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The concept of discrete description of plant ontogenesis and cellular automata models of plant populations

A.S. Komarov [a,*], M.M. Palenova [b], O.V. Smirnova [c]

[a] *Institute of Physicochemical and Biological Problems in Soil Science of the Russian Academy of Sciences, Pushchino, 142290 Moscow, Russia*

[b] *All-Russian Research and Information Center for Forest Resources, 69 Novocheremushkinskaya, 117418 Moscow, Russia*

[c] *Center of Forest Ecology and Productivity of the Russian Academy of Sciences, 69 Novocheremushkinskaya, 117418 Moscow, Russia*

Abstract

The article represents a link between the concept of discrete description of the ontogenesis of plants and the cellular automata approach for the spatial-temporal modelling of plant population dynamics. The continuous process of individual plant development may be subdivided into several stages on the basis of morphological indicators reflecting functional importance of plants at different stages. The number and duration of age stages may vary from species to species, among life-forms within species, and under different environment conditions. The duration of age stages and the probability of transition from one stage to another for a given plant depend on the plant's neighbourhood pattern, the type of ontogenesis and the site conditions. Such data are available from numerous field studies.

The presented approach allows simulation of a plant population as a set of cellular automata located on a plane. The age stages of these automata can be changed according to simple rules, which reflect the types of plant ontogenesis, different life spans of age states, and different sizes of plants in the neighbourhood. This approach is different from matrix models, which are usually used for this purpose, in that here we can directly simulate the role of space interactions in the population dynamics. We constructed some cellular automata models based on experimental data, which reflect the ontogenesis types and life-forms of plants. The models demonstrate that simple rules of plant development with simply defined local interactions lead to complicated dynamics. The results show new possibilities of applications of discrete simulation modelling for analysis of plant populations and community dynamics.

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Keywords: Cellular automata; Ontogenesis; Plant population dynamics; Age states; Random extinction; Phase transition; Critical probability

1. Introduction

The fixedness of plants, their spatially explicit positions and interactions with a set of nearest neighbours are the main characteristics of a plant population life. Plant population represents a spatially distributed set of separate individuals of various size and age. These individuals are able to disseminate their offsprings in various ways and with different spatial pattern. Obviously, these circumstances should lead to complex spatial dynamics of plant communities.

For the sake of simplicity we considered the development of a plant community from the ontogenetic

* Corresponding author.

E-mail addresses: komarov@issp.serpukhov.su (A.S. Komarov), palyonova@mtu-net.ru (M.M. Palenova), smirnova@cepl.rssi.ru (O.V. Smirnova).

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point of view, i.e. as a set of complementary processes of both individual and population development. A comparative study of the ontogeny of all species constituting the community could be considered as a basic tool for exploring the community functioning and development. An adequate concept for comparison of ontogenetic features of various species has to be introduced.

Ontogeny is a continuous process. Its duration may be characterized not only by physical time (years, months, etc.), but also by biological time inherent to an organism's life (Harper, 1977). Division of the continuous ontogenetic process into functional stages allows obtaining the coherent scales of biological time for different species with different life span. This approach has been developed by Russian botanists and is known as "the concept of discrete ontogeny" (Rabotnov, 1950, 1978; Uranov, 1975; Gatzuk et al., 1980; Serebryakova, 1976, 1977; Zaugol'nova et al., 1988; White, 1985).

From mathematical point of view this biological concept allows to describe the development of an individual plant as a sequence of states of finite automata. Analysis of interactions between nearest neighbours or vegetative propagation of daughter plants in the neighbourhood of a mother plant leads to construction of the cellular automata model. Such complex spatially distributed methods of computer modelling have been well developed (Toffoli, 1984; Gerhard et al., 1990; Vanag, 1988). The first applications of the cellular automata approach to simulation of plant populations or community dynamics were developed in 1980 (Edelstein, 1982; Komarov, 1982; Czaran, 1984; Inghe, 1989, 1990). A summary of the results is given by Ermentrout and Edelstein-Keshet (1993). It is necessary to mention a number of papers by Silvertown et al. (1992, 1993, 1994). A short review with a list of references to cellular automata models in ecology is given by Balzter et al. (1998).

The aims of this study are (1) to link the concept of discrete description of the plant ontogeny and cellular automata models; (2) to formulate the main assumptions of plant population life in discrete terms with two-dimensional spatial presentation; and (3) to demonstrate applications of this approach in some areas of plant population ecology.

2. The discrete description of the plant ontogenesis

Division of the continuous ontogeny process into functional stages allows for definition of coherent scales of biological time for different species with different life spans.

A detailed study of the ontogeny of a large number of species in various communities allows us to state the main principles of the concept of discrete description of plant ontogenesis (Gatzuk et al., 1980; Smirnova et al., 1999).

1. The continuous process of individual plant development may be subdivided into several stages which reflect functional importance. These stages defined on the basis of structural indicators as: the presence or absence of embryonic, juvenile, or mature morphological features; the ability of an individual to reproduce or to propagate vegetatively; the ratio between the living and the dead, as well as the ratio of growing and non-growing plant parts.
2. Ontogeny stages are universal and apply to plants of all life forms.
3. Individual development may be expressed in different ways, which reflects both temporal and structural diversity of ontogeny pathways (Zhukova, 1986; Zhukova and Komarov, 1990). Temporal variations are expressed as:
   (a) developmental delays, i.e. a longer duration of certain ontogenic stages under unfavourable conditions as compared to the duration of the same stages under optimal conditions;
   (b) omission of some ontogenic stages;
   (c) recurrence of earlier ontogenic stages.

