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From the Editorial Board

The Editorial Board of the *Russian Journal of Ecology* always gives close attention to ecological studies carried out in different regions of Russia. In keeping with this tradition, this issue brings to our readers the most interesting and significant reports presented at the Third All-Russia Population Seminar "Ontogeny and Population" (February 7–11, 2000) held by the Department of Botany, Ecology, and Phytophysiology of Mari State University (the organizing committee was headed by N.V. Glotov).

The problem "Ontogenesis and Population" is one of the central problems of modern population biology. It is now apparent that any analysis of fundamental and applied aspects of the life of natural populations should be based on the concept of life organization levels, such as the cell, organism, population, and biogeocenotic levels. The population level is of special significance, as trends and events occurring at all other levels are reflected in the life of populations. Since the publication of classical works in population zoology, especially the work of S.S. Schwartz and his colleagues, it has become clear that the age composition of a population is very important; in other words, it is necessary to consider the entire "ontogenetic spectrum" of a population, from zygote to dying individuals. Population botany is now following the same trend. As the actual age of many plants is impossible to determine, T.A. Rabotnov, A.A. Uranov, and their followers use the concept of the age (ontogenetic) state. Since the age state reflects the biological age of plants, this approach is often even more reasonable than the use of chronological age.

The program of the seminar included the following topics: genetics of individual development, morphogenesis, spatial and age structure of populations, and

adaptation at different ontogenetic stages. The studies were conducted on various species (plants, animals, and man) using a broad spectrum of methodical approaches (morphological, physiological, biochemical, and mathematical).

At the All-Russia Population Seminars, it became traditional to hold memorial sessions. At the first seminar, this session was dedicated to the memory of L.F. Semerikov, a remarkable researcher who was a major contributor to the development of plant population ecology until his untimely death. The second seminar was dedicated to the memory of T.I. Serebryakova, a distinguished plant morphologist whose works were fundamental for the development of the concept of plant age states. In 2000, the scientific community commemorated the 100th anniversary of the birth of N.V. Timofeeff-Ressovsky, an outstanding Russian scientist who made major contributions to the development of basic fields of natural sciences, such as genetics, radiation biogeocenology, and the theories of population and the biosphere. A special session was dedicated to his memory at the third seminar.

The Fourth All-Russia Population Seminar was conducted at the Koltsov Institute of Developmental Biology, Russian Academy of Sciences, May 18–19, 2000 (the organizing committee was headed by V.M. Zakharov). Proceedings of the seminar will be published in *Ontogenez* (Russian Journal of Developmental Biology, 2001, no. 5). The Fifth All-Russia Population Seminar—"Populations, Communities, and Evolution"—is to be held in Kazan at the Institute of Ecology of Natural Systems, the Academy of Sciences of Tatarstan, in October 2001.

Ontogeny and Population: Developmental Stability and Population Variation

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Abstract—By definition, the ontogenetic and population organization levels are fundamentally different. Studies at these levels are traditionally independent. However, it becomes increasingly evident that special analysis of individuals in terms of ontogeny is necessary for correct estimation of populations and their spatiotemporal dynamics, as well as for understanding the mechanisms of population processes.

Key words: ontogeny, population, developmental stability, population variation

By definition, the ontogenetic and population organization levels are fundamentally different. While studies at the ontogenetic level deal with individual development, the subjects of population studies are aggregates of individuals (populations). Studies in these two fields are traditionally independent from each other. When studying individuals, the organism's state at a certain developmental stage and the dynamics of development (the study of ontogeny per se, whose scope is often restricted to embryonic development) and its spatial heterogeneity (the analysis of differences between individuals) are considered. Studies on populations deal with the state of the aggregates of individuals at a fixed moment of time, as well as its dynamics (analysis of population dynamics) and spatial heterogeneity (analysis of interpopulation and interspecific differences). Usually, the study of populations does not take into account that each individual is an example of ontogeny, so that the assessment of a population is a cross section of ontogenetic trajectories. If this fact is taken into account, the possible ontogenetic changes are regarded as an obstacle to the population assessment and the researcher's task is to eliminate them by analyzing individuals of the same age. However, a special analysis of an individual in terms of its ontogeny is necessary for correct estimation of populations and their spatiotemporal dynamics, as well as for understanding the mechanisms of population processes.

Here, I attempt to analyze the advantages of the methodology based on population assessment, with ontogenetic changes taken into account, for solving the main problems of population biology, including the estimation of population dynamics, interpopulation differences, and interspecific differences.

ESTIMATION OF THE STATE OF POPULATIONS

Estimation of the state of populations is the essence of the population approach. At the population level, the

estimation is based on demographic parameters, such as population size, age and sex composition, and reproductive success (the ratio of the number of progeny to the number of reproducing individuals). From the ontogenetic point of view, the estimation may be based on the state of individuals with regard to developmental stability. In this case, we should estimate the normality, or perfection, of developmental processes, whose main characteristics are developmental disturbances and ontogenetic noise. Whereas developmental disturbances, or phenodeviations, are characterized by substantial morphological changes and are rarely found in natural populations at frequencies more than several percent, ontogenetic noise may serve as an operational criterion for assessing natural populations (Zakharov, 1987). Ontogenetic noise (Waddington, 1957), also called random spontaneous developmental variation (Astaurov, 1978) or realization variation (Strunnikov, 1991), may be most accurately and simply estimated from fluctuating asymmetry of bilateral structures. The advantage of this approach is that the norm (reference point), i.e., the state that must be observed in the absence of perturbations, is known. This normal state is an absolute symmetry, deviations from which constitute the ontogenetic noise. The almost identical phenotypic effects on the left and right sides of the body, which are achieved independently in the course of ontogeny, is maybe the most impressive evidence for the power and accuracy of genotypic determination of the phenotype.

Analysis of ontogenetic noise allows us to estimate the effects of population processes, including evolution, on individual organisms. The estimation of ontogenetic noise seems also promising as a measure of fitness, which, in this case, is estimated as individual's health, rather than as the number of progeny and the contribution to the next generation (which would hardly be possible with natural populations). The advantages of this approach are integrated and sensitive estimations, operational effectiveness, and wide applicability. To illustrate

the usefulness of the proposed approach, let us consider the experimental estimation of the effects of polychlorinated biphenyls (PCB) on American minks *Mustela vison* (Borisov *et al.*, 1997). In the control group, developmental stability in stillborn minks was considerably lower (i.e., the asymmetry was higher) than in live-born animals. Conversely, in the experiment with PCB poisoning, the developmental disturbances were approximately the same in stillborn and live-born minks. Thus, developmental stability is disturbed when the organism's state worsens due to various factors, but this disturbance does not cause the organism's death. Therefore, this characteristic can be used as a sensitive indicator of the organism's state. Consider its applicability to solving the aforementioned problems in population biology.

Population dynamics. This remains a key problem of population biology. The main questions, in the context of this work, are as follows. How does the state of the population change in the course of population cycles? How are these changes related to population density? What is the role of biotic and abiotic factors? What is the role of population density in the changes of the population size? Studies in this field were performed on the common shrew *Sorex araneus* (Zakharov *et al.*, 1991). A negative correlation between developmental stability and population size was found in the cyclic central Siberian population, whose size is presumed to be self-regulated. Therefore, the developmental stability is disturbed (and, hence, the animals' state is considerably altered) at the peak of the population size due to excessive population density. This leads to the subsequent decrease in the population size. Conversely, in the noncyclic southern Finland population of shrews, developmental stability positively correlated with the number of animals. The apparent effect was inverse because both the population size and developmental stability decreased in response to climatic changes. When the population size increases under favorable conditions, the developmental stability is also high. The results obtained indicate that the proposed approach is promising for uncovering the mechanisms of population dynamics: a positive correlation between developmental stability and population density suggests a greater role of environmental factors, whereas a negative correlation suggests self-regulated population cycles, with an increase in population density being a stress factor for the population.

Interpopulation differences. Assessment of the periphery, ecological rather than geographic, of the species range is among the most interesting problems when studying interpopulation variation. A decrease in developmental stability indicates a worse state of organisms at the ecological periphery of the range. For example, we found that the developmental stability of the sand lizard *Lacerta agilis* was disturbed at the southern periphery of its range (Zakharov, 1987). Note that conditions of the ecological periphery of the range may now be found everywhere due to anthropogenic

impact on the environment. In addition, these conditions may emerge in various parts of the range for natural reasons. This is especially distinct in plants. For example, we found that developmental stability in European white birch (*Betula pendula*) in shaded areas was considerably lower than in well-illuminated areas (Zakharov and Krysanov, 1996). Thus, the development of population studies aimed at determining the contributions of geographic isolation and environmental conditions to interspecific phenotypic diversity is currently high on the agenda.

The level of developmental stability is usually similar in many populations, including those located far apart. However, considerable variation in environmental conditions even within a small area is accompanied by deviations of environmental stability. This indicates that, notwithstanding certain differences, many populations of the same species have similar optima of developmental stability. Therefore, it is possible to detect the populations that exist under suboptimal conditions. Each species is adapted to certain conditions, and populations where "something has begun" may be found at the periphery of the species range. In these areas, disturbances of the developmental stability are the cost of living under new conditions.

Different species. Sympatric populations of different species are most interesting objects, as studying them permits comparison of the responses of different species to the same conditions. Such data have been obtained for insects and reptiles (Zakharov, 1987). If the responses are different, this indicates that the same environmental conditions are optimal for some species and suboptimal for others. These differences indicate that "something has already happened," the population has developed certain adaptations, and it can safely exist under the new conditions.

The significance of the approach. The approach based on assessment of natural populations with the use of ontogenetic characteristics has the following main advantages: (1) the possibility to find out not only what occurs but also how it occurs and (2) a high sensitivity, which allows alterations to be detected as early as in the first generation, whether the conditions deteriorate or improve.

