— index of Hopkins (A), ------ the mean height of population (d), ·–·–· density of individuals (ρ).

of which one individuals is excluded, this being one of the pair of individuals which has minimal distance, $v_{\min}(m)$, among the m remaining individuals $(m \leqslant n)$. The procedure is stopped if $v_{\min}(m) \geqslant 2K$. As a measure of aggregation of the m individuals we shall take the statistics of Clark and Evans (see equation 4):

$$R(m) = 2\bar{v}(m)\sqrt{\rho(m)} \qquad (6)$$

where $\rho(m)$ is the population density, and:

$$\bar{v}(m) = \frac{1}{m} \sum_{i=1}^{m} v_i(m)$$

in which $v_i(m)$ is the distance of ith individual to its nearest neighbour where m individuals are present.

We shall show that the following implication holds:

$$m - \sqrt{m(m-1)} > v_{\min}(m)/\bar{v}(m) \Rightarrow R(m-1) > R(m) \tag{7}$$

Proof: Simple book-keeping shows that for $m > 1$ the left-hand side of implication (7) is equivalent to:

$$2\bar{v}(m)\sqrt{\frac{m}{A}} < 2\frac{m\bar{v}(m) - v_{\min}(m)}{m-1}\sqrt{\frac{m-1}{A}} \tag{8}$$

Moreover, it is easy to see that:

$$\bar{v}(m-1) = \frac{\sum_{i=1}^{m-1} v_i(m-1)}{m-1} \geqslant \frac{m\bar{v}(m) - v_{\min}(m)}{m-1} \tag{9}$$

Substitution of (9) in inequality (8) gives the right-hand side of implication (7), which completes the proof.

For a purely regular pattern, $v_{\min}(m)/\bar{v}(m) = 1$. If $m > 1$, then $m - \sqrt{m(m-1)} < 1$. Hence, in the case of a regular pattern $R(m)$ must decrease at least in the first step. When the pattern goes from a regular to an aggregative one, the value of $v_{\min}(m)/\bar{v}(m)$ decreases, which implies that the statistic $R(m)$ becomes more likely to increase. Let us now give a rough estimate of what happens if the pattern is random.

It is reasonable to consider that m is not too small. For $m > 4$ we obtain:

$$m^2 - m^2 + m > 2\sqrt{m} > \sqrt{m} + \sqrt{m-1} = \frac{\sqrt{m^2} + \sqrt{m(m-1)}}{\sqrt{m}} \tag{10}$$

Division of equation (10) by $m + \sqrt{m(m-1)}$ yields:

$$m - \sqrt{m(m-1)} > \frac{1}{\sqrt{m}} \tag{11}$$

which gives us (together with implication (7)) the following implication:

$$1/\sqrt{m} \geqslant v_{\min}(m)/\bar{v}(m) \Rightarrow R(m-1) > R(m) \tag{12}$$

The cumulative distribution function of the distance v to the nearest neighbour in the case of a random pattern is:

$$F(v) = 1 - \exp(-kv^2) \tag{13}$$

where $k = k(m, A)$ denotes the mean number of individuals per circle of unit radius (Pielou, 1977). The mean of v is:

$$E(v) = \frac{1}{2}\sqrt{\frac{\pi}{k}} \tag{14}$$

The distribution function of the random variable $v_{\min} = \min_{i=1,2,\ldots,m} v_i$ is then:

$$G(v_{\min}) = 1 - (1 - F(v))^m \tag{15}$$

From equations (13) and (15) we obtain:

$$E(v_{\min}) = \frac{1}{2}\sqrt{\frac{\pi}{mk}} \tag{16}$$

Let us now consider a pattern in which $\bar{v}(m) = E(v)$ (equation 14), $v_{\min}(m) = E(v_{\min})$ (equation 16). From (12) it follows that $R(m)$ increases in that case (at least in the first step). This indicates that $R(m)$ tends to increase if the pattern is random.

DISCUSSION

The importance of spatial processes for dynamics of populations and communities of sedentary organisms was emphasized many times (e.g. Czárán, 1984; Yodzis, 1978). Similarly, we found differences in the course of self-thinning among cases with different initial spatial pattern.

Changes in the spatial pattern of even-aged population of sedentary organisms are due to mortality of individuals. It depends, particularly in densely closed canopy, on the competition of neighbours. The growth of individuals under strong competition stress is suppressed first and then these individuals die in the undercanopy position. Comparing the patterns of canopy (dominant) and undercanopy (suppressed) individuals, the canopy ones are usually spaced more evenly (cf. Ford and Diggle, 1981; Malik et al., 1976). It is in accordance with the results of our simulation. The competition among neighbouring individuals seems to be the crucial factor, influencing the development of the spatial pattern of a single, even-aged population. Its omission (as in Kent and Dress, 1979, 1980) in models causes their inability to explain some real phenomena.

The random pattern may be observed as a result of changes of the initial aggregated pattern caused by competition among neighbours; hence it is incorrect to deduce the independence of individuals within population from the observed random pattern. Hence, intensity of spatial pattern should never be taken as a measure of community organization, as its use has been attempted (e.g. by Kershaw, 1973, pp. 57–64).

We have considered a single even-aged population in a homogeneous area. This case is, however, not very common in the field. Are there any features of spatial pattern development that can be used to explain the behaviour of real populations? It should be noted that nearly all phenomena which we have omitted may be considered to be the causes of aggregation; a small heterogeneity of plot may have an important influence on survival of plants, particularly of seedlings; new individuals appear almost always in groups (e.g. vegetatively dispersed plants, young trees in 'gaps' in canopy, cf. Shugart, 1984). Catastrophic events often cause aggregated pattern (cf. Sprugel, 1976). The interspecific competition often has a similar influence (e.g. if one of the species exhibits aggregated pattern, it is highly probable that there is aggregated pattern also in its competitors). Seeds in soil are often distributed contiguously (Greig-Smith, 1979; Laessle, 1965). If we consider all the above-mentioned factors, it is obvious that the initial pattern is almost always aggregated. Further development depends on the proportion of the influence of the above-mentioned factors and the influence of competition among neighbours. The influence of the above-mentioned factors often decreases with the age of individuals (e.g. seedlings are more sensitive to external factors than mature plants) and the remaining factor which determines mortality is competition among neighbours. Hence, the decrease of intensity of aggregation is often observed (Cooper, 1961; Kershaw, 1963, 1973, pp. 59–64; Laessle, 1965; Tagawa, 1965; Anderson, 1971; Greig-Smith, 1979; Phillips and MacMahon, 1981; Prach, 1981) in an even-aged population. In the uneven-aged population it was found that mature plants exhibit a low tendency of aggregation (or are distributed randomly or even evenly), although in seedlings and immature plants high intensity of aggregation was found (Malik et al., 1976; Christensen, 1977; Whipple, 1980).

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