   Structural variations are expressed as:
   (a) different vitality;
   (b) different life forms;
   (c) different types of propagation.
4. There is no direct correlation between ontogenetic stage and absolute age.

We shall consider several properties of the discrete description of the ontogenetic stages of plants in more detail, bearing in mind their applications in modelling.

An example of ontogenetic stages of a plant is shown in Fig. 1. The distinction between ontogenetic stage and age was made on the basis of morphological and ecological studies.

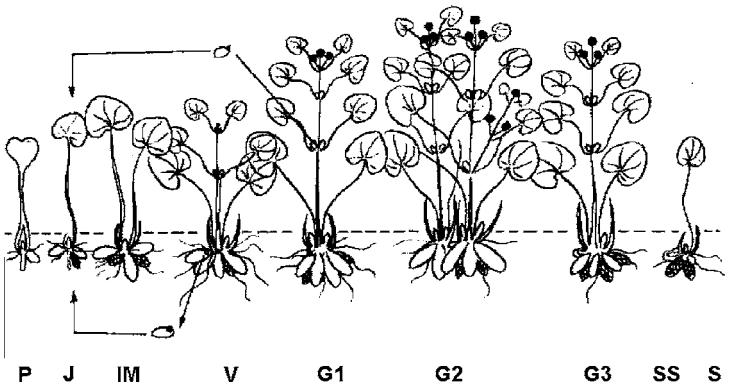


Fig. 1. Example of age states (*Ficaria verna* L.).

The ontogenetic stages of plants have the following main features (The Coenopopulation of Plants . . . , 1977, 1988; Gatzuk et al., 1980; Smirnova et al., 1999):

Seed (*se*) is characterized by size and biomass, degree of embryo development, duration and type of dormancy, nutrient storage.

Seedling (*pl*) usually possesses a partially heterotrophic nutrition type, i.e. it uses both the substances of the maternal plant stored in the seed and its own assimilates. It usually consists of a primary shoot and a primary root.

Juvenile plant (*j*) is usually simple in structure. Some embryonic structures may still be present. Juvenile plants have features not found in mature plants, such as different forms of leaves, shoot and root systems.

Immature plant (*im*) has a structure which is transitional between juvenile and mature. A plant begins to branch at this stage, so its shoot system consists of branches of a low order. The leaves or needles have mature form and structure; exceptions are the species with compound leaves. The root system includes either the entire primary root or its remains, lateral roots of the second and higher orders and, for some species, adventitious roots.

Virginile plant (*v*) has most features of a mature plant with the exception of reproductive organs. It may be difficult to distinguish between immature and virginile plants of some species, since both age states cover the transition from a juvenile to a mature structure. For trees this stage is of fundamental importance, because their light demand increases. Seeds are not produced, but the leader shoot has maximal annual increment.

Young reproductive plant (*g*1) is similar to the adult plant. The reproductive structures appear; but seed quantity is low. Formation of new parts prevails over death of old parts, and is reflected in the balance between living and dead parts, and between actively-growing and fully-grown structures. Height growth is rapid. Trees in the ontogenic stages from *j* to *g*1 are generally in the phase of exponential growth.

Mature reproductive plant (*g*2) shows a relative equilibrium in the processes of formation and death of structures. They usually show the maximal yearly increase in biomass and maximal seed productivity. These individuals are at the peak of ontogenic development. Trees have a decreasing rate of vertical growth, while the radial increment increases to a maximum. The crown and root system attain their maximal size and branching order.

Old reproductive plant (*g*3) is characterized by prevailing of death of its parts over the formation of new ones, the reproductive activity is diminished, as is the rate of root and shoot formation. For trees the size of both crown and root system decreases because many frame branches and anchor roots have already died off. A secondary crown may in some cases replace the primary one.

In *subsenile* (*ss*) and *senile* (*s*) plants flowering and fruit development practically ceases and the veg-

etative structure is simplified. Juvenile leaves appear once more and growth rate decreases. The differences between subsenile and senile plants are usually quantitative.

The description of plant population in terms of age states of plants is more important than knowledge of their absolute age. The reasons at the population level are as follows:

- different individuals of the same species reach certain age state at different absolute age, but they have a similar role in population or community dynamics because they have the same developmental stage;
- plants of different species or life forms pass similar age states at different age, so the comparison of their population role may be done in different ways;
- determination of absolute age for some plant species of herbs or grasses is accompanied by destruction of the plant, for example, via digging out the root system.

Thus, we have a way of describing of the development of each plant in discrete terms. This allows for investigating the age state spectrum which consists of the relative proportions of each age state in a population. The examples of such spectra are well known from experimental data and can be useful for calibration and verification of the discrete models. Numerous populations of different species in a range of ecological, geographical and successional situations have now been investigated; these studies show the similarities and differences of age-state spectra of particular plant growth forms (Zaugolnova and Smirnova, 1978; Zaugol'nova et al., 1988). Information on variations in age-state spectra in time and space, and how such variations are related to environmental changes, is available (Serebryakova, 1976, 1977).