Various characteristics of developmental homeostasis, including immunological, cytogenetic, and physiological parameters, have been found to correlate with the estimate of developmental stability (Zakharov and Krysanov, 1996). Therefore, analysis of developmental stability yields estimates not only of the characteristics of morphogenetic processes but also of the general state of the organism. In addition, these estimates correlate with reproductive success, which is a general population characteristic (Zakharov *et al.*, 1991). In general, these data indicate that our approach is promising for assessing the state of populations and is more sensitive than other approaches that are currently in use.

The approach also proved to be promising for practical applications, including background monitoring (under natural conditions) and estimation of anthropogenic impact. The main advantage of this ontogenetic approach is the possibility of detecting alterations in the organism's state in response to various types of pollution when the alterations cannot be detected based on either biodiversity parameters (at the community level) or population characteristics (Zakharov and Krysanov, 1996).

NATURE OF OBSERVED DIVERSITY

An approximate estimation of the nature of observed phenotypic diversity is essential for population studies. Usually, even such an approximate estimation is difficult in natural populations. Genotypic diversity is generally assumed to be the main cause of phenotypic diversity. This is only partly true and sometimes completely wrong. It has been found that a considerable proportion of the total phenotypic variation (50% or even more) in natural populations may be accounted for by ontogenetic noise. This variation may largely determine the dynamics of phenotypic diversity observed in natural populations. One example is the aforementioned data on common shrew population dynamics in different regions. In the noncyclic shrew population of southern Finland, the level of variation determined by ontogenetic noise changes in parallel with the general phenotypic diversity, whereas this variation in the cyclic population of central Siberia dramatically increases during stress and largely determines phenotypic diversity at a peak of the population size (Zakharov *et al.*, 1997).

MECHANISMS OF EVOLUTION

The population–ontogenetic approach permits tracing the development of differences between different forms. Such studies have been performed on several models. Consider the following example. More than 10 forms of barbel were found in Lake Tana (Ethiopia) during a special study. They were regarded as either separate species or intraspecific forms. All fish had approximately the same size but represented different life forms. The morphological differences between them were greater than the differences usually observed between genera. The estimation of a set of morphological characters (dimensions) made it possible to trace the divergence of these forms into different ontogenetic channels (so-called creods). Some of them were found to diverge at late ontogenetic stages (Mina *et al.*, 1996).

In addition, the population–ontogenetic approach may help to determine why and how the observed phenotypic differences between the forms emerge. For example, the ontogeny of the blunt-nosed and pointed-nosed forms of lenok (*Brachymystax lenok*) was also

found to diverge into creods. Heterochrony is the main mechanism of their differences (Alekseyev, 1994). Another example is the fast- and slow-growing forms of the char (*Salvelinus alpinus*). The ontogeny may be monitored using the recording structures; in the given case, these are fin rays. This method allowed Alekseyev *et al.* (1998) to estimate the growth rate and its possible changes during ontogeny for different individuals in a population. On other objects, it was demonstrated that fast-growing forms had a higher developmental stability (Zakharov, 1987). In general, the analysis of recording structures is an important independent line of research (Klevezal, 1988); it substitutes for the experimental approach in the case of long-lived species, where the latter is almost impossible.

The population–ontogenetic approach can also be used for experimentally estimating processes in natural populations, with certain environmental factors being taken into account. The simplest method of this estimation is to incubate the offsprings of animals from different parts of the species range at different temperatures (Zakharov, 1993). For example, fruit flies (*Drosophila subobscura*) from Norwegian and Italian populations exhibited the same pattern of the dependence of wing length on temperature; however, the respective experimental curves were parallel, shifted in the direction of the modificational changes that were similar in both populations. Significant interpopulation differences at all temperature regimes studied indicate that the new reaction norm is determined genetically. Similar data were obtained for lizards of the genus *Lacerta*. The dependence of the number of femoral pores on temperature had also the same pattern for all forms studied; the experimental curves were parallel and shifted in the direction of modificational changes, namely, from the northern to the southern *Lacerta agilis* subspecies (*L. agilis exigua* and *L. agilis bohémica*, respectively) and then to the southern species, *L. striata*. These data suggest that the current interpopulation and interspecific differences have developed via genetic determination of a new reaction norm based on a modificational response. Estimation of the developmental stability has revealed that what only emerges at an increased temperature and disturbed development in one form may appear at a lower temperature and high developmental stability in another form. The results of the aforementioned comparison between two species under natural conditions indicate that this microevolutionary process has actually occurred, and, as a result, suboptimal conditions have become optimal.

Thus, evolutionary transformation begins from ontogenetic changes rather than mutations. In terms of population genetic models, nothing at all occurs in this case. Therefore, we may describe the main stages of evolutionary transformation as follows.

A population originally lives under optimal conditions and is characterized by high developmental stabil-

ity and genetic coadaptation (stage 1). In the case of environmental stress under new conditions, developmental stability decreases; this decrease occurs in the form of the organism's direct response to environmental factors as early as in the first generation (stage 2). If many generations of the population live under these conditions, adaptive genetic changes usually occur, which allow the population both to survive and to adapt better to the new conditions, so that environmental stress considerably decreases. However, homeostasis is not yet improved at this stage. Apparently, this is mainly due to genetic stress caused by the genetic changes that ensure survival under the new conditions but disturb the preexisting genetic coadaptation (stage 3). Subsequent genetic transformations may result in a new genetic coadaptation and restore homeostasis, which turns the suboptimal conditions into optimal (stage 4).

The entire four-stage cycle is a microevolutionary transformation determining adaptation of the population to the new conditions. This is accompanied by a change of optimum: originally suboptimal conditions become optimal. Apparently, this cycle is often not completed; it may be stabilized at any of the above stages. Such situations are usually described as the ecological periphery of a species range. Decreased homeostasis in these populations is the cost of survival under new conditions, at the breaking point of the species' potential.

Unfortunately, it is difficult to follow the entire process from the beginning to the end, mainly because this would require a long time. However, it is possible to test the model described above by comparing the populations that are at different stages of the cycle. Considerably lower developmental stability at the ecological periphery of the species range than in the populations living under usual conditions, which has been observed in many studies (Soule, 1967; Soule and Baker, 1968; Zakharov, 1987), fits stages 2 and 3 of the cycle. Differences in the level of developmental stability between sympatric populations of related species are evidence that disturbed developmental stability may be restored by means of gradual adaptations (i.e., the transition between stages 3 and 4 is possible). Disturbances of developmental stability at the ecological periphery of the ranges of widespread species and high developmental stability in the populations of specialized species indicate that these species respond differently to the same conditions. The zone of sympatry may be an ecological periphery for one species and an optimal habitat for the other. Correspondingly, the conditions of this zone disturb developmental stability of the former species and ensure a high stability of the latter one.

In general, analysis of natural populations with regard to ontogenetic changes in them seems to be a promising avenue of further development of population studies. This approach will help us to go from phenomenology to the mechanisms, to uncover the causes of

the observed differences, and to turn from studying populations and species within the framework of population-genetic models of evolution and speciation to estimation of the state and dynamics of populations and mechanisms of their evolution.

We have recently witnessed an impressive intervention of genetic views into population studies. The warning that an organism is not "a sac of beans" (genes) proved to be justified for the most part. At the same time, the insistent call to put on "genetic glasses" has distorted the "eyesight" of many researchers in the field of population biology, so that they started seeing genotypic alterations looming behind any phenotypic change. The importance of "ontogenetic glasses" now becomes increasingly obvious. An ever-increasing number of researchers realize that they see worse and worse without such glasses.

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Diversity of Ontogenetic Pathways in Plant Populations

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Abstract—Population heterogeneity in caespitose, fibrous-rooted, brevirhizomatous, stoloniferous, and tap-rooted herbaceous and woody plants is described. This heterogeneity is caused by the multivariant character of plant ontogeny (i.e., its dimensional, morphological, rhythmological, and temporal multiversality), which is regarded as the main adaptation mechanism operating in plant populations because it provides for the diversity of ontogenetic pathways under different ecological conditions.

Key words: ontogeny, multivariant development (with respect to dimensions, morphology, reproduction, rhythms, and dynamics), biomorphs, morphogenesis, population, age states, ecotope, anthropogenic impact

Profound knowledge of the population life of plants is a prerequisite for developing the theoretical bases of ecological monitoring and assessing the state of renewable natural resources, which implies the necessity of studies on plant population heterogeneity from the population–ontogenetic aspect (*Ekologiya...*, 1998; *Zhizn' populyatsii...*, 1998). In this context, an important task is to distinguish ontogenetic groups as the sets of individuals (or vegetative ramets) of the same biological age within populations. This task is impossible to accomplish without the detailed analysis of ontogeny in taxonomically different plants of different biomorphs.

In the 20th century, numerous independent attempts to divide plant ontogeny into periods were made by Russian and foreign scientists. Rabotnov (1950) proposed a general scheme of periodization by the criterion of biological age. Uranov (1975), who approached the problem in terms of energetics, estimated the energy value of each age state and introduced the coefficient of cenopopulation akeness. This periodization of plant ontogeny was elaborated and appended in subsequent studies (*Tsenopopulyatsii...*, 1976; Zhukova, 1983, 1995; Smirnova, 1987; Zaugol'nova *et al.*, 1988; *Vostochnoevropeiskie...*, 1994; *Ontogeneticheskii atlas...*, 1997; Gatsuk *et al.*, 1980).

According to modern views, the complete ontogeny of perennial polycarpic plants includes four periods and 12 ontogenetic (age) states, including the cryptogenerative state (g_0 , the first stage of the generative period) described by E.V. Shestakova (*Ontogeneticheskii atlas...*, 1997). In addition, three groups of temporarily nonflowering generative plants—young (g_{1v}), middle-aged (g_{2v}), and old (g_{3v})—are distinguished. In monocarps (including annuals), the generative period completes ontogeny, as the postgenerative period is absent.

To date, the validity of this concept has been confirmed by the detailed descriptions of ontogenetic states in more than 540 species of higher plants, ferns (Shorina, 1991), and lichens (Suetina *et al.*, 1997). The proportions of different ontogenetic groups in the age spectrum of a population determine its demographic structure and the stage of its development in the population flow (Uranov, 1975). The classification of populations is based on identification of groups making the most notable contributions to the “adult” part of the age spectrum (*Tsenopopulyatsii...*, 1976; Zaugol'nova *et al.*, 1988; *The Population...*, 1985). Hence, the ontogenetic spectrum is an important parameter of each population, as it characterizes the current state of the population and allows estimation of prospects for its future development.

The purpose of this work was to analyze the factors providing for realization of different ontogenetic pathways and specific features of population diversity in different ecological situations.

MATERIALS AND METHODS

Material was collected in natural meadow cenopopulations (CPs) in central, northwestern, and northern regions of European Russia; forest and meadow phytocenoses of the Mari El Republic; and plantations of medicinal herbs at the agrobiological stations of Moscow State Pedagogical University and Mari State University. The conventional population–ontogenetic methods of sampling were used. Studies were performed on *Chelidonium majus* L., a tap-rooted paucennial plant (12 CPs); perennial herbs, including fibrous-rooted *Valeriana officinalis* L. (25 CPs), *Plantago major* L. (71 CPs), and *Polemonium caeruleum* L. (18 CPs); caespitose *Dactylis glomerata* L. (24 CPs); brevirhizomatous *Plantago lanceolata* L. (17 CPs); and stoloniferous *Trientalis europaeum* L. (23 CPs).

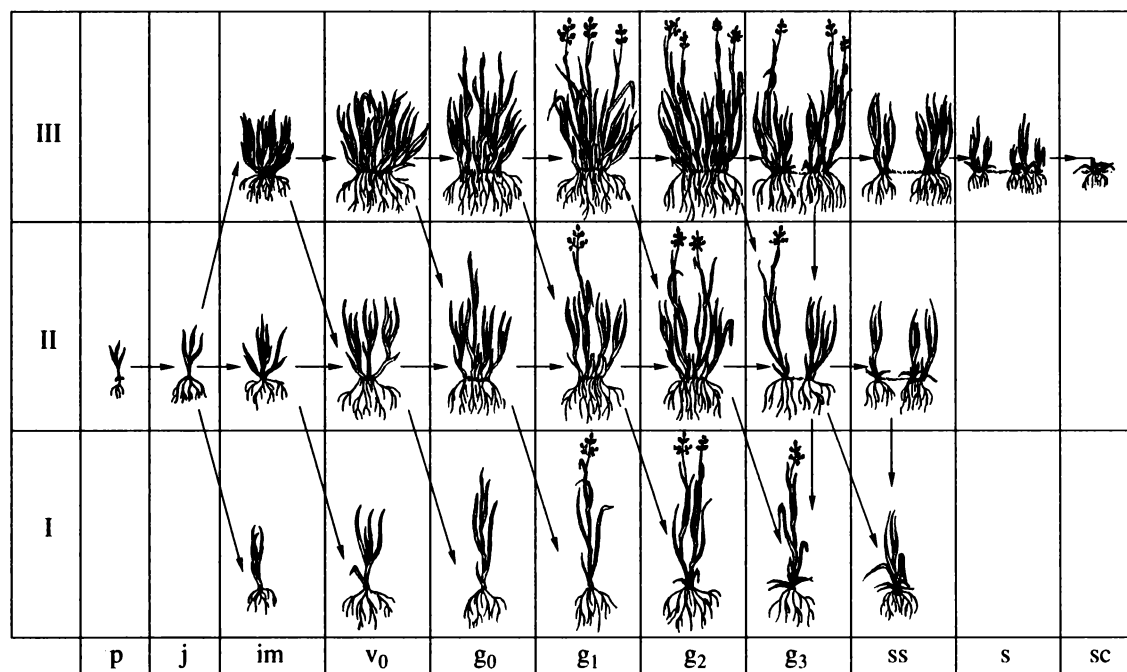


Fig. 1. Dimensional variants of ontogeny in *Dactylis glomerata*. Ontogenetic states: (p) seedling, (j) juvenile, (im) immature, (v₀) virginal, (g₀) cryptogenerative, (g₁) young generative, (g₂) adult generative, (g₃) old generative, (ss) subsenile, (s) senile, (sc) senescent; (I–III) levels of vitality (low, medium, and high), arrows indicate possible transitions from level to level.

Woody plants were represented by *Betula pendula* Roth. (4 Cps).

RESULTS

The complexity of natural phenomena, including individual development, does not fit in the framework of concepts regarding the ontogenetic states as static. In population studies of the 1970s and 1980s, different variants of ontogenetic states were discovered (Tsenopulyatsii..., 1976; Zaugol'nova, 1988; Zhukova, 1995) and, on this basis, the concept of multivariant ontogeny (in other words, ontogenetic multiversality) was formulated. The basic factor providing for a high plasticity of plants include their modular organization, unlimited growth, attached mode of life, and the presence of multipotent meristematic cells (Zaugol'nova *et al.*, 1988; Zhukova, 1995). These properties manifest themselves in a broad spectrum of structural units (modules or phytomers), their various combinations in different biomorphs, and differences in the rate of their formation and the duration of their existence. Hence, plants in any age state may demonstrate a wide range of variation in the structural organization, vitality, methods of reproduction, and developmental rate within the limits of a species-specific genetic program of ontogeny (Glotov and Zhukova, 1995).

Abundant factual material accumulated to date provided the basis for classifying ontogenetic multiversality into two supertypes, (I) structural and (II) dynamic; the first includes three types: dimensional, morpholog-

ical, and reproductive multiversality; the second includes the multiversality of growth rhythms and the developmental rate (Zhukova and Komarov, 1990; Zhukova, 1995). Population heterogeneity within each ontogenetic group can be described according to this classification.

Dimensional multiversality. Individual diversity in each ontogenetic group is described using a set of additional quantitative characters (morphological, anatomical, etc.) characterizing the life state (vitality) of an individual. In other words, vitality is a parameter characterizing the degree of an individual's thriving in the cenosis and prospects for its future development (Zlobin, 1989; Ermakova and Zhukova, 1985). Vitality is estimated in grades (3–8) from the strength of the vegetative and reproductive organs and resistance to adverse influences (Fig. 1). When the age–vitality spectra are constructed, the proportions of the subgroup differing in vitality are determined within each ontogenetic group.

To estimate the dynamics of vitality, Ilyushechkina (1998) proposed the coefficient of switching between the life states of an individual, which is determined as the number of changes in the level of vitality during ontogeny. The analysis of generalized data on the number of such switches per individual in cultivated *V. officinalis* plants showed that vitality remained unchanged in 28% and changed once in 25.9%, twice in 35.2%, three times in 25.9%, and four times in 11.1% of the plants. Five changes were observed in only one case, at

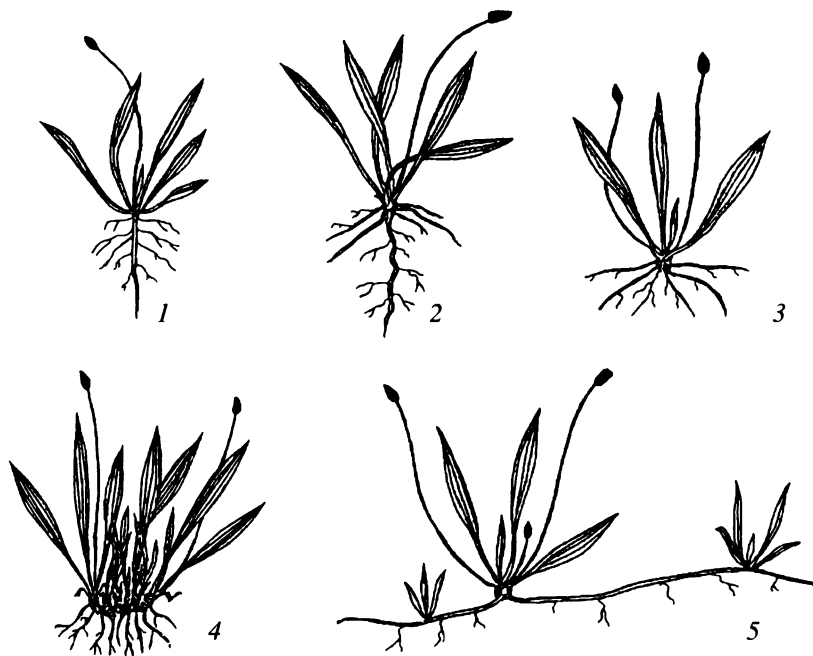


Fig. 2. Different biomorphs of *Plantago lanceolata* in the young generative state. Monocentric biomorphs: (1) tap-rooted, (2) brevirhizomatous–tap-rooted, (3) brevirhizomatous–fibrous-rooted; (4) cryptopolycentric, multirosette brevirhizomatous biomorph; (5) polycentric, creeping-rooted biomorph.

the maximum planting density (10×10 cm). The dimensional variability of plants in different ontogenetic states and changes in vitality during ontogeny were also observed in woody plants, such as *Euonymus verrucosa* Scop., *Quercus robur* L., and *Picea schrenkiana* Fisch. et Mey. (Vostochnoevropeiskie..., 1994).

Thus, the diversity of life states (variants of vitality) of the same plant during its individual development offers the possibility of choosing between numerous ontogenetic pathways, which provides for more efficient adaptation to permanently changing environmental conditions in plants of different biomorphs.

Morphological multiversality underlies the formation of different biomorphological groups within the same CP. The shoot and root systems of herbaceous plants in each ontogenetic state are fairly labile and can be within and between CPs. Upon strong anthropogenic stress, this can lead to malformations or the appearance of several variants of a certain biomorph in conspecific adult plants.

Thus, Zhukova and Osmanova (1999) described three types and five variants of biomorphs in young generative *P. lanceolata* plants (Fig. 2): (I) the monocentric type included (1) tap-rooted and (2) brevirhizomatous–tap-rooted plants, in which ramet separation and rejuvenation occur relatively rarely, and by (3) typical brevirhizomatous one- or few-rosette plants; (II) the cryptopolycentric type comprised (4) brevirhizomatous multirosette plants; and (III) the polycentric type was

represented by creeping-rooted plants (5) with a high degree of ramet rejuvenation and intensive vegetative reproduction. The set of these biomorphs in different *P. lanceolata* CPs (Fig. 3) apparently depended on both the granulometric composition of soils and the type of anthropogenic influences. Their occurrence in the same CP could be determined by the micromosaic structure of an ecotope, which promoted the implementation of different genetic programs of individual development and, hence, made possible the choice between different ontogenetic pathways.

In the course of studies on fibrous-rooted plants, *V. officinalis* and *P. major*, diverse manifestations of the morphological multiversality of vegetative and generative organs were observed at different stages of plant ontogeny. In *V. officinalis*, changes in the morphological structure of leaf blades, inflorescences, and flowers in many plants were described (Ilyushechkina, 1998). The highest level of morphological diversity was observed in the group of young generative plants g_1 of *V. officinalis* and some other species (*Primula veris* L., *Lysimachia nummularia* L., and *L. vulgaris* L.), and the lowest level, in the group of old generative plants g_3 (Zhukova 1995; Ilyushechkina, 1998). The latter was probably explained by the early death of plants with morphological abnormalities, i.e., by implementation of the programs of incomplete ontogeny. This also follows from the incomplete composition of *V. officinalis* CPs growing near roads, in which up to 80% of plants

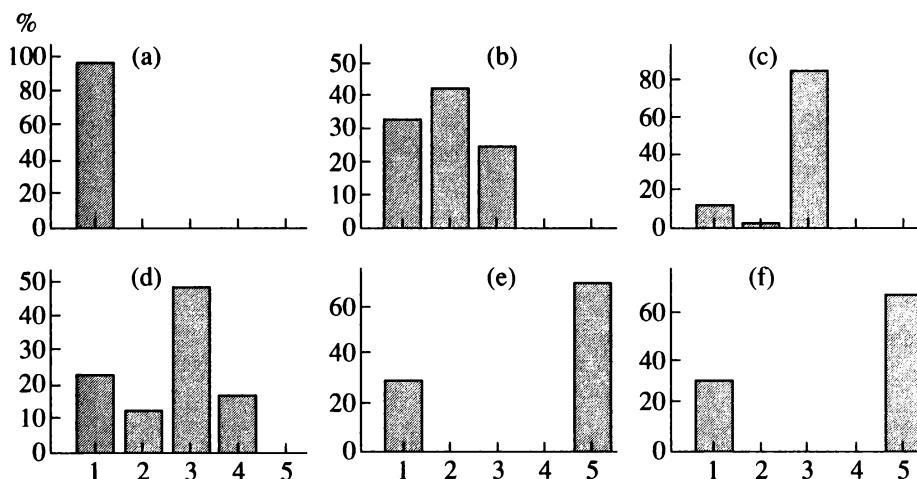


Fig. 3. Frequencies (%) of various biomorphs in *Plantago lanceolata* cenopopulations growing in different habitats: (a) upland meadow (safety strip, sandy substrate); (b) ecotonal cenosis on a forest margin (rubbly substrate); (c) pasture on a floodplain meadow (loam); (d) upland meadow (sandy loam); (e, f) transitional meadows on the slopes of an irrigation channel with compacted and loose soils, respectively. For other designations, see Fig. 2.

develop according to an altered morphogenetic program.

In ecologically clean habitats, morphologically multivariant ontogeny in *V. officinalis* is an extremely rare phenomenon. In *P. major*, Zhukova and Shestakova (1995) described changes in the type of shoots under the effect of pathogenic fungi or herbicides and the appearance of birossette and suprasemirosette shoots and paniculiform inflorescences in addition to rosette vegetative shoots and semirosette generative shoots. According to T.A. Polyanskaya (unpublished data), *Trientalis europaeum*, a polycarp that forms underground stolons, is characterized by a highly variable morphological structure of the suprarosette shoot. Its variants are as follows: the appearance of one larger leaf in the upper rosette and assimilatory leaves (instead of squamiform) in the elongated part of the shoot; the formation of second-order suprarosette shoots in the axils of squamiform leaves and specialized stolons, which initially grow above the ground but subsequently penetrate the litter and form tubers; and, finally, the formation of additional flowers. The increase of the assimilatory surface in the former three instances improves the vitality of shoots, whereas the formation of additional flowers and stolons changes the course of ontogeny and can provide for more intensive seed or vegetative reproduction. Thus, changes in the genetically determined program of vegetative or generative shoot morphogenesis can amend the general program of complete and incomplete ontogeny and, at the same time, make additional methods of reproduction (*multivariant reproduction*) possible, such as the formation of root suckers in *P. lanceolata* and *Taraxacum officinalis* L., underground stolons in *Ranunculus*

repens, and epigeogenic rootstocks in *Dactylis glomerata* L.

The *rhythmological multiversality* of ontogeny manifests itself in the asynchronous onset of a certain phenophase in plants of the same cenopopulation and different local populations. The comparison of flowering rhythms in *B. pendula* trees growing under urban conditions showed that the timing of corresponding processes varied depending on the ontogenetic state. In g_2 trees, the process of flowering was usually less extended in time, whereas g_1 and g_3 trees had broader spectra of phenophases on each date of observation (Fig. 4). The diversity of phenorhythms in the groups of trees in each ontogenetic state is a stabilizing factor providing for the self-maintenance of *B. pendula* populations in urbanized areas (Solov'eva, 2000).

The fifth, least studied, type of multivariant ontogeny concerns its *temporal multiversality*, i.e., the existence of variants differing in their developmental rate. This phenomenon, which also accounts for the diversity of ontogenetic pathways, can be observed in the course of long-term monitoring of marked plants. Observations showed that the proportion of plants developing at the normal rate does not exceed 20% in natural populations and ranges from 3 to 80% in plantations (table). Retarded development is more frequent among perennial plants than among annuals, such as *Chelidonium majus* (Skochilova, 1999). Plants often enter the state of secondary dormancy. This phenomenon was recorded at different ontogenetic stages in *D. glomerata*, *P. lanceolata*, and *P. major* but was not observed in *Ch. majus* and *V. officinalis*. In some cases, a plant repeatedly enters this state in the course of its ontogeny. The flowering of juvenile and immature plants—an illustrative example of accelerated development—is also fairly common (e.g., in *P. major*; Zhuk-

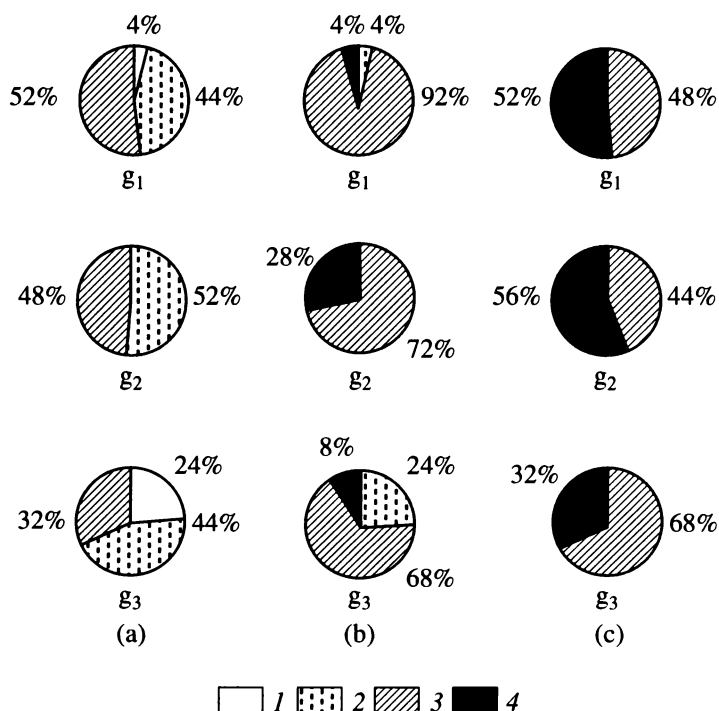


Fig. 4. Specific features of flowering rhythms in *Betula pendula* trees at different ontogenetic stages as of (a) April 26, (b) April 28, and (c) April 30, 1999: (1) budding, (2) onset of flowering, (3) mass flowering, (4) end of flowering.

ova *et al.*, 1996). This specific kind of neoteny was described in many species used in our research. In *P. major* and *V. officinalis*, for example, some pregenerative plants directly entered the postgenerative period, so that up to five ontogenetic stages were missing. The reduction of ontogeny occurs under the effect of both abiotic factors (drought, treatment with herbicides, high doses of mineral fertilizers, etc.) and biotic factors (intra- and interspecific competition).

Reversions to earlier ontogenetic stages may be either slight (from the subsenile to the old generative state) or, in many cases, more profound (to the young generative, immature, or juvenile state), as was observed

in *P. major* (Fig. 5). The latter is observed in the ramets in which additional foci of the meristem appear or dormant buds awake.

The data on temporally multivariant ontogeny in *P. major* ssp. *major* Pilger, obtained by Zhukova (1995) in experimental plantations and Ivshin (1999) in natural populations, provided conclusive evidence that possible combinations of different developmental rates in the course of individual plant development can provide for the diversity of ontogenetic pathways owing to differences in the duration of each age state and variation in their sequence (Fig. 5). This improves the adaptation potential of a population in different ecological situa-

Frequencies (%) of classes of temporally multivariant development in cenopopulations of tap-rooted, fibrous-rooted, and brevirhizomatous plant species

Class	Species					
	1	2	3	4	5	6
Normal development	3.4–50.2	9.1–100.0	4.7–23.0	5.0–83.0	13.3–93.3	5.0–80.0
Accelerated development	19.3–69.6	9.1–100.0	27.3–85.7	79.0–86.0	0–33.3	2.3–90.0
Retarded development	24.7–32.7	9.1–90.9	0–42.0	0–24.0	6.7–33.3	75.0–100.0
Temporary dormancy	–	–	9.5–39.5	0–9.0	0–26.7	2.3–5.0
Rejuvenation	–	0–44.4	3.3–6.0	10.0–42.0	0–13.3	–

Note: (1) *Chelidonium majus*, (2) *Valeriana officinalis*, (3) *Polemonium caeruleum*, (4) *Plantago major*, (5) *P. lanceolata*, (6) *Dactylis glomerata*; (–) classes not recorded in the cenopopulations studied.

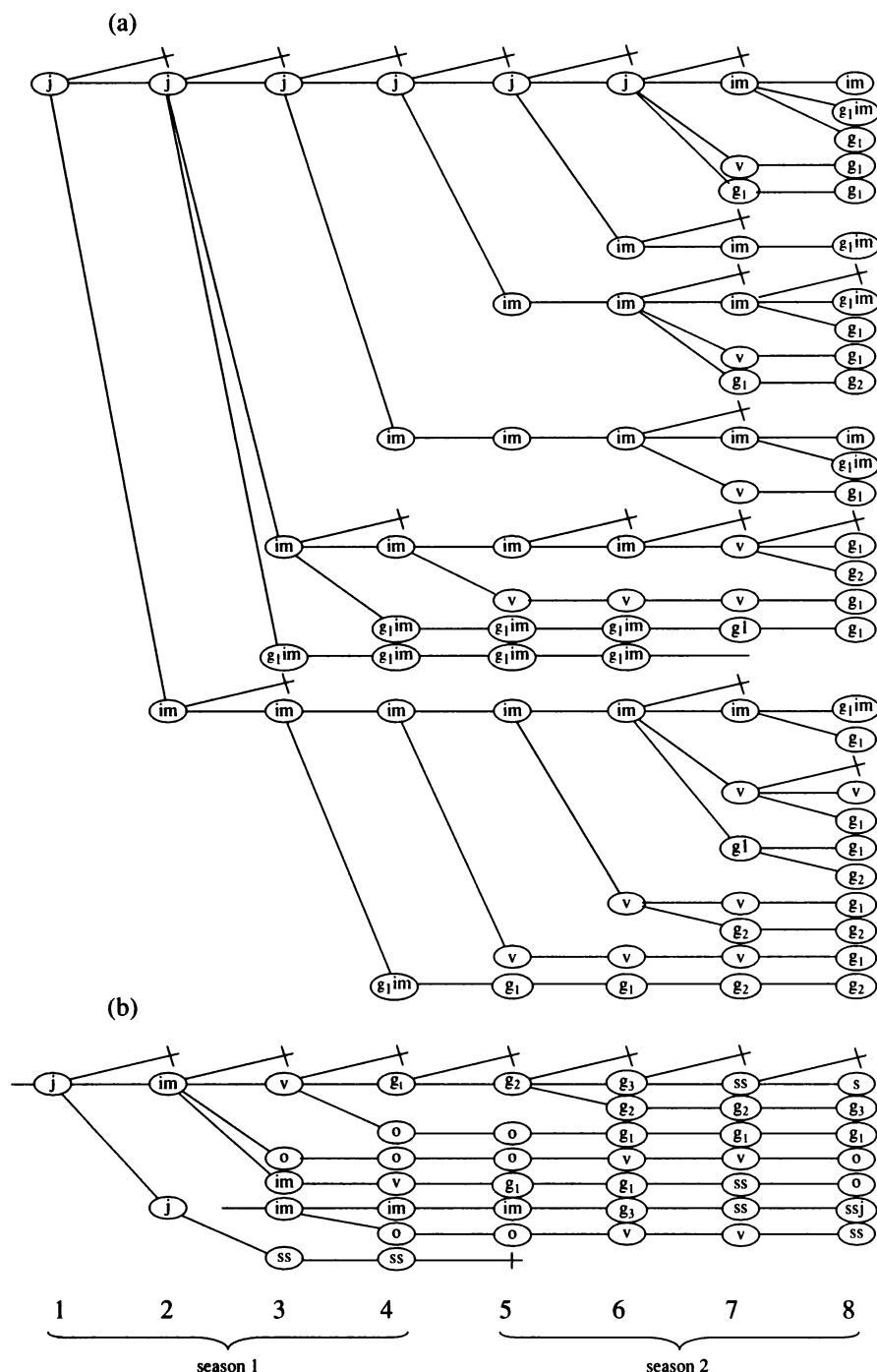


Fig. 5. Diversity of ontogenetic pathways in *Plantago major* in natural and cultivated populations of (a) the Marii El Republic and (b) Moscow oblast. A line shows transition to the next state; a line with a cross indicates plant death; (o) the state of secondary dormancy; (1–8) dates of observation. For indices of the ontogenetic states, see Fig. 1.

tions and provides for its permanent heterogeneity and, hence, stability.

Computer simulation experiments with the use of discrete algorithmic models (Zhukova and Komarov, 1990) showed that the removal of plants with retarded or accelerated development from a population can

sometimes bring it to the critical state. Polenova (1991) observed interfamilial differences in the rate of individual plant development in cultivated *Trifolium repens* L. Statistical analysis revealed families with the retarded or accelerated transition to the generative state. The pattern of variation in this trait was interpreted as evidence for its genetic nature.

Thus, each ontogenetic group may include several subgroups differing in the vitality, biological and morphological parameters, growth rhythms and developmental rate, and, in some cases, physiological, biochemical, and other characteristics.

Numerous studies on ontogeny in more than 450 higher plant species provided conclusive evidence that, in most cases, there are both the basic (modal) ontogenetic pathway and numerous additional pathways, which are related to dimensional, morphological, or dynamic multiversality of individual plant development. Multivariant ontogeny aids in broadening the ecological niche of a species, reducing plant elimination under constantly changing environmental conditions, and maintaining population density. On the one hand, this provides for a high genetic heterogeneity of plant populations; on the other, as noted by Raff and Kaufman (1986), the existence of different developmental pathways based on the same genome, along with the complexity morphogenetic programs, is a mechanism providing "raw material" for evolutionary transformations. Different developmental pathways represent the differential behavior of genetically similar individuals under changing environmental conditions.

Thus, multivariant ontogeny in all its manifestations is a widespread mechanism of adaptation operating at the population level, which determines heterogeneity and, hence, stability of plant populations in ecosystems. Therefore, the assessment of ontogenetic diversity and various manifestations of multivariant development in plant populations can indicate optimal measures aimed at natural resource conservation and rational use.

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Tree Ontogeny and Its Reflection in the Structure and Dynamics of Plant and Soil Covers

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Abstract—Based on the results of our own long-term experiments and the analysis of published data, the process of individual development (ontogeny) of trees and the parameters of ontogenetic stages are described. Changes in the environment-forming (edificatory) role of a tree in the course of ontogeny and upon its completion are characterized. The performance of this role leads to the formation of the following components of biogeocenosis heterogeneity: phytogenic fields of trees, “gaps in the tree canopy,” and windfall–soil complexes. The data concerning the interrelation of structural transformations of the plant and soil covers in the course of forest vegetation and soil formation on the primary substrate are reviewed.

Key words: ontogeny, ontogenetic stages, gaps in the tree canopy, windfall–soil complexes, heterogeneity and mosaic structure of plant cover

Modern ecological concepts, such as “gap mosaic” and the “mosaic-cycle concept of ecosystems” (*The Mosaic-Cycle...*, 1991; Smirnova, 1998a, 1998b) provide the methodological basis for solving the problems of biodiversity conservation. The essence of these concepts is that the maximum taxonomic diversity is characteristic of the communities with greater structural diversity and high environmental heterogeneity. Studies on the population structure of communities show that intracenic environmental heterogeneity strongly depends on the peculiarities of population life of the species representing different kingdoms, primarily plants and animals. The population life of edificators (Sukachev, 1975), or environment-forming species, is a factor integrating the population life of numerous species in a community (Smirnova *et al.*, 1993). Edificators form the largest and long-lived population mosaics, which involve the largest proportion of energy and matter into the cycle of generation change. In the process of ontogeny—individual development from birth to death—individuals of these species significantly transform the environment, which concerns changes in the dynamics of PAR (photosynthetic active radiation), hydrologic and temperature regimes, micro- and mesorelief, the structure of the soil cover, etc. Environmental heterogeneity, formed as a result of continuous generation change in the populations of edificators, provides the possibility of sustainable existence for subordinate species with different cenotic and ecological properties.

Trees with different types of strategies, primarily competitive and tolerant (*Vostochnoevropeiskie...*, 1994), are the main environment-forming species in forest

biogeocenoses. Knowledge of the features of their individual development and the methods of environment transformation makes it possible to propose measures to protect and restore the species diversity of forests.

The purpose of this work was to reveal specific features of the environment-forming effects of trees in different periods of their ontogeny on the vegetation and soils of forest biogeocenoses.

BRIEF DESCRIPTION OF TREE ONTOGENY

The descriptions of ontogeny in different tree species of Eastern European forests were published earlier (*Diagnozy i klyuchi...*, 1989; Smirnova *et al.*, 1999). We present short generalized diagnoses of the ontogenetic states of trees. Since trees exert their environment-forming influence within the stratified structure of cenoses, it is noted to which layer the plants of each ontogenetic stage belong. The classification of layers is given by life forms (Korchagin, 1976). The following layers are distinguished: (A) adult tree layer (in forestry, the main stand, or overwood); (B) adult shrub layer (in forestry, underwood); (C) the layer of herbs and dwarf shrubs.

Seedlings (pl)—nonbranching plants formed from a seed in the year of its germination. They have an embryo root and a shoot with seed lobes, which can be located both above (in most species) and under the ground (in oak).

Juvenile trees (j) usually have no seed lobes but retain juvenile (infantile) structures. The epicormic shoot (trunklet) is nonbranching, and the leaves or needles are of a juvenile form; the root system consists of

an embryo root and a small number of branch roots. Seedlings and juvenile individuals are the components of the herbaceous–dwarf shrub layer and have a high shade tolerance.

Immature trees (im) are intermediate between juvenile and adult plants. The shoot system consists of branches of the 2nd to 4th–5th orders; the crown has not yet been formed; the total number of branches is small; and trunk diameter is no more than two times greater than the diameter of large branches. The trunk increments insignificantly exceed in the length and diameter the increments of branches, and, hence, the tree crown is rounded. Leaves or needles have the adult structure, except for the trees with complex leaves (ash). The root system includes the embryo root (or its basal part) and branch roots; in some species, additional roots develop. Immature trees come to the shrub layer, and their light demand increases. If illumination proves to be lower than required, the development of trees is inhibited and they die off.

Virginal trees (v) have virtually all the features of adult trees but have not yet begun to produce seeds. They have a well-developed trunk and crown; the height increment is greater than at any other ontogenetic stage. The annual increment of trunk length significantly exceeds the increments of large branches; hence, the crown is elongated and pointed at the top. The trunk diameter is more than three times greater than the diameters of the skeletal branches. The shoot system is composed of the branches of the 4th to the 7th–8th orders. The root system includes the main root (or its base), lateral roots of different orders, and secondary roots. The trunk is covered with periderm (usually, the cortex has not yet begun to develop). Virginal plants begin their development in the shrub layer and complete it in the tree canopy. In all tree species, the light demand in this ontogenetic state is maximal.

Young generative trees (g_1) look like adult trees and produce seeds for the first time. The organs of seed production are localized in the upper part of the crown. The number of seeds is small. The trunk growth in height is intense, branching is of 7th to 9th–10th order and more. The cortex begins to form in the lower part of the trunk.

Generative trees of middle age (g_2) have crowns ranging in shape from oval or tapering, with a pointed top, to rounded or bluntly cone-shaped. The order of branching and size of the crown and the root system are maximal. The cortex becomes coarser and covers a significant proportion of the trunk. Seeds develop in the upper and middle parts of the crown. The number of seeds is maximal. The trunk increment decreases in height, the apical growth of some large branches ceases, dormant buds on the trunk and skeletal branches wake up, and some anchoring roots die off.

Old generative trees (g_3) practically cease to grow in height, and the trunk increment decreases significantly in diameter. The crown and the root system decrease in size, as some skeletal branches and anchor-

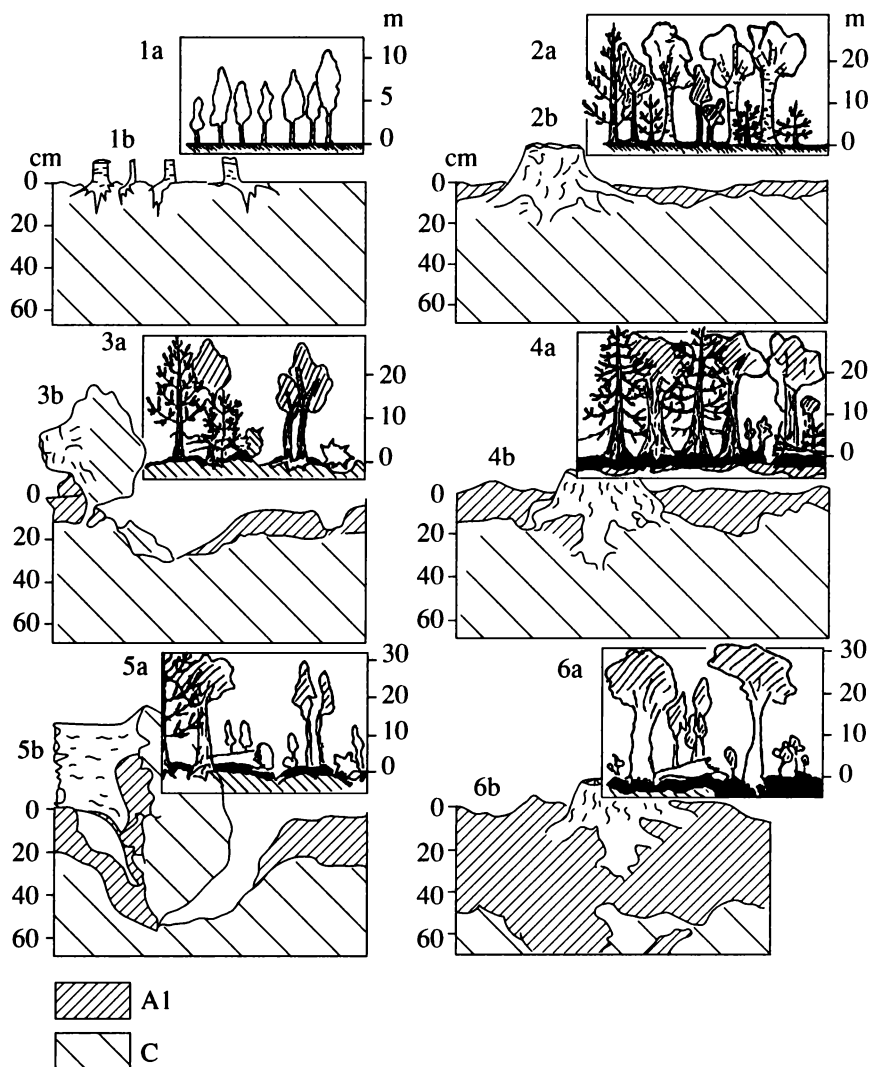
ing roots die off. This is more pronounced in leaved trees and pine and less pronounced in dark coniferous trees (spruce and fir), because dormant buds in the latter wake up along the entire length of skeletal branches and form many needled shoots. In leaved trees, dormant buds wake up only on the trunk or at the bases of skeletal branches. In some cases, the secondary crown may completely replace the primary crown. Seeds appear irregularly, and their number is small.

Senile trees (s) in most species have only the secondary crown, and leaves or needles can be of a juvenile type. The upper parts of the crown and trunk die off, so that only the lower half or third of the trunk remains alive in many leaved trees and pine. The root system is largely destroyed. Trees cannot produce seeds.

FORMATION OF HETEROGENEOUS STRUCTURE OF FOREST BIOGEOCENOSES AS A RESULT OF TREE LIFE AND DEATH

The process of plant and soil cover formation as a result of tree growth on bare (freshly exposed) parent rock has been studied in detail in the case of soil formation on loamy substrates (Gennadiev *et al.*, 1987; Rubilina and Kholopova, 1991; Bobrovskii, 1998; Ponomarenko, 1988, 1999). The upper layer of the bare loamy substrate quickly consolidates, and its drying causes cracks in the consolidated mass, which play the role of channels for mineral substances and moisture migration. The establishment of vascular plants becomes possible when these cracks appear. Upon grass cover formation (sodding), substrate differentiation is governed by the following processes: (1) the removal of substances by plant roots, (2) the input of substances with plant debris and moisture coming to the substrate surface, and (3) vertical transport of substances by the mesofauna and their migration in solutions. In the first few years, most of the debris comes from herbs, as individuals of the pioneer tree species (*Betula pendula* Roth, *Populus tremula* L., *Salix caprea* L., *Pinus sylvestris* L., etc.) of the first generation are at the initial stages of development (juvenile and immature) and their environment-forming effect is minimal. They successively come through the layers of mosses, herbs, and shrubs and accumulate substances for building the bulk of the forest canopy.

When the crown develops (at the virginal stage), the phytogenic field begins to form under it (Kozhevnikova, 1982; Dem'yanov, 1983). The prevalence of leaf and woody debris over grass debris is a characteristic feature of this field. The accumulation of debris under the tree crown entails the appearance and development of forest herb and dwarf shrub species and the specific soil mesofauna, and this makes the plant cover significantly more mosaic (Figure 1, 1) At the same time, earthworms become more active. They collect leaf debris from the sites adjoining the cracks and bury it untreated (leaf blocks) or in the form of humus-



Formation of tree synusia (1a–6a) and soils (1b–6b) on the bare loamy substrate (C). Stages: (1) the first generation of trees (pioneer species) on the bare substrate; (2) the appearance and development of broad leaved and coniferous species under the canopy of the pioneer species, the onset of humus horizon (A1) formation on the loamy substrate; (3) the pioneer species die off, the onset of wrench mosaic formation; (4) the formation of multispecific tree synusia with the prevalence of climax species and species characteristic of the late stages of succession; (5) the aforementioned species die off, and a mosaic of new gaps and WSCs is formed; (6) the mature dark soil with an extensive and deep humus horizon is formed.

enriched coprolites, thus performing its initial treatment. The rate of humus horizon growth strongly varies in different parts of the substrate surface. The possibility of its growth is minimal under the base of a tree trunk and large roots formed by the beginning of coprogenesis and is maximal in the peripheral part of the crown projection. Substrate differentiation by the degree of soil horizon development, which depends on the development of trees at certain points, is the initial stage of mosaic pattern formation in the soil cover (Figure 1, 2).

When trees are in the middle of the generative period (the adult generative state), the phytogenic fields are finally formed under the combined effect of shading, litter accumulation, changes in moistening, etc. These fields are specific microsites for many subordi-

nate species of plants and soil animals. The assimilatory surface of trees in the old generative and senile states decreases because of the lower branching intensity and the loss of some branches; as a result, the illumination intensity in the undercrown space increases, which leads to changes in the basic ecological regimes and the composition of subordinate species at this microsite.

Observations showed that trees of the pioneer species in the first generation have a short life span (ontogeny) and begin to die off approximately 40–60 years after being established on a bare substrate. As one or several old trees die and fall down, a new habitat is formed, referred to as an opening, or gap, in the forest canopy. The duration of ontogeny in years varies in

trees of even the same generation, and old trees do not die simultaneously. Hence, the mosaic of gaps of different age and size appears at early stages of forest community formation, when the first generation of pioneer species dies off.

Tree fall is accompanied by soil disturbances: clods of earth are wrenched off (Figure 1, 3), and windfall-soil complexes (WSCs) are formed (Skvortsova *et al.*, 1983). At this time, the following microsites can be distinguished in the resulting gap: (1) the area of undisturbed development (beyond the hole), with the undamaged herbaceous-dwarf shrub cover and the humus horizon of medium thickness, free of coarse fractions, and enriched with silty fractions; (2) the area where the ground vegetation is covered with the wrenched soil, the humus horizon has the maximum thickness and includes nonhumous material from the C horizon; (3) the wrenched clod of earth, with the bare substrate being nonhumous or slightly humous; (4) the hole formed after tree fall, which represents the primary substrate not transformed by the processes of soil formation, accumulates precipitation and snowmelt water, and is often the site of local soil gleying; (5) dead tree (fallen wood), a new biogenic substrate whose decay significantly increases the local humus content in the soil.

By the onset of wrench mosaic formation, the next generation of competitive and tolerant tree species (*Quercus robur* L., *Tilia cordata* Mill., species from genera *Acer*, *Picea*, *Abies*, etc.) develops under the canopy of pioneer tree species (Figure 1, 4). The development of this and subsequent generations is accompanied by the appearance of new gaps and WSCs (Figure 1, 5). After two to three tree generations (400–600 years), most of the area will be exposed to soil wrenching and the mosaic of soil cover will be formed, which represents the combination of WSCs differing in age; the thickness of the humus horizon; and the parameters of soil moisture content, porosity, and granulometric composition. The subsequent turnover of the soil profile accounted for by wrenching and activities of the mesofauna, moles, and other animals leads to the formation of a thick and dark humus horizon (60–100 cm thick) with a wavy lower boundary (the consequence of wrenching), which lies on the parent rock (Ponomarenko, 1988, 1999; Bobrovskii, 1998).

COMPOSITION AND SPECIFIC FEATURES OF PLANT COVER DEVELOPMENT IN GAPS AND WSCS

Spontaneous development of the plant cover in gaps (openings in the forest canopy) has been described in detail for Eastern European forests (Skvortsova *et al.*, 1983; Dyrenkov, 1984; Smirnova *et al.*, 1995; Samokhina, 1997; Shirokov, 1998; Leonova, 1999). For example, tall grasses dominate in coniferous-broadleaved forest at the first stage of gap development (two to four years after the death of a small group of old trees).

Among them, the nitrophilous light-demanding species *Urtica dioica* L. is dominant and the recovery of populations of both coniferous and leaved tree species is suppressed. At the next stage, which continues for one to two decades, tall grasses remain dominant, but their species composition becomes more diverse, with the prevalence of *Rubus idaeus* L., *Calamagrostis arundinaceae* (L.) Roth., *Aconitum septentrionale* Koelle, etc. Simultaneously, the reestablishment of spruce (*Picea obovata* Ledeb.) and fir (*Abies sibirica* Ledeb.) begins on decaying tree trunks and at the periphery of the gap, respectively. At the following stage, which continues for many decades, tall grasses gradually lose dominance as the gap becomes shaded by surrounding trees. In this course, nemoral species (*Aegopodium podagraria* L., *Asarum europaeum* L., etc.) become prevalent at sites where linden (*Tilia cordata* Mill.) with its vegetative undergrowth or aspen (*Populus tremula* L.) grew before the gap formation. Boreal species (*Oxalis acetosella* L., *Trientalis europaea* L., etc.) grow at the sites where fir and spruce develop successfully,

In the same forests at the first stages of gap existence, the wrenched clod of earth is the optimal substrate for the establishment and development of pioneer tree species (*Betula pendula* Roth., *Populus tremula* L., and *Salix caprea* L.), shrubs (*Sambucus racemosa* L.), and herbs. In the hole, conditions are favorable for the existence of nitrophilous trees and herbs that tolerate stagnant moistening and local gleying (*Ranunculus repens* L., *Chrysosplenium alternifolium* L., *Filipendula ulmaria* (L.) Maxim., *Padus avium* Mill., *Ulmus glabra* Huds., etc.). Dead trees at different stages of gap development serve as the optimal substrate for mosses and many species of herbs, shrubs, and trees. Moreover, moderately decomposed trees are the most favorable substrate for the reestablishment of Norway and Siberian spruce (*Picea abies* (L.) Karst. and *P. obovata* Ledeb.) (Dyrenkov *et al.*, 1970; Skvortsova *et al.*, 1983; Dyrenkov, 1984; *Vostochnoevropeiskie...*, 1994; Smirnova *et al.*, 1995).

Thus, normal tree ontogeny is associated with the permanent formation of gaps (openings in the forest canopy) and windfall-soil complexes, which provides for the maintenance of high intracenic heterogeneity in forest biogeocenoses. A great variety of microsites differing in their size, composition and structure of plant and soil covers, duration of development stages, and other parameters is created in forest biogeocenoses. Such features of the latter determine the high species, ecological, and cenotic diversity of subordinate species.

ACKNOWLEDGMENTS

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Population Biology of Gametophytes in Homosporous Polypodiophyta

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Abstract—Modern data on the diversity of morphology and morphogenesis of gametophytes in homosporous ferns, their vegetative reproduction, and the existence of their colonies growing separately, independently of sporophytes, are reviewed. The ontogenetic states of gametophytes are identified and characterized. The problem of gametophyte chemical interactions mediated by antheridiogen, an exohormone, is discussed. These intrapopulation interactions determine the polyvariant character of gametophyte ontogeny and the complex age and sex structure of their colonies.

Key words: gametophytes, populations, antheridiogen, ontogenetic states of plants, age and sex structure of populations

Homosporous ferns (Polypodiophyta) have a reproduction cycle with the antithetical alternation of two independently living heteromorphic generations: agamic (sporophyte) and sexual (gametophyte). The generations at different levels of morphological organization, cormophytic (sporophytes) and thallomic (gametophytes), alternate in the reproduction cycles of homosporous ferns.

In studies on the population biology of ferns, only sporophytes are usually considered (Seraya *et al.*, 1980, 1985; Nauyalis, 1977, 1980, 1984; Gureeva, 1987; Lashchinskii and Shorina, 1985). Gametophytes are either not taken into consideration at all or the authors restrict themselves to notes about their presence or absence. There has been a long-standing concept that the role of these minute plants is only limited to realizing the sexual process and that their colonies are short-lived and have no complex population structure. In recent years, however, specialists have been attempting to study the natural colonies of gametophytes by the methods developed in plant demography and population biology (Nauyalis, 1979; Nauyalis and Filin, 1983; Shorina, 1991; Gureeva, 1996). Difficulties in this research are associated with poor knowledge of the morphology and ontogeny of gametophytes and the methods of their reproduction and self-maintenance of natural colonies.

MORPHOLOGY OF GAMETOPHYTES

A widespread opinion is that gametophytes of the Polypodiophyta are externally uniform. They are usually described as small horizontal cordiform green plates with rhizoids and gametangia on the lower surface. The central parts of these plates are composed of several (up to eight) cell layers and are named veins, or

archegonial cushions. The marginal parts, or wings, are single-layered.

Gametophytes are short-lived. They live for several weeks to several months and are usually proterandrous; i.e., antheridia develop before archegonia, and prothalli successively pass through the male and then the female phases of development. This facilitates interprothallium fertilization.

However, such a type of gametophytes is not characteristic of all homosporous ferns (Atkinson and Stokely, 1964; Gladkova, 1978; Filin, 1978; Shorina, 1987) but only of many (but not of all!) representatives of the class Polypodiopsida. More ancient classes, Ophioglossopsida and Marattiopsida, have different types of gametophytes. The Ophioglossopsida have perennial underground heterotrophic gametophytes that are colorless and of a cylindrical, tuber-like, discoid, or flabellate shape. They are radially symmetrical and live together with endophytic fungi. They live for dozens of years (for example 10–20 years in *Ophioglossum vulgatum*), but annual gametophytes are also found (in *O. crotolophoroides*). The upper parts of gametophytes sometimes extend above the ground and become green. Gametangia are large, massive, and immersed and are distributed throughout the gametophyte surface. The gametophytes of Ophioglossopsida generally look like the prothalli of Lycopodiopsida, which is the reason for regarding them as the most primitive ferns (Bierhorst, 1971).

The gametophytes of Marattiopsida are autotrophic dorsoventral plants, which are relatively long-lived (several years) and large (more than 2–3 cm in length). They are multilayered, often band-shaped, can branch (bifurcate), and continue to grow after the formation of sporophytes. There is no distinct differentiation into the archegonial cushion and wings. Antheridia are large,

multicellular, and immersed; archegonia are formed on both the upper and lower surfaces of prothalli (Gladkova, 1978). Bierhorst (1971) regarded this fact as evidence that the band-shaped dorsoventral gametophytes originated from the cylindrical radially symmetrical ones.

The order Osmundales, the most ancient among Polypodiopsida, has gametophytes similar to those of Marattiopsida but even larger, up to 30 cm in length (Bobrov, 1978).

In the order Schizaeales, two genera (*Actinostachys* from the family Schizeaceae and *Stromutopteris* from the family Stromatopteridaceae) have colorless underground gametophytes resembling the prothalli of Ophioglossopsida (Popova, 1978). In other representatives of this class, gametophytes are green and autotrophic. In most families, adult prothalli are cordiform but aberrant forms are also found: they can be filamentous, looking like algae (in the genera *Schizaea*, Schizeaceae, and *Trichomanes*, Hymenophyllaceae), or filamentous and taeniate in some species of the subfamily Vittariaideae (Adiantaceae) and in the family Grammitidaceae. Bierhorst (1971) considered them to be evolutionary advanced, having originated via neoteny from the cordiform ones.

VEGETATIVE REPRODUCTION OF GAMETOPHYTES AND SELF-MAINTENANCE OF THEIR COLONIES

The appearance of neotenic forms of gametophytes was often accompanied by the tendency toward vegetative reproduction via gemmae (Shorina, 1987a, 1987b; 1991), which has significantly increased the life span of sexual generation in the reproduction cycles. In some ferns, gametophytes even became capable of living independently of sporophytes. The most notable example of such an independent existence of fern gametophytes was found in the Appalachian Mountains by Wagner and Sharp (1963). They discovered colonies of sterile gametophytes which formed aggregations up to 10–100 cm in diameter on rocks and stones. These gametophytes reproduced by means of brood buds and did not form gametangia. Externally, they resembled the gametophytes of *Vittaria lineata* (L.) J. Sm., the sporophytes of which live hundreds of miles to the south. Farrar (1967) managed to achieve the formation of gametangia and to grow sporophytes, and this allowed the exact species identification of prothalli. It was found that the gametophytes belonged to three epilithic and epiphytic species of tropical rain forests: *Vittaria lineata* (L.) J. Sm. (Vittariaceae), *Hymenophyllum thanbridgense* (L.) J. Sm. (Hymenophyllaceae), and *Grammitis nimba* (Jenm.) Proctor (Grammitidaceae). It is noteworthy that another species of genus *Vittaria*—*V. ensiformis*—also has vegetatively reproducing gametophytes, but they regularly form gametan-

gia and sporophytes in nature, so that the sexual and asexual generations are not separated territorially.

The adaptive significance of the longer phase of sexual generation and its relative independence apparently consists in the increase of ecological range of species, because gametophytes are poikilohydrous and can live in drier and colder places, compared to sporophytes (Sato and Sakai, 1980, 1981; Sato, 1982; Nauyalis, 1989a, 1989b; Rumsey and Scheffeld, 1996).







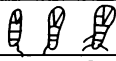



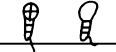



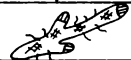
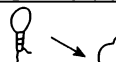





MORPHOGENESIS AND ONTOGENETIC STATES OF GAMETOPHYTES

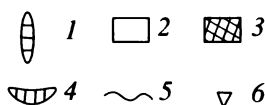
The pattern of morphological diversity of gametophytes becomes even more complex if we take into consideration the course of their morphogenesis and the possibility of convergence in the formation of "typical" cordiform prothalli. Nayar and Kaur (1971) demonstrated the existence of at least seven types of morphogenesis in autotrophic gametophytes (figure). They were identified using the following indicators: (1) the methods of reorientation of cell divisions upon the transition from unidimensional filamentous growth to two-dimensional planar and three-dimensional spatial growth; (2) the presence or absence of a pyramidal initial cell; (3) the initial position of the meristem, apical or intercalary (lateral); (4) the degree of development, number, and location of multilayered fragments, the so-called archegonial cushions; (5) the shape of adult gametophytes (cordiform, bifurcate, or band-shaped); and (6) the distribution of rhizoids. As can be seen from the figure, cordiform gametophytes are formed at the final stages of at least four types of morphogenesis: in *Adiantum*, *Drynaria*, *Aspidium*, and *Ceratopteris*. The authors emphasize that gametophytes are very pliable, and the course of their morphogenesis can change depending on environmental conditions and is specific not for species but for genera and families.

We attempted to distinguish discrete periods in gametophyte ontogeny on the basis of principles accepted in plant population biology (Rabotnov, 1950, 1964; Uranov, 1975). In laboratory cultures, ontogenetic states were determined in gametophytes of the following ferns: *Polypodium vulgare* L. (Polypodiaceae), *Pteridium aquilinum* (L.) Kuhn (Hypolepidaceae), *Athyrium filix-femina* (L.) Roth, *Gymnocarpium dryopteris* (L.) Newm. (Athyriaceae), *Asplenium ruta muraria* L., *Phyllitis scolopendrium* (L.) Newm. (Aspleniaceae), *Dryopteris expansa* (C. Presl) Fraser-Jenkins et Jermy, *D. carthusiana* (Vill.) H.P. Fuchs, and *D. filix-mas* (L.) Schott (Dryopteridaceae).

Four periods of ontogeny and nine ontogenetic (age) states of gametophytes were distinguished (Shorina, 1991). Here is their brief description.

Period I, initial dormancy (sp). Dormant spores. Page (1990), Nauyalis (1989a, 1989b), and Komarova (1987) reported about the existence of the soil pool of fern spores.

Type	P h a s e s				
	protonema	beginning of planar growth	young	mature	old
1 Marattia					
2 Osmunda	⊖	⊕ ⊕			
3 Adiantum					
4 Drynaria					
5 Kaulinia					
6 Aspidium					
7 Ceratopteris					



Morphogenesis of gametophytes (according to Nayar and Kaur, 1971, modified). (1) Filamentous gametophytes, (2) single-layered and (3) multilayered parts of gametophytes, (4) marginal meristem, (5) rhizoids, (6) initialia.

Period II—young sporophytes—includes four ontogenetic states. (1) Germs (p): the onset of spore germination, the formation of the first rhizoid and the growth of the protonema filament; mixed nutrition owing to the substances stored in spores and via photosynthesis. (2) Juvenile (j): the filamentous phase, or protonema; the growth is one-dimensional; cells are divided by walls perpendicular to the longitudinal axis of the filament; cell number varies from 2–3 to 10–17 (in *Pteridium*). (3) Immature (im): reorientation of cell divisions; the onset of two-dimensional planar growth; the prothallium plate is oval, without a notch and multicellular meristem; spore envelope and the filament of protonema are well-preserved. (4) Adult immature gametophytes, in which the archegonial cushion has not yet been formed (v). The plate of the gametophyte is linguiform, with a blunt top and, rarely, a weakly expressed notch.

Period III—definitive—is characterized by the transition to spatial (three-dimensional) growth. The multilayered archegonial cushion (vein) is formed, and the development of archegonia is possible. The prothallium plate is cordiform, with a well-expressed notch at the apex and multicellular meristem in it. Depending on the size of the gametophyte, preservation of the filamentous part, the abundance of gametangia, and the degree of goffering of the “wings,” definitive prothalli can be assigned to young (d_1), medium-age (d_2), or senescent (d_3).

Period IV, senile (s). Gametophytes are losing the meristematic part, the notch disappears, the shape of

the prothallium becomes roundish, and wing goffering is typical. Gametangia are no longer formed.

As can be seen from the description of gametophyte ontogeny, one of the age-related (ontogenetic) criteria is the formation of archegonia, which only occurs in the definitive prothalli with multilayered archegonial cushions. As for antheridia, they can be formed at any ontogenetic stage, beginning from juvenile. As early as in 1907, Lagerberg found antheridia on the three-cell juvenile gametophytes of *Pteridium aquilinum*. Hence, the appearance of antheridia, as opposed to archegonia, cannot be used as an age-related (ontogenetic) criterion.

CHEMICAL INTERACTIONS OF GAMETOPHYTES

It was found in the 1950s that the substrate on which *Pteridium aquilinum* gametophytes were grown contained a substance that stimulated the formation of antheridia on the prothalli of both this and other fern species (Döpp, 1950). This substance was named antheridiogen. Its chemical and structural formulas, determined in the 1970s (Naf *et al.*, 1975), proved to be close to those of gibberelic acid (gibberellin). Antheridiogen is produced by gametophytes of not only *Pteridium*, but also of another genera, such as *Lygodium*, *Onoclea*, and *Aneimia*. However, antheridiogens of different ferns differ slightly from one another chemically.

Only the large definitive female prothalli with a well-expressed meristem in the notch produce antheridiogen, as the meristem proper is the source of anthe-

ridiogen. This was demonstrated experimentally: when the meristematic parts of large female prothalli were cut out, antheridiogen production ceased (Naf *et al.*, 1975). It was also shown experimentally that large female prothalli release antheridiogen into the substrate and, thus, can chemically affect other prothalli at a distance of several centimeters, stimulating the formation of antheridia in 1000 neighboring smaller (primarily juvenile) gametophytes (Voeller, 1971). Antheridiogen accelerates the formation of antheridia in the neighboring gametophytes; inhibits the growth and development of juvenile, immature, and adult immature gametophytes; and stimulates spore germination in the dark.

The j, im, and v gametophytes are most sensitive to antheridiogen. Definitive prothalli shortly after the formation of the multicellular meristem become the sources of antheridiogen themselves and practically cease to respond to it. The loss of sensitivity to antheridiogen is explained by the production of specific antibodies in adult cordiform gametophytes. Chemical interactions through the antheridiogen-containing substrate give rise to different variants of gametophyte ontogeny. In laboratory cultures, three basic variants were found: (1) rapidly developing unisexual female prothalli (they are the main source of antheridiogen); (2) ambisexual proterandrous prothalli, whose ontogeny is considered typical; and (3) neotenic filamentous male prothalli with retarded development. The percent ratio of these three groups was approximately 25 : 75 : 5 (Naf *et al.*, 1975).

Hence, the colonies of gametophytes acquire a complex age and sex structure, which is determined by intrapopulation chemical interactions. Antheridiogen, the exohormone entering the substrate, regulates the rate of morphogenesis and the sex of gametophytes and, thus, promotes their ontogenetic diversity and interprothallium fertilization (Shorina, 1986, 1987). In fact, antheridiogen acts as a pheromone, i.e., a substance transmitting biological information from individual to individual. It is noteworthy that antheridiogen regulates the repeated formation of antheridia in the same prothallium in ferns with large long-lived gametophytes (*Osmunda*, *Lygodium*, *Aneimia*). The role of antheridiogen as a pheromone affecting the intrapopulation diversity of prothalli apparently increased in the course of gametophyte evolution (Naf *et al.*, 1975).

THE STRUCTURE AND DYNAMICS OF GAMETOPHYTE COLONIES

The complex sex and age structure of gametophyte populations has been repeatedly studied in laboratory experiments (Naf, 1958; Naf *et al.*, 1975), but its detailed analysis with regard to the ontogenetic states of gametophytes has not yet been performed. I studied the dynamics of age and sex composition of *Polypodium vulgare* L. and *Phyllitis scolopendrium* (L.) Newm. populations under laboratory conditions for nine months (Shorina, 1987a, b). These populations

proved to have a complex age structure throughout the period of observations. During these nine months, the ontogenetic spectra changed from incomplete left-handed (months 1 and 2) to unimodal, with the prevalence of adult immature and definitive gametophytes (months 3–7), and, finally, to right-handed, with the prevalence of aging definitive and senile prothalli (months 8 and 9). Thus, the transformation of the ontogenetