RUSSIAN JOURNAL OF DEVELOPMENTAL BIOLOGY

A JOURNAL OF RUSSIAN ACADEMY OF SCIENCES

Editor-in-Chief
Sergei G. Vassetzky

PLEIADES PUBLISHING

Distributed by Springer

Ontogeny of Different Life Forms of Plants and Specific Features of Age and Spatial Structure of Their Populations

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Received April 18, 2001

Abstract—Materials have been generalized that were accumulated in population-ontogenetic studies of plants and leading features of the ontogeny of plants have been noted that determine specific structural features of their populations. The described patterns allowed the authors to develop simulation models of plant population dynamics. The results of simulation are provided, and they are compared to the empirical data. Problems have been considered that concern the influence of specific features of development of different plant biomorphs on the genetic structure of populations and biocoenotic processes.

Key words: plants, biomorph type, genet, ramet, ontogeny, population, mathematical models, cell automata.

Studies of the mechanisms and principles of regulation of the populational processes are impossible without using the concepts and patterns of the organism. The aim of this study is to investigate the influence of specific features of ontogeny in different life forms of plants on the formation of the age and spatial structure of population and to discuss possible evolutionary consequences of plant ontogeny.

The concept of the system of plant life forms developed by the Serebryakovs' school (Serebryakov, 1962, 1964; Serebryakova, 1971, 1981) is based on comprehensive studies of the morphological structure of plants and its development in ontogeny. The ontogeny of plants characterized by the attached mode of life takes place in time and space, and, hence, there are two aspects of this process: temporal and spatial.

ONTOGENY AS EVENTS IN TIME

Every individual of a population can be characterized by the absolute, or calendar, age, which represent a period of time from its appearance to the moment of observation, as well as by relative or biological age—specific set of morphological, anatomical, and physiological characters, whose community determines its ontogenetic state (*Tsenopopulyatsii…*, 1976).

Determination of the ontogenetic state is much more important for population studies than the determination of the biological age. This is explained by the following: (1) different conspecific individuals reach a certain ontogenetic state at different calendar times, but, since they are at the same developmental stage, their role in the population or coenosis is similar; (2) individuals of different species or life forms pass through the same ontogenetic states during different periods of time, and, hence, their comparative estimate can only be based on the determination of the biological age (Tsenopopulyatsii…, 1988). In addition, determination of the absolute age of most plants is practically impossible because of the constant renewal of its perennial parts, while classification by ontogenetic state is quite practical.

It was shown that plant ontogeny may be expressed in terms of the discrete description of the ontogeny (Rabotnov, 1950; Uranov, 1975; *Tsenopopulyatsii…*, 1976, 1977, 1988; Gatsuk *et al.*, 1980; The Population Structure…, 1985; Smirnova, 1987; Zhukova, 1995). It is essential that the concept of biological rather than calendar age is used for description, and, thereby, the ontogeny is presented as the transition of the plant from one ontogenetic state to another. Nowadays, when describing the complete ontogeny of plants, the periodization is used, which was proposed by Rabotnov (1950), added by Uranov (1975) and his students (*Tsenopopulyatsii…*, 1976; *Ontogeneticheskii atlas…*,
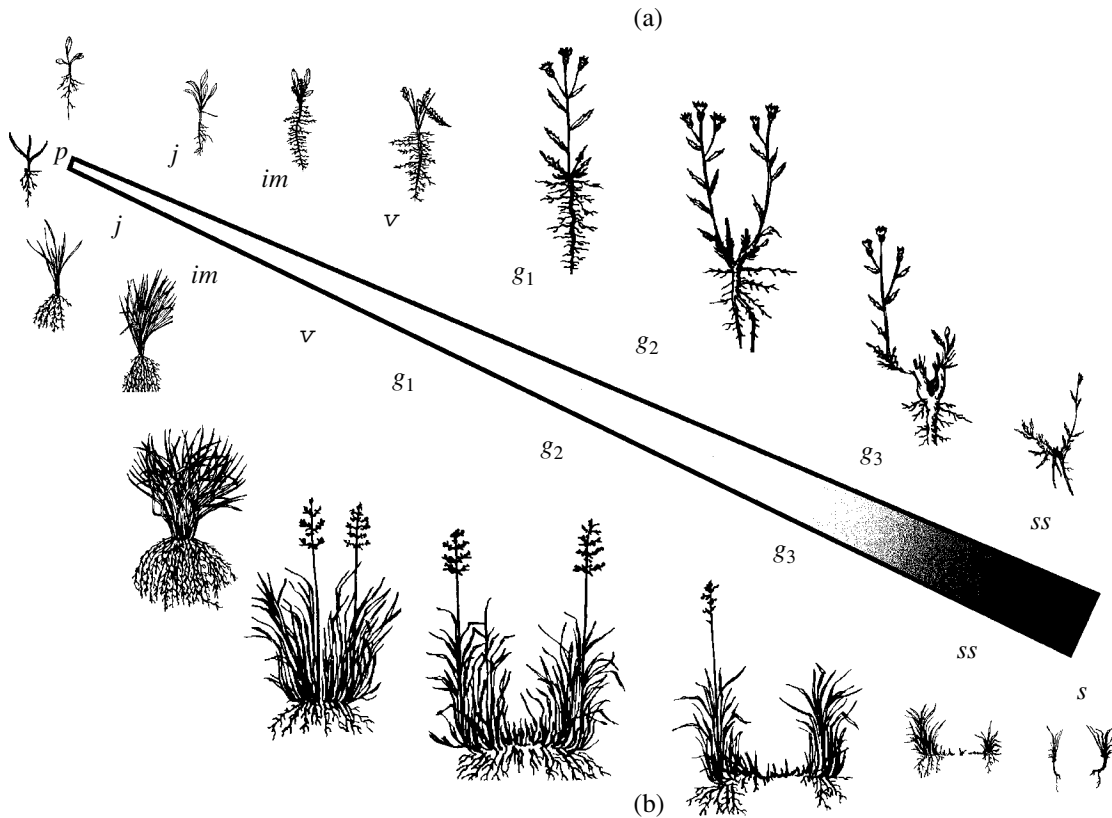
(a)