3. Ontogenesis as spatial events

Ontogenesis is a process of consequential changes of the morphological structure of a plant. In general, morphological transformation appears in form of consequential changes of plant organs (shoots and roots) in space. All other aspects of development specify the way of formation of different types of spatial structure for different life forms of plants. On the contrary, from a population point of view the consideration of a plant or its part (for example, connected by shoot or root) as an independent element of population leads to three variants of spatial structure.

Three types of plant morphological structures have been defined: (i) monocentric, (ii) dense polycentric and (iii) sparse polycentric (The Coenopopulations . . . , 1976). The last two types may be seen as a representative process of morphological disintegration of an individual plant (genet) into separate and self-sufficient parts (ramets). Disintegration appears at different age states and occurs in various forms. Completed morphologic disintegration is vegetative reproduction. Despite the great variety of morphologic variants of vegetative reproduction, the distinction of two types of ontogenesis is essential from the population perspective: (1) with rejuvenation of ramets and (2) without rejuvenation (Figs. 2 and 3). This characteristic defines main features of the age structure of population.

The above description of ontogenetic development could be used for comprehensive simulation of a variety of plant life forms and for analysis of the population dynamics. Generalization of numerous field experiments shows that every plant population with similar ontogenesis characteristics (morphology spatial type and extent of ramet rejuvenation) possesses the same population dynamics.

For monocentric plants with restricted vegetative propagation, the population size is maintained through seeds. High mortality of young plants requires a reserve of the plants of this group and age-state spectrum is left-sided. Similar left-sided spectrum is typical for the populations of dense polycentric plants in the case of strong rejuvenation of offsprings. In this case the spectrum maximum increases due to mixed seed and vegetative reproduction (Fig. 4A).

In the case of absence of rejuvenation of ramets the ontogenetic spectrum represents bimodality with maximum value at the pregenerative age due to seed reproduction, and a second maximum at the old generative and post-generative plants age state due to vegetative propagation (Fig. 4B).

Ontogenetic spectrum for the populations of sparse polycentric plants demonstrates a maximum at the young and middle-aged generative plant states. Sometimes plants in certain age-states are missing (Fig. 4C).

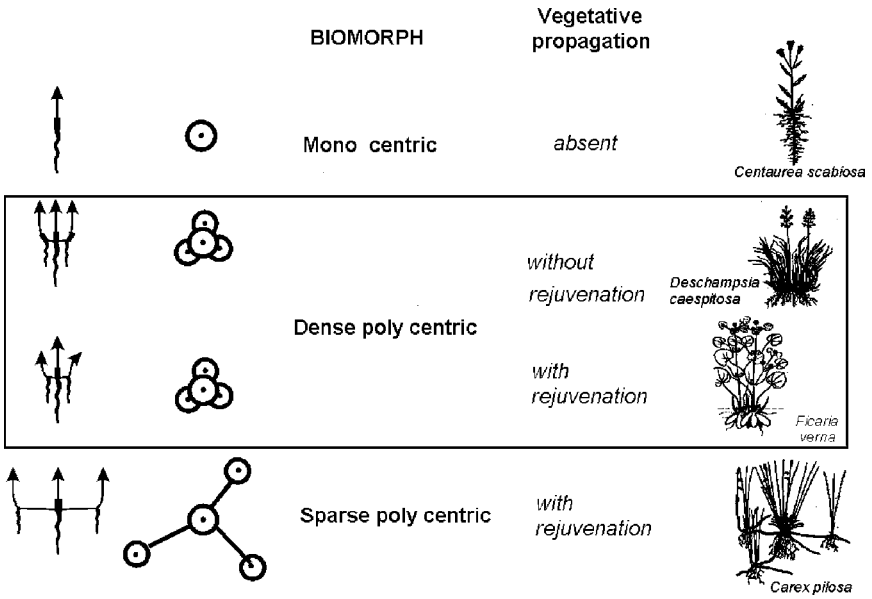
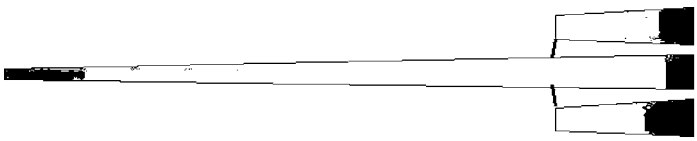
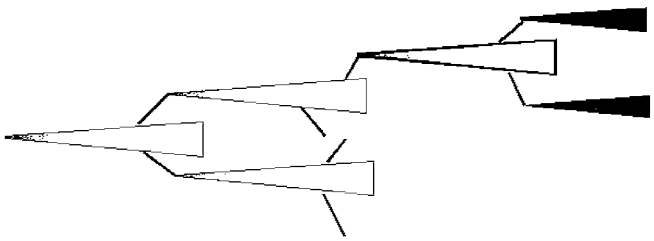


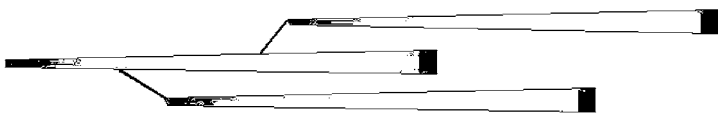
Fig. 2. Types of ontogenesis for three types of plant morphological structures.



at the end of ontogenesis without ramet's rejuvenation



in the middle of ontogenesis with ramet's rejuvenation
abridged ontogenesis



in the middle of ontogenesis with ramet's rejuvenation
full ontogenesis

Fig. 3. Different types of spatial resolution of ramets.