(b)

Fig. 1. Schematic diagram of the ontogeny of plants (genets) of the polycentric (a) and monocentric (b) biomorph types.

1997, 2000) and now includes ten ontogenetic states (Fig. 1). It looks as follows.

Periods	Ontogenetic state	Indices of states
I. Latent	1. Seed	*se*
II. Pregenerative	2. Germling	*p*
	3. Juvenile	*j*
	4. Immature	*im*
	5. Virginil (young vegetative)	*v*
III. generative	6. Young (early) generative	g_1
	7. Middle-aged (mature) generative	g_2
	8. Old (late) generative	g_3
IV. Postgenerative	9. Subsenile	*ss*
	10. Senile	*s*

Each state is considered as a key moment of development characterized by specific features of morphogenesis, certain relations between *de novo* formation and dying, morphological markers, and specific physiologobiochemical processes (Zhukova, 2002). Ontogenies of more than 500 plants have been described, including sporophytes and gametophytes of some ferns (Shorina, 1981) and some lichens (Suetina and Zhukova, 1997).

The ontogenies were described in terms of the above concept for the plants from broad-leaved forests (Starostenkova, 1971; Smirnova and Toropova, 1974; Smirnova and Cheremushkina, 1975; Toropova, 1977;
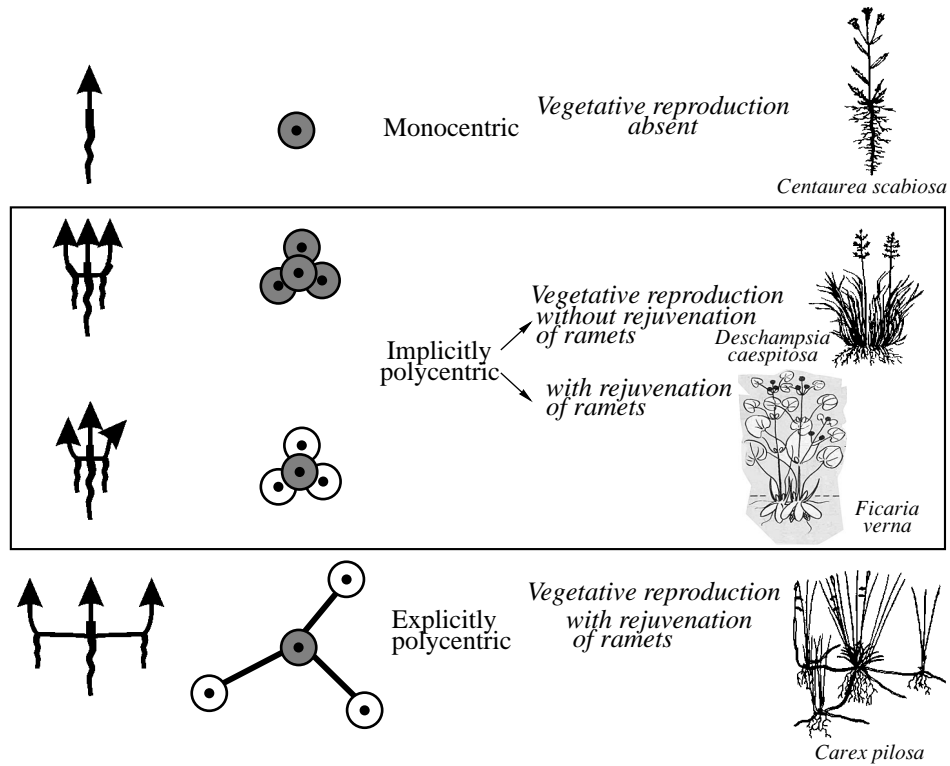
Fig. 2. Types of biomorphs.

Smirnova, 1987; Istomina and Bogomolova, 1991; Evstigneev *et al.*, 1992; *Vostochnoevropeiskie…*, 1994), flood plain and mainland meadows (*Diagnozy…*, 1980, 1987, 1989), steppes and semideserts (Kozhevnikova and Trulevich, 1971; Vorontzova and Zaugolnova, 1985), mountain phytocoenoses (Onipchenko, 1983, 1984; Malinovskii *et al.*, 1984), as well as for weed and ruderal plants (Markov, 1980, 1992; Lebedev, 1984; Zlobin, 1984, 1989).

ONTOGENY AS EVENTS IN SPACE

The plant ontogeny can be considered in a structural-spatial aspect as successive changes in the plant morphostructure. On the one hand, if the most general features of this process are described, the plant morphostructure transformation alteration is reduced to successive changes in the position of its parts (shoots and roots) in space. All other details of the description are only made more precise with the help of what structures or adaptive modifications of the shoot or root systems a certain type of spatial structure is realized in plants of different life forms. On the other hand, if the plant spatial structure is viewed from the populational position, i.e., if we postulate that the "plant parts" in question are "elementary sources of the phytogenic field, centers of influence on the environment, which are spatially separated from other such centers" (Uranov, 1965), only three variants of spatial structure (biomorph types) can be found among the entire diversity

of life forms of the plants that can be formed by the plant. The monocentric, implicitly polycentric, and explicitly polycentric types of biomorphs have been distinguished (Figs. 1, 2) (*Tsenopopulyatsii…*, 1976). Classification of plants by the biomorph types is essential for determining the volume of a countable unit (element of the population) and studying the patterns of regulation of the population abundance and spatial structure. Comparative-population studies can be car-
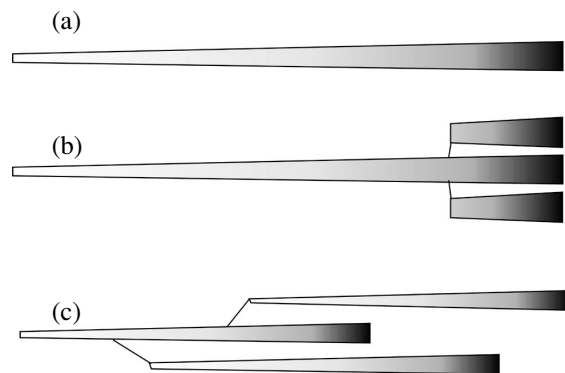

Fig. 3. Types of ontogenies of plants of different biomorph types: (a) monocentric without vegetative reproduction; (b) polycentric, vegetative reproduction without rejuvenation of ramets; (c) polycentric, vegetative reproduction with rejuvenation of ramets.

Types of biomorph and variants of vegetative reproduction of plants

Variants of vegetative reproduction	Biomorph types		
	monocentric	implicitly polycentric	explicitly polycentric
Absent	Tap root, cespitose, tuberiferous, and bulbiferous herbaceous plants; single-trunk (monopodial and sympodial) trees; aeroxilic vegetative-immobile shrubs; cushion plants without auxiliary rooting		
Present, without rejuvenation		Particulating tap root, raceme root, short rhizome, dense cespitose, loose shrub, tuberiferous, and bulbiferous herbaceous plants; sub-shrubs, shrubs, and cushion plants with auxiliary rooting	
Present, with rejuvenation		Bulbiferous, bulbotuberiferous, tuberiferous, rhizomatous raceme root, and short-rhizomatous herbaceous plants; epigenous-geoxilic shrubs; multi- and few-trunk trees	Long-rhizomatous, rhizomatous tap root, stolon forming, and creeping herbaceous plants; subshrubs and aeroxilic vegetative-mobile shrubs; hypogenous-geoxilic shrubs and subshrubs; elfin wood; grove-forming trees

ried out only on the basis of the formalization of the biomorph types.

The names of biomorph types are given according to two features of the spatial structure of adult individuals: the number of growth centers (mono- or poly-) and the degree of expression of individual centers (explicitly or implicitly), which is determined to the degree of their separation from each other (Smirnova, 1987). In adult individuals of monocentric biomorphs, the roots, shoots, and reproduction buds are concentrated in a single center, which is the center of growth; i.e., an adult individual is an elementary source of the phytogenic field.

Adult individuals of explicitly polycentric biomorphs are characterized by the presence of several distinct centers of concentration of the roots, shoots, and reproduction buds interconnected by communications (hypogeogenic rhizomes, stolons, loops, etc.). They act as centers of growth and, at the same time, are relatively autonomous; i.e., they can exist independently and give rise to new centers at natural or artificial separation. Adult individuals of implicitly polycentric biomorphs, like the previous ones, have several growth centers (centers of concentration of roots, shoots, and reproduction buds). However, these centers develop so close to each other in ontogeny that they are difficult to distinguish.

The formation of polycentric biomorphs is related morphological disintegration, which can be defined as a process leading to the appearance of distinct structural elements (ramets) capable, when separated, of an independent existence and development. In the aforementioned three types of biomorphs, morphological disintegration is expressed at different times and to a different extent. Its aspects can be considered: early late (ontogenetic state of mother plants), complete and partial, specialized and unspecialized, and with and without rejuvenation of daughter ramets. Complete morphological disintegration is taken to mean vegetative reproduction.

Thus, vegetative reproduction is another important feature characterizing the plant ontogeny. Given the entire diversity of variants of vegetative reproduction in plants of different life forms, it is essential (from the position of population consequences) to distinguish two types of ontogeny: with and without rejuvenation of developing ramets (Fig. 3). This characteristic of ontogeny determines to a great extent specific features of the age structure of a plant population.

These characteristics suffice for comprehensive description of variants of the ontogenies of diverse life forms of plants (table) and prognostication of specific structural features of their populations. Generalization of the results of numerous field studies suggests that each group of plants distinguished on the basis of specific features of their ontogeny (type of biomorph of adult individuals and degree of ramet rejuvenation) has a common structural feature of their population. The spatial and age structure of populations of plants of different life forms can be prognosticated on the basis of specific features of the ontogenies of individuals that comprise a population.

The results of studies of many kinds of life forms in different coenoses suggest that the age composition of normal coenopopulations is characterized by a certain ratio of ontogenetic groups (*Tsenopopulyatsii…*, 1976, 1988; Smirnova, 1987; Chistyakova, 1988; Zhukova, 1995). Hence, it became possible to distinguish a char-
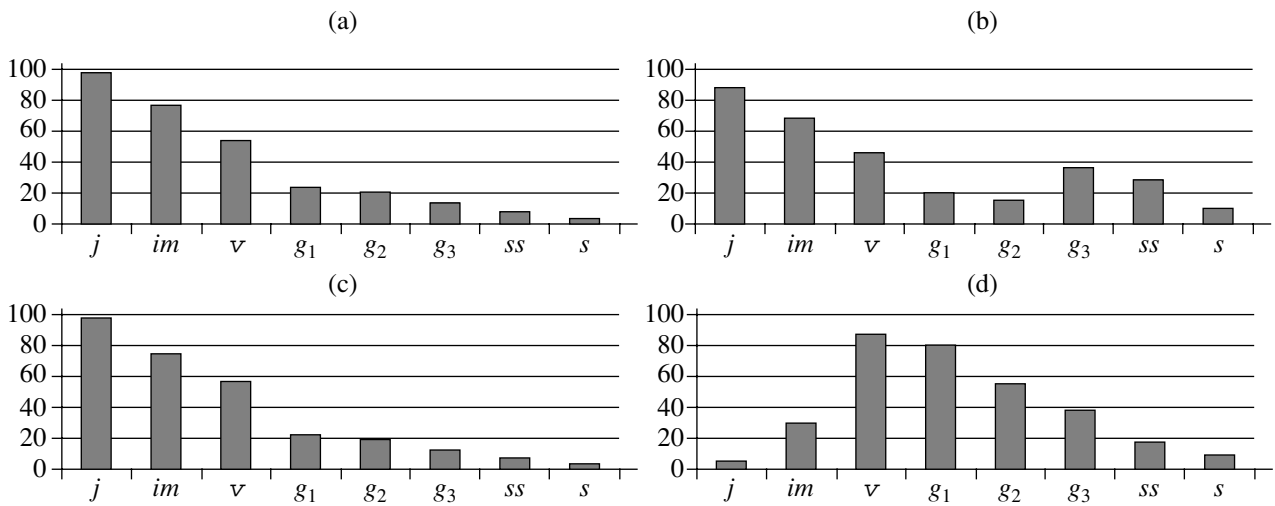
Fig. 4. Age spectra of populations of plants of different biomorph types: (a) monocentric, without vegetative reproduction; (b) implicitly polycentric, vegetative reproduction without rejuvenation of ramets; (c) implicitly polycentric, vegetative reproduction with rejuvenation of ramets; (d) explicitly polycentric, vegetative reproduction with rejuvenation of ramets (results of computer simulation).

acteristic species-specific ontogenetic spectrum (*Tsenopopulyatsii…*, 1988). Populations of plants with the same biomorph type have close variants of characteristic ontogenetic spectrum, since the mean indices of the involvement of ontogenetic groups are determined by the biological characteristics of the species and, above all, specific features of its ontogeny. Variations are related to different environmental influences, such as coenotic situation and climatic, zoogenic, and anthropogenic disturbances.

Let us provide generalizing descriptions of the characteristic ontogenetic spectrum based on field studies of populations of plants of different biomorph types. In plants of monocentric biomorphs (with a limited ability of vegetative reproduction), the self-maintenance of populations is realized by the seed pathway and pregenerative plants predominate (a significant reserve of the plants of this ontogenetic group in a population is necessary because of a high mortality of plants). A sinistral ontogenetic spectrum is also characteristic for that group of implicitly polycentric plants, which form deeply rejuvenated ramets: a maximum in the spectrum is produced due to a mixed (seed and vegetative) self-maintenance of a population. Many implicitly polycentric plants that form nonrejuvenated ramets as a result of vegetative reproduction are characterized by a bimodal ontogenetic spectrum: peaks on the pregenerative group (active seed renewal) and on the group of old generative and subsenile plants (vegetative reproduction). The ontogenetic spectrum of explicitly polycentric plants is characterized by the position of an absolute maximum on young and middle-aged generative individuals, and it is often incomplete.

The spatial structure of plant populations is, to a significant extent, determined by specific features of distribution and interaction of individuals, i.e., above all by the type of their biomorph, due to the attached mode of life of constituent elements. Thus, it was shown (Smirnova, 1987; *Vostochnoevropeiskie…*, 1994) that the spatial structure of populations of monocentric plants is characterized by a mosaic of relatively large spots, comparable to the plant phytogenic field, where individuals of the same ontogenetic state are concentrated. The spatial structure of implicitly polycentric species is characterized by a smaller mosaic of spots. In populations of explicitly polycentric species, plants with different ontogenetic states are relatively uniformly distributed in space.

The patterns described constituted the basis of a mathematical model that prognosticates the dynamics of numbers, density, and age and spatial structure of model populations on the basis of algorhythmization of behavior of the population elements (analog of the description of specific features of the ontogeny).

MATHEMATICAL SIMULATION

The so-called cell-automaton approach in simulation is nowadays the most convenient method for describing the population dynamics of different species consisting of discrete immobile individuals. Von Neumann (1966) was the first to introduce cell automata as mathematical objects for the construction of schemes of self-reproduction of simple engineering devices. In such schemes, the time and spaces were considered as discrete, while interactions between devices were defined only locally, i.e., only between the closest neighbors in space. Later, as the computing technique developed, the cell automata proved to be a flexible tool

allowing simulation of complex spatial structures. Moreover, the schemes using cell automata proved to be more informative in many physical problems than partial differential equations (Toffoli, 1984; Gerhard *et al.*, 1990).

The cell-automaton approach was first used for simulation of plant populations in the 1980s (Komarov, 1982, 1988; Edelstein, 1982; Czaran, 1984; Inghe, 1989, 1990), and this trend was continued by Silvertown *et al.* (1992, 1993, 1994). The application of cell automata in ecology was briefly reviewed (Grabovskii, 1997; Balzter *et al.*, 1998).

Studies of natural populations have shown that the formation of age and spatial structure is affected by both specific features of ontogeny and specific ecological and coenotic situations (*Tsenopopulyatsii*…, 1976; Smirnova, 1987; Zhukova, 1995). The use of the technique of imitation simulation (Komarov, 1982, 1988) allows one to carry out a "pure" experiment, i.e., to follow the development of a model population, not distorted by the influence of above environmental factors, and reveal specific features and leading dependencies of the population level on the ontogenetic characteristics. In such computer experiments, the researcher can test his/her hypotheses and estimate their adequacy. In other words, he/she can see how changes in the ontogenetic characteristics of the population elements (their biological properties) affect the formation of the plant population structure.

Ontogeny of model plants of a "computer" population (for model description see Komarov and Palenova, 2002) is set by parameters like duration and number of ontogenetic states, presence/absence of vegetative reproduction in the course of development, age state of mother plants at vegetative reproduction, age state of daughter ramets, and the number of forming daughter ramets. These parameters are at the same time parameters of the model work. In addition, random appearances of new plants of the youngest age with a certain probability (analog of seed reproduction) and their random extermination, also with a certain probability (analog of external disturbances), are set in the model. Thus, the main population events are simulated: growth and development of plants, seed and vegetative reproduction, and natural or random death of individual plants.

In the model, the space is defined as a regular square lattice, in the nodes of which model plants may be located. This allows an easy determination of the distances between the plants (in lattice steps) and to their closest neighbors.

In the model, the population element, i.e., the ramet or genet at early developmental stages, before the formation of daughter ramets, has always a monocentric structure. Daughter ramets are formed in a close neighborhood to the mother plant (one step). In terms of the model for the plant of implicitly polycentric biomorph) or at a certain distance from the mother plants (three to five lattice steps in terms of the model for the plants of explicitly polycentric biomorph). The ontogenetic state may also be older or younger than that of the mother state.

The authors carried out four series of computer experiments to study, according to the above generalizations, the effects of ontogenetic parameters on the formation of the age and spatial structure of a population of model plants. The plants differed in the biomorph type and degree of rejuvenation of the daughter ramets, which was expressed in the following model parameters: presence/absence of vegetative reproduction, ontogenetic state, and distance between daughter ramets and mother plants. Only one parameter underwent changes from one experimental series to another (variant a—inhibition of vegetative reproduction; b—vegetative reproduction, distance of one step between daughter ramets and mother plant, without rejuvenation of daughter ramets; c—vegetative reproduction, distance of one step between daughter ramets and mother plant, with rejuvenation of daughter ramets; d—vegetative reproduction, distance of five steps between daughter ramets and mother plant, all other model parameters being fixed).

These computer experiments have shown a significant influence on the biomorph type and degree of rejuvenation on the formation of the age structure of populations. Figure 4 demonstrates the variants of the age structure of model populations from different series of computer experiments. As a result of simulation of the populations of monocentric plants, a distinct sinistral ontogenetic spectrum was formed with an absolute maximum on the group of young plants due to the seed pathway of self-maintenance of the population (Fig. 4a). The populations of implicitly polycentric plants with rejuvenation of ramets had a very similar ontogenetic spectrum (Fig. 4c), with the only difference that the young ontogenetic groups of the population comprised predominantly individuals of vegetative origin-ramets. The model populations of implicitly polycentric plants without rejuvenation of ramets were characterized by a bimodal age spectrum (Fig. 4b) with one maximum on the young part of the population and another, on the old one. The model population of explicitly polycentric plants had a maximum of ontogenetic spectrum on the plant of virginil and young generative states (Fig. 4d). Similar types of ontogenetic spectra were described in natural populations as characteristic spectra for plants with the corresponding type of ontogeny (Smirnova, 1987; *Tsenopopulyatsii*…, 1988; Zaugolnova *et al.*, 1991; Zhukova, 1995). Thus, it was shown that changes in a single parameter characterizing the ontogeny of population element lead to a significant alteration of a leading population characteristic.

SPECIFIC FEATURES
OF PLANT ONTOGENY AND POSSIBLE
EVOLUTIONARY CONSEQUENCES

The influence of ontogeny of plants with different biomorph types on evolutionary events in the populations and communities is one more aspect implicitly avoided in demographic studies of plant populations. Investigation of population dynamics in demographic studies is concentrated, above all, on studying the survival and reproduction of individuals (elementary countable units of populations). Such an approach is justified for most animals and monocentric plants, unlike for the explicitly and implicitly polycentric plants.

As shown above, polycentric plants are characterized by vegetative reproduction, as a result of which a clone is formed at a certain stage of genet ontogeny. The genet-clone can be considered as a population locus formed by the ramets with identical genotypes. The description of ontogeny of the plants of different biomorph types has principal distinctions: in the case of monocentric plants (Figs. 1a, 3a), we described the ontogeny of a population element, the ontogeny of an individual, while in the case of polycentric plants (Figs. 1b, 3b, 3c), we describe at the initial stages the ontogeny of a genet, individual (population element) and have to describe thereafter (but do not describe in most studies) the ontogeny of a genet-clone as a community of ramets. It can be seen that, in the ontogeny of polycentric plants, transition to the superorganismic level takes place, since the description of the ontogeny of a genet-clone is already a description of a certain population locus, i.e., an object of the population level.

Polycentric plants are difficult objects for demographic studies at the genet level, since, first, their genets usually live for a long time and, second, individual genets can hardly be identified in natural populations. The latter feature is related to the brevity of morphological relations between the daughter and mother ramets and diffuse spatial structure of clones of many such plants. An additional, purely methodical, difficulty of demographic studies at the level of genets of the population of polycentric plants is the stereotype of traditional description of the ontogeny of these species. First, a successive series of elementary units of the seed origin (genet-individuals) is described, such as primary shoot, primary frutex, loose frutex, turf, grove, etc., and then a successive series of elementary (countable) units of the vegetative origin (ramets) is described, such as tillering, system of partial shoots or frutexes, partial frutex, etc. The ontogeny of the plant as a whole (now genet-clone) is not described, since the characterization of the initial stages of genet ontogeny is replaced by the description of the middle and end of incomplete ontogeny of ramets of the species in question.

Most population studies of polycentric plants are concentrated on the investigation of the rate of ramet appearance and death, and, hence, we can speak in most cases only about the spatial and age structure of ramet populations.

Thus, the ontogeny of explicitly and implicitly polycentric plants is characterized by the transition of their genets during development from the organismic level to the population level; i.e., the ontogeny of the genets of the polycentric plants takes place in a flow of ramet generations (Fig. 5a). This usually escapes attention but is favored by the data itself (Smirnova, 1987). Formalization of the ontogeny description within the framework of the population mathematical model leads to the same conclusion and such an approach has already been realized in some studies of the population life of genets (Palenova, 1993; Falinska, 1995). This concept is essential for understanding the formation of the genetic structure of populations of plants of different biomorphs. The number of individuals (ramets) of the same genotype actually involved in sexual reproduction may differ one-thousand-fold for the genets, "successful" and "unsuccessful in space" (Fig. 5b), which is determined by the number of ramets of specific genotypes present in the population "at a given moment." The involvement (or, in other words, influence on the population gene pool) of genets, "successful" and "unsuccessful in time," may also differ ten- or one-hundred-fold (Fig. 5c). "Unsuccessful" genets were described in literature as a phenomenon of "quasisenility" (Smirnova et al., 1984). Preservation of "unsuccessful" genets in a population leads to a great diversity of free combinations and genetic heterogeneity of the population, which is a significant reserve of hereditary variations. This specific feature of plant ontogeny is an adaptation mechanism of the population level enhancing an increased population stability.

Hence, the population dynamics of polycentric plants may be studied at both the ramet and gene level. Most population studies of the plants of these biomorph types were carried out at the level of ramets. However, studies at the level of genets have also been reported (Eriksson, 1993).

The changes in the genetic structure of a population of clonal plants were described. The number of genets in local populations of some species, which reflects the level of the population genetic diversity, may be determined by the number of first cohort germlings and their subsequent survival (Hartnett and Bazzaz, 1985). A local population of ramets may be formed by a single genet (Oinonen, 1967), but this is an extreme situation. In populations of other species, new germlings-genets appear continuously, and the local population comprises a mixture of genes of different cohorts. Such a situation was described for *Trifolium repens*, in which new germlings appear in the population every year. This process is usually accompanied by microdisturbances. It was shown for *Oenocarpus mapora* (De Steven, 1989) that in the disturbed forests, a high density of genets and multiple seed renewal were observed, while, in the intact forests, the seed renewal is insignif-
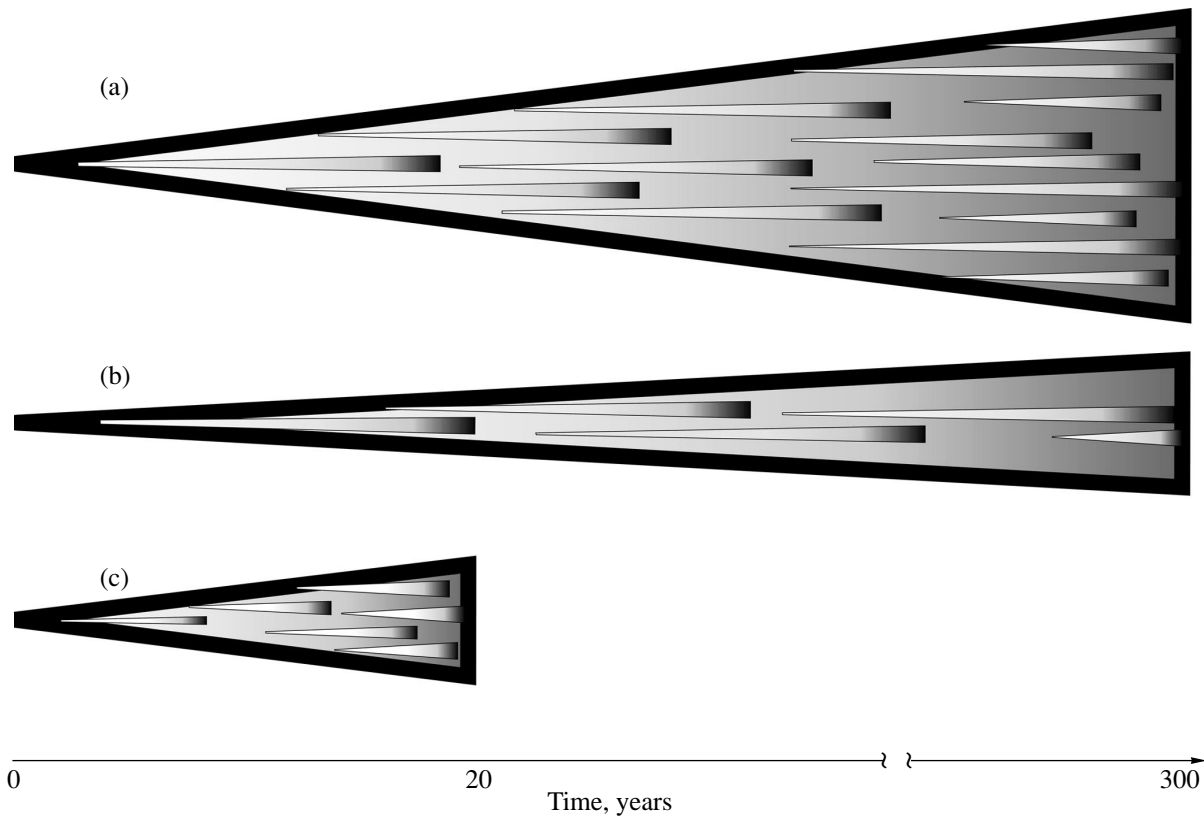
Fig. 5. Schematic diagram of development of different (in "success") genets in a flow of generation of ramets: (a) "successful";
(b) "unsuccessful" in space; (c) "unsuccessful" in time

icant and the population consists of a small number of
huge genets. Similar results were obtained for *Rubus
saxatilis* (Eriksson and Bremer, 1993).

The influence of specific features of the ontogeny of
plants of different biomorphs is significant in the course
of succession processes in communities. A large occu-
pied space and long life of the genets of polycentric
plants, as well as relatively uniform colonization of the
space by genets may lead to its monopolization
(Smirnova, 1987) and, thereby, to a "freezing" of the
community spatial structure. This delays the rate of
invasion of new species in the community or com-
pletely stops the invasion (Smirnova and Korotkov,
2001). As a result, progressive succession is markedly
slowed down or its direction changes to the alternate
one (regressive succession). The huge size of genets of
some polycentric plants (more than 1000 m^2) allows the
populations to have a significant poll of diaspores
(buds), and, hence, fast recolonization of such popula-
tions is possible (Oborny and Bartha, 1995).

In the scale of a plant community, the clone spatial
structure may exceed the habitat structure. Thus, ramets
of the same genet may encounter different conditions
above and under ground, where different selective
forces are active. As a result of selection in such condi-
tions, specialization of individual genets-clones to sub-
niches of the community is possible. Hence, the long

life of genets of polycentric plants insures their popula-
tions against changes of the conditions in time, while
their large size, against changes of the conditions in
space.

Note, in conclusion, that diverse factors affect the
formation of the population structure: from the bio-
coenotic situation, which determines specific values of
the factors of population dynamics to genetic processes
that run in the populations and are, finally, realized as
individual ontogenetic differentiations. In order to
reveal the leading mechanisms of population life, it is
necessary to study and describe events at all levels and
emphasize their significant features. At the level of
individuals, it is advisable to reduce the entire diversity
of life forms plants to three biomorphs and two types of
rape rejuvenation for preliminary estimation of the age
and spatial structure of their populations. This conclu-
sion was confirmed by the construction and investiga-
tion of models of plant population behavior. The results
of simulation suggest that each type of ontogeny corre-
sponds to a certain, repetitive in a series of computer
experiments, type of the age and spatial structure of the
population. It was shown that the ontogeny of a popu-
lation element has such features that changes in a single
parameter lead to significant changes of the leading
population characteristics. For a better understanding
the population dynamics and evolutionary features of

explicitly and implicitly polycentric plants, it is necessary to focus attention on the level of genets and take into account the dynamics of genets, since genetic variability, except somatic mutations, is expressed at this level.

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Estimation of Developmental Stability of Small-Leaved Lime on Reserved and Urbanized Territories

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Received April 24, 2001

Abstract—The developmental stability of small-leaved lime (*Tina cordata* Mill.) was estimated in populations on territories of the Kerzhenskii State Nature Reserve, Nizhni Novgorod District, and in an industrial region of Nizhni Novgorod. The developmental stability was estimated according to the fluctuating asymmetry of the leaf measurements. The results obtained suggest that, in the urbanized territory, the homeostatic developmental mechanisms are weakened, as expressed in the increased degree of leaf asymmetry.

Key words: developmental stability, population, fluctuating asymmetry, leaf system.

The development of methods that allow us to quickly obtain safe information on the natural environmental state and suitability of life activities of humans and other living beings is at present a current task. Studies of the effects of individual anthropogenic factors on living beings does not seem very promising in view of the increasing diversity of anthropogenic influences. The methodology of integral biological estimate of the natural environment was developed (Zakharov, 1993). It is based on the estimation of the state of living beings occurring in the territory in question according to developmental homeostasis.

Fluctuating asymmetry, small nondirected deviations from the organ symmetrical structure, can serve as a measure of efficiency of the homeostatic mechanisms allowing the normal morphogenesis in a certain range of conditions (Zakharov, 1987). The sensitivity of this criterion to the conditions of internal and external medium was demonstrated in a series of investigations. However, most studies were carried out on animals (Zakharov, 1987; *Developmental Stability…*, 1992; *Developmental Homeostasis…*, 1997; Zakharov *et al.*, 2000), while plants were rarely used for such studies (Freeman *et al.*, 1994; Kryazheva *et al.*, 1996; Zakharov *et al.*, 1997).

The aim of this work was to estimate the developmental stability of the small-leaved lime according to the value of fluctuating asymmetry of the leaf system on urbanized and reserved territories.

MATERIALS AND METHODS

The materials were collected in six sites in August 2000. Three of them were located in the Kerzhenskii State Nature Reserve and three others, in an industrial zone of the city of Nizhni Novgorod, near the "GAZ" car plant.

The Kerzhenskii reserve is located on the Nizhegorodsko-Mariiskii Transvolga plain in the subzone of mixed broad-leaved–fir forests. Its area amounts to 46 940 hectares. In site 1 (quarter 73), the leaves were collected in a mixed fir-lime forest, where bracken and whortleberry predominated in the lower layers. Site 2 (quarter 129) was set in the Kerzhenets River floodplain terrace in the lime–maylily–sorrel forest. Site 3 (quarter 179) is located near the settlement of Chernoozer'e.

Site 4 in Nizhni Novgorod is an avenue of limes in a recreation center, 83 hectares in area, located at a distance of 1 km from the car plant. Site 5 is located at a distance of 500 m from the car plant in a small square, 7.6 hectares in area, which is surrounded on three sides by auto routes with the traffic intensity of about 50 vehicles per minute. At site 6, the leaves were collected from the trees represented an avenue running along the lively auto route directly near the car plant walls with the traffic intensity of 60 vehicles per minute. Note that according to the data of the State Committee of Environment Protection of Nizhni Novgorod, the "GAZ" car plant is one of the main polluters of the city's air (*Nizhni Novgorod…*, 1999).

At all sites, the leaves were collected from ten trees, ten leaves from each, and all samples were represented by 100 leaf blades. The leaves were subjected to morphometric analysis. The system of morphological characters was similar to that proposed for the birch (Kryazheva *et al.*, 1996). The following characteristics were measured: the width of leaf halves; the length of the second order vein, second from the leaf base; the distance between the bases of the second order veins, second and third from below; the distance between the ends of these veins, and angle between the principal vein and second vein of the second order.
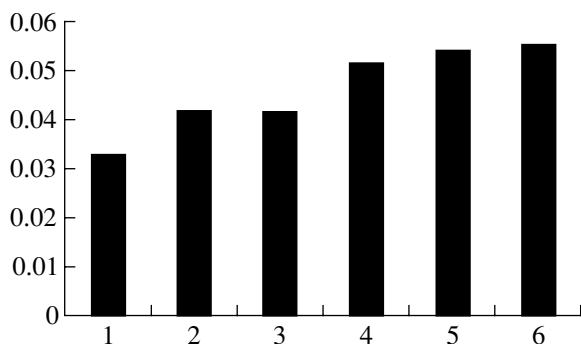
The value of fluctuating asymmetry of measurements (ordinate) in small-leaved lime leaves collected at different sites in the district of Nizhni Novgorod (abscissa).

The level of fluctuating asymmetry, an integral index of developmental stability of plants, was estimated according to the value of mean relative difference per character (arithmetic mean of the ratio of difference to the sum of right and left leaf measurements referred to as a characteristic). It is assumed that the higher this index, the lower the developmental homeostasis. Student's *t*-test was used to evaluate the significance of differences between the samples.

RESULTS AND DISCUSSION

In all three sites in the reserved territory, the level of fluctuating asymmetry of the small-leaved lime leaves was relatively low: 0.0333 ± 0.0017, 0.0421 ± 0.0019, and 0.0422 ± 0.0020 at sites 1–3, respectively (figure). It corresponds to point 1–2 of the five-point scale of deviations from the normal level, proposed earlier for the birch (Zakharov, *et al.*, 2000).

In the city, the developmental stability was much lower. It decreased with the distance from the car plant: 0.0518 ± 0.0021 and 0.0549 ± 0.0024 at sites 4 and 5, respectively. The lowest population index of developmental stability was recorded at site 6, where the trees grow in the direct vicinity of the car plant and, in addition, are subjected to the effect of exhausts: 0.0554 ± 0.0027. (This level corresponds to the critical state of the organism: point 5 of the five-point scale of deviations from the normal level.)

Thus, all studied plots can be divided into two groups. The small-leaved lime populations growing in the Kerzhenskii State Nature Reserve are characterized by a higher level of developmental homeostasis, which is expressed as lower indices of fluctuating asymmetry of leaves than those of the populations on the urbanized territory ($p < 0.01$). In the conditionally control sites of the reserve, the life conditions appear to be the closest to the optimal conditions. On the contrary, the populations of trees on the urbanized territory had higher indices of fluctuating asymmetry of leaves. Homeostatic mechanisms appear to be weakened under the pressure of anthropogenic factors, which is expressed at the morphological level as an increased asymmetry of the leaf system.

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