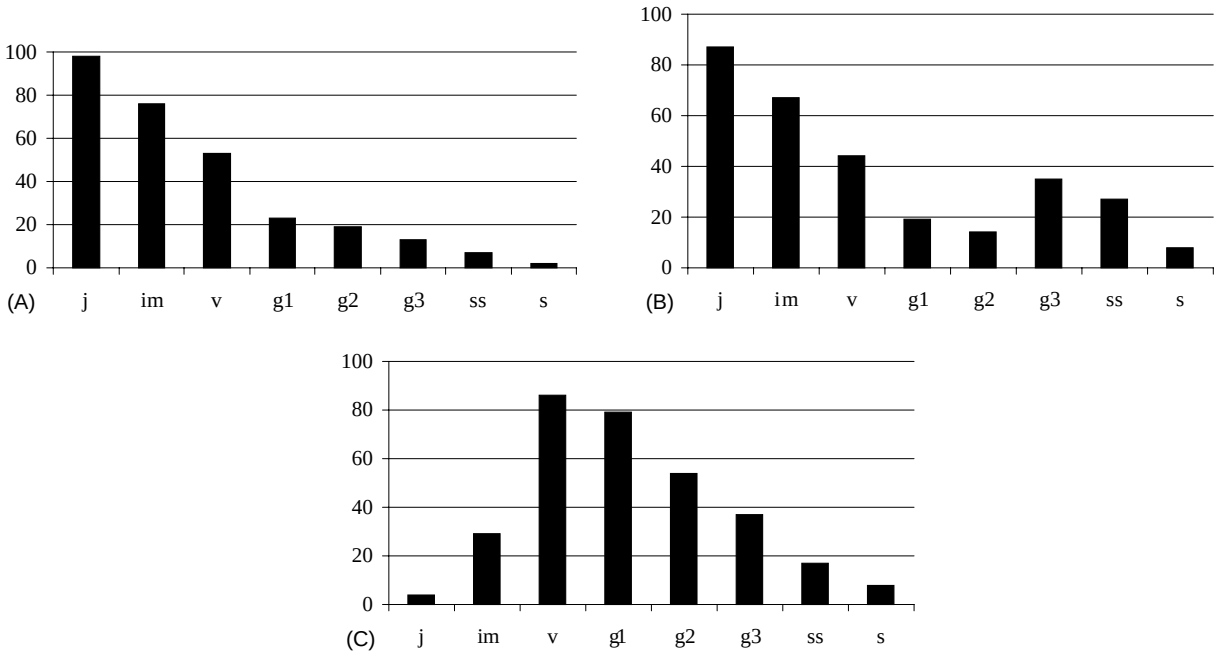


Fig. 4. (A) Typical age spectrum for monocentric plants with restricted vegetative propagation or for the populations of dense polycentric plants in the case of strong rejuvenation of daughter ramets. (B) Age spectrum in the case of absence of rejuvenation of ramets. (C) Ontogenetic spectrum for the populations of sparse polycentric plants.

Examples mentioned before show that it is possible to link the spatial and age structures of plant population of different life forms on the basis of the ontogenesis characteristics of its constituents.

4. Simple cellular automata model of plant population divided by age-state classes

Let us consider a simple example of a cellular automata model of one-species population of short-rhizome plants. We shall assume that the plants are located in the cells of a bounded two-dimensional integer lattice with no more than one plant per cell. In each cell, a finite automaton with N states is defined. Automaton transition from one state to another depends on the previous state of the automata, the longevity of its residence in the current state as well as on external factors. If transitions are dependent on the current state of the automaton and the states of neighbouring automata, then these automata are known as cellular (von Neumann, 1963). We shall illustrate that the population of short-rhizome plants can be simulated in terms of cellular automata in agreement with the main characteristics of plant ontogenesis described above.

The following rules define the population dynamics of formal plants:

- plants are assigned to bounded cells of a two-dimensional integer lattice $Z(i, j)$, $(i = 1, \ldots, N;\ j = 1, \ldots, M)$ with cells (i, j). The lattice is transformed into a torus-like surface to avoid boundary effects;
- population consists of plants which originate either from seeds or ramets (vegetative dissemination);
- no more than one plant can live in a cell (i, j) from its birth until death;
- a neighbourhood $Q(i, j)$ is defined for each (i, j), which contains all lattice cells at distance (number of lattice ribs) K_m from (i, j);
- time step is provisionally equal to 1 year and longevity of age states is assumed to be equal;
- the element of population consequently changes age state τ_i to next τ_{i+1}; in the age state τ_{veg} the plant spreads its daughter plants of age τ_{juv} into its neighbourhood $Q(i, j)$;

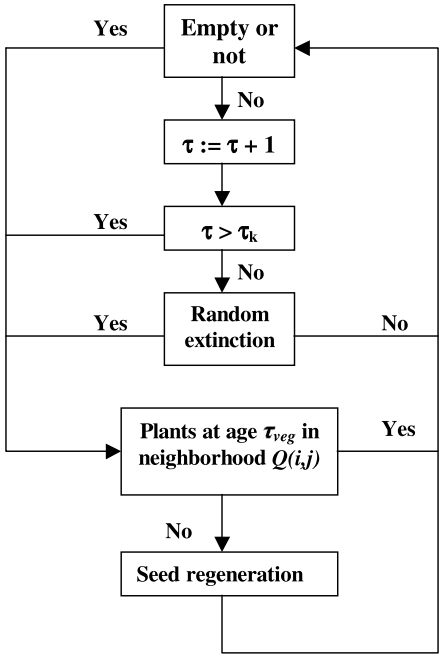


Fig. 5. The consequence of elementary operations at *i*th time step.

- the limiting age-state τ_k exists, on reaching this state the plant dies, which makes the corresponding cell vacant;
- cells can be made vacant as a result of an external destructive impact; every plant in the lattice cell is assumed to be excluded (trampled) independently at each time step with a probability P_d;
- seed rain is defined as a probability of random appearance of a plant in juvenile age state P_s in an empty cell (i, j).

The consequence of elementary operations at *i*th time step is shown in Fig. 5. At each time step we obtain age and spatial structure of the population and its number.

5. Results of simulation

The model parameters were set as follows: $P_s = 0.1$, $\tau_k = 5$, $\tau_{veg} = 2$, and $P_d = 0$. Vegetative reproduction takes place in the first half of a plant's life cycle, and the model population does not undergo random extinction. The fraction of lattice cells occupied by plants θ_t demonstrates oscillations (Fig. 6A). The reason of these oscillations is as follows: the plants either propagate through their offsprings or generate seeds which occupy the whole lattice. No vacant cells are available; hence there is no possibility for new plants to emerge. The plants that occupy the cells become old and are no longer capable of vegetative reproduction. Further, after a certain number of time steps the plants reach their limiting age and intensive mortality is observed. The lack of young plants severely restricts the vegetative propagation prospects of the population.

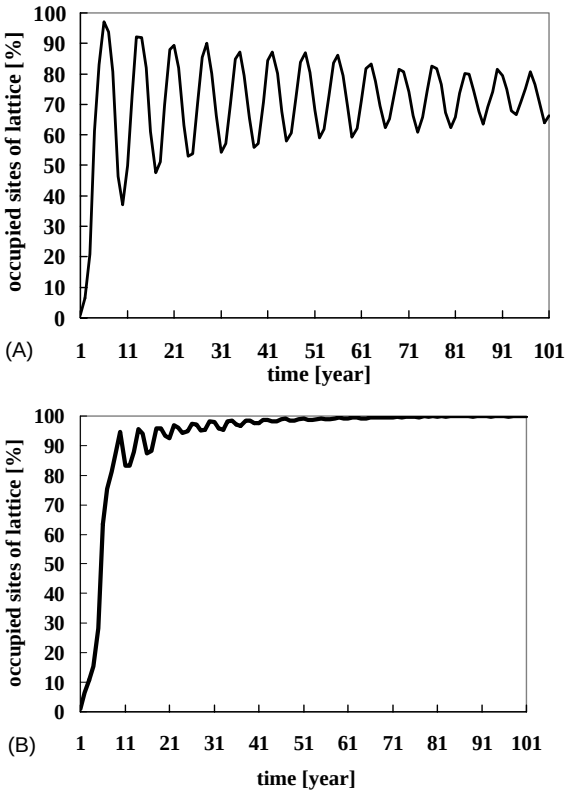


Fig. 6. Dynamics of population with plants' propagation abilities at different periods of its lifetime: (A) $P_s = 0.1$, $\tau_k = 5$, $\tau_{veg} = 2$; (B) $P_s = 0.1$, $\tau_k = 5$, $\tau_{veg} = 3$.

New plants which start to occupy the vacant cells are of seed origin only. However, as the number of dead plants increases more cells become vacant and new plants capable of vegetative reproduction have more cells to occupy. Ultimately, the amount of young plants counterbalances the mortality rate and then the

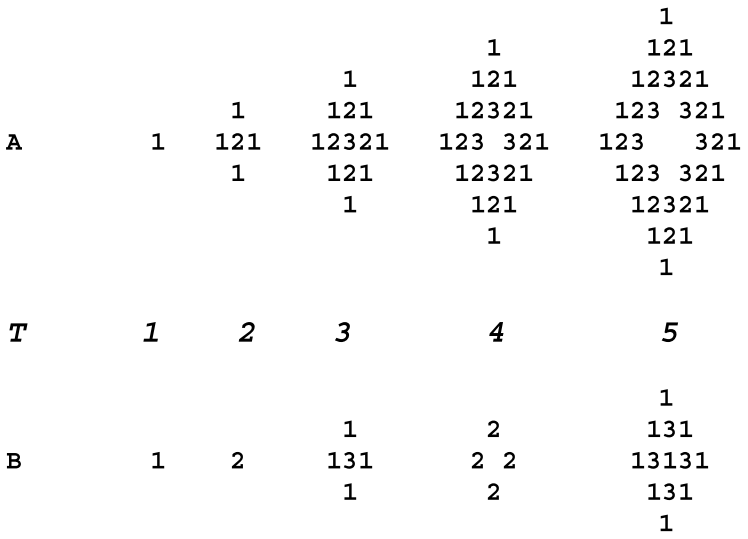


Fig. 7. Different mutual displacement and its dynamics of plants with different age states: (A) $\tau_k = 5$, $\tau_{veg} = 2$; (B) $\tau_k = 5$, $\tau_{veg} = 2$.

total amount of plants starts to increase. The cycle is then repeated.

Let us shift the vegetative propagation age of mother plants towards the second half of the life cycle, i.e. $\tau_{veg} = 4$. Values of all other parameters remain unchanged. We find that the oscillations have disappeared and the population dynamics has changed (Fig. 6B). This change can be explained by the fact that mutual displacement of plants at different age states has a different spatial structure. In the first case, the propagation of offsprings takes the form of a spatial auto-wave with expanding circles (Fig. 7A). If the parent plant produces its offsprings in the second half of the life cycle, then spatial displacement of parent and the new-borns is different from the previous case: the new-borns have a possibility to penetrate into the interior of an expanding circle (Fig. 7B). This simple example shows the role of spatial structure in dynamic processes in the populations of sessile plants.

Certain observations can be made with regards to the changes in the plant numbers, which occur if the intensity of random extinction is altered. If the intensity increases then the amplitude of oscillations of plant amount decreases. Moreover, at any P_d different from zero no oscillations occur. Changing in the number of plants appears to be a stationary random process without any distinct harmonic component (Fig. 8). Starting from a certain time step, θ_t appears to be a sample function of stationary random Gauss process with discrete time and can be described in terms of expectation θ_{av} and the corresponding variance.

We shall now simplify the model by removing the seed regeneration process. We shall assume that the young plants of the initial age randomly appear at one of the lattice boundaries spreading into empty neighbouring lattice cells by daughter ramets. Once the whole lattice is filled in the lattice is then wrapped into a torus-like surface in order to avoid boundary effects. In this case the spreading wave of new-born plants circulates along the torus. Such description enables examination of internal effects inherent to the structure of the population not effected by seed rain.

We shall consider the response of a simplified model community to intensive single extinction. Two kinds of extinction can be distinguished in this theoretical experiment: background extinction at each time step P_d and single extinction at a certain step with intensity P_{single}. Fig. 9 shows an example of a background extinction at $P_d = 0.1$ and of a single strong ($P_{single} = 0.9$) extinction at a certain step (bottom line). Single extinction causes a sharp decrease in θ_t value followed by a further decrease at the subsequent steps due to the identical age of the 90% of plants imposed by the single impact. Upon reaching a certain minimum gradual restoration of the population takes place, and the stationary state is achieved. The possibility of the sys-

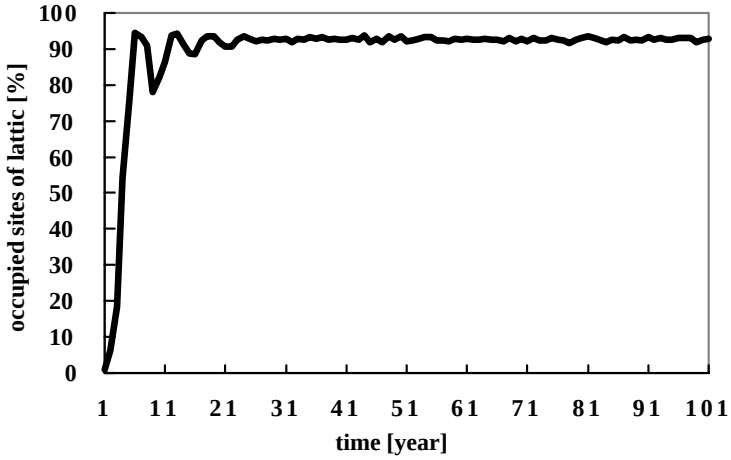


Fig. 8. An example of response of population to random extinction with intensity $P_d = 0.1$ and other parameters similar to Fig. 6A.

tem restoration after a strong single impact is a phenomenon of a particular interest. Though when compared to the results of a similar ($P_{single} = 0.9$) system impact under conditions of more intensive background influence at $P_d = 0.7$ (Fig. 9), the restoration rate proves to be higher in last case.

This effect can be explained by the quantitative ratio of plants of different age. According to the assumptions above, the vegetative shoots can originate from young plants only, and, thus, the restoration rate is highly dependent on their quantity. The probability of a plant's survival to it's age k is well presented by equation $(1 - P_d)^k$. The higher is the P_d value, the lower is the number of mature plants. Stronger background influence results in the corresponding increase of young plants amount. Evidently, the greater is the background disturbance, the faster the system returns to its stationary state. The intensity of random extinction must be restricted because there is a critical intensity at which the population dies out. We evaluated

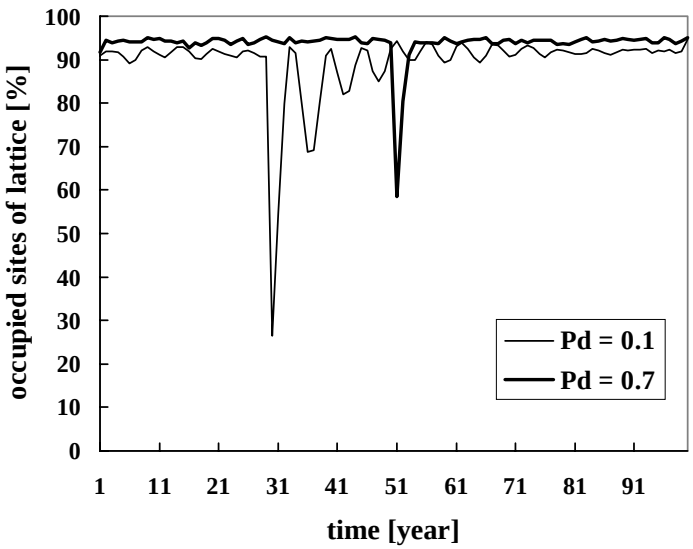


Fig. 9. "Adaptation" of population to different intensity of extinction.

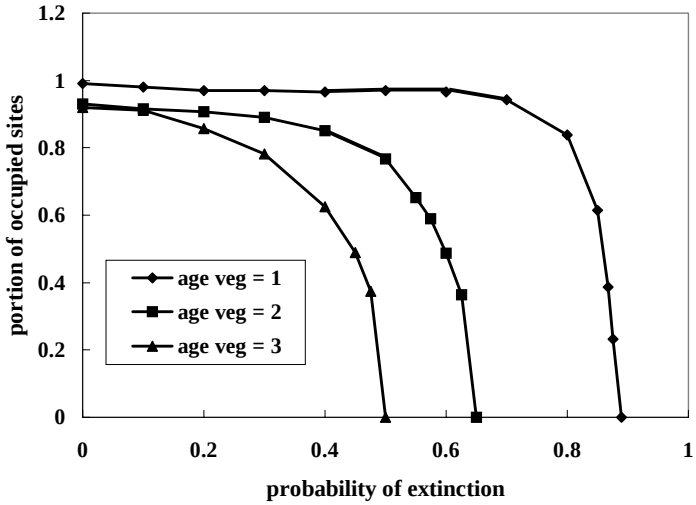


Fig. 10. Dependency between intensity of random extinction and average numbers of population.

this critical intensity via a computer modelling experiment. It was mentioned before that the sample function θ_t might be presented in terms of expectation θ_{av} and the corresponding variance. The dependency of the expectation θ_{av} from the intensity of extinction P_d is shown in Fig. 10. A relatively small alternation of θ_{av} within a broad range of P_d is worthy of noting, so as the sharp shift in the critical area, where θ_{av} changes considerably. The process is no longer stationary at $P_d > P_c$ (P_c is the critical intensity of extinction), and the population size falls to zero from any initial state at $P_d > P_c$.

The above described effect can be demonstrated by a real life example: a footpath through a grass lawn is affected by intensive trampling. We shall make a suggestion that the intensity of trampling follows a Gauss distribution with the mean at the centre of the pathway (Fig. 11), and a certain variance, which reflects the width of the footpath. In the suggestion that trampling upon grass occurs randomly, it may seem reasonable to expect a diffuse edge of the path. A highly determined sharp edge of the path can be explained by the critical intensity P_c as shown in Fig. 11.

6. Discussion

The age and spatial dynamics of many plant communities can be well presented with the help of the model described above. The model also indicates that a complete absence of destructive impacts (i.e. under the conditions of "strict preservation") has the same after-effect as a very strong destructive impact due to weak restoration capacity.

The mechanism of fluctuations is usually associated with the hypothesis of self-contamination, changes in weather conditions and other factors. It is likely that these factors can initiate the fluctuation. However, on the basis of the described simple simulation model it may seem apparent that such fluctuations may also arise due to the geometrical structure of the plant spatial pattern under the conditions of limited seed regeneration. For the first time a similar observation was made by Watt (1947). Moreover, it can be easily observed that under certain environmental conditions (e.g. a drought) the age of vegetative propagation is shifted towards the second half of the plant's life cycle. The number of plants may differ considerably due to mutual geometrical displacement of individual plants of different age states.

The plant dynamics may vary depending on the relations between the position of plant in reproductive age-state and the duration of life cycle. The response of a model community to intensive single extinction depends on previous background extinction. If the population is subject to a weak extinction at each time step, then the restoration rate proves to be higher. Although not raised in the present paper, it is evident that

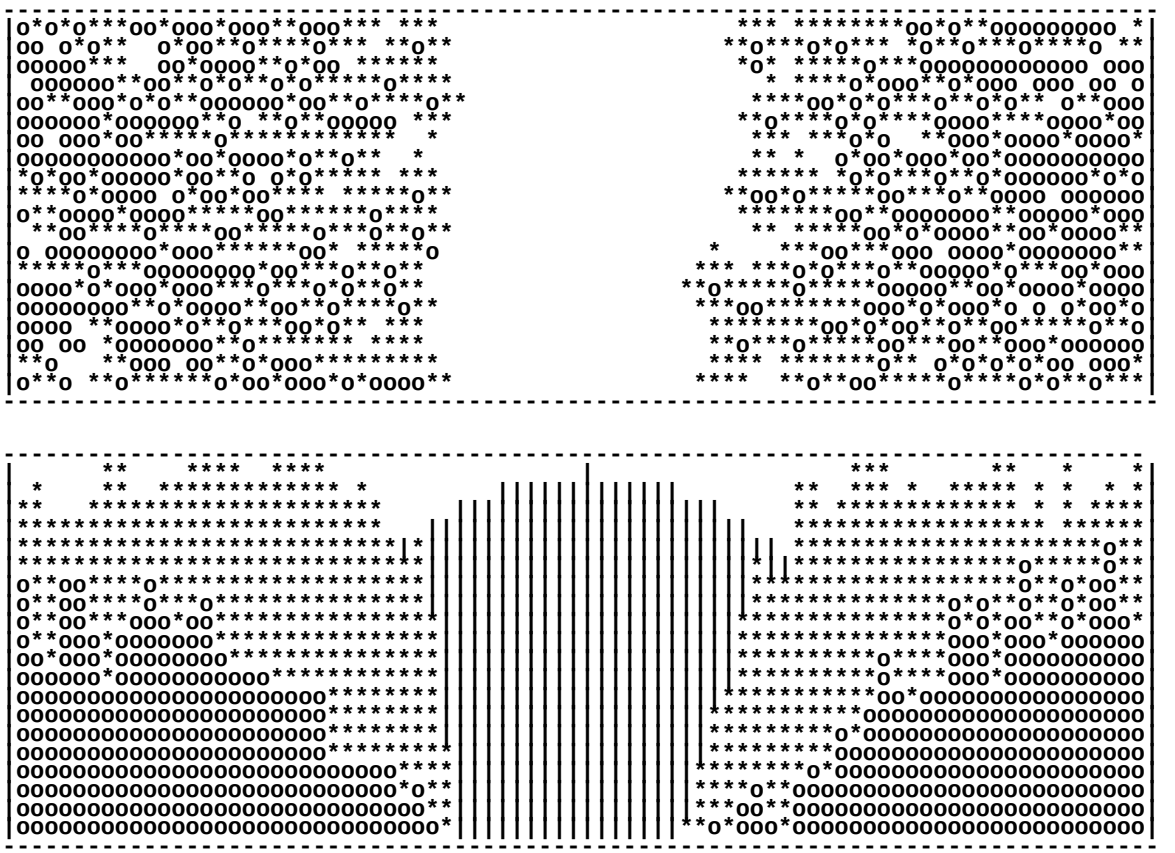


Fig. 11. Originating of sharp edge of pathway at Gauss intensity of extinction. Upper figure is a planar presentation of the pathway ($\tau_k = 5$, $\tau_{veg} = 1$). Lower part of figure represents the histogram of intensity of extinction (|, central part) and histograms of proportion of plants in the vertical lattice rows in different age stages (○, non-generative plants, ∗, plants in the generative stage).

probabilistic transitions from one age state to another lead to the increased stability of the population under random extinction.

The dependency shown in Fig. 10 is similar to the phase transition in the Ising model of spontaneous magnetization (Kerzon Huang, 1963). In our view, the analogy with phase transitions in the theory of spontaneous magnetization is not coincidental and the importance of this interrelation may become obvious if a more detailed study is carried out.

Descriptions of age status exist for more than 500 plant and tree species, but for the boreal and temperate zones only (Zhukova, 1997, 2000). However, there is a lack of knowledge of the shifts in numerical values of physiological and ecological parameters of tree or plant species at various age, ontogenic and vitality stages. Certain experimental data were obtained from permanent sample plots with marked individuals. Several times in a year the age state of each marked plant was determined (Serebryakova, 1985; Zhukova, 1995; Onipchenko, 1994). This method of investigation allows an evaluation of transition probabilities of changes of age states under various conditions. These probabilities take into account the above mentioned ontogeny multi-ways. These probabilities are possible to use in matrix models to study the dynamics of a vector of population numbers grouped by stage, size or age (Leslie, 1945; Lefkovich, 1965; Sarukhan and Gadgil, 1974; Law, 1983; Caswell, 1986; Csetenyi and Logofet, 1989; Logofet, 2002; Ulanova et al., 2002). There are, however, at least two unfavourable properties associated with these probabilities. Firstly, the

probabilities vary depending on the calendar age of plants. Secondly, they depend on population conditions, such as population density (Zhukova and Komarov, 1990, 1991), or more generally on the spatial interactions of plants with neighbours. Such matrix models, therefore, have restricted use and do not reflect some important aspects of the population dynamics.

The main difference between matrix models and the above described cellular automata models is that the latter one allows to use a more extended presentation of a plant as a cellular automaton with finite number of states. These states reflect the age states of and their role in the population dynamics. The concept of discrete description of plant ontogenesis may be used further for constructing simple, and yet, thorough simulation models of populations and communities of plants.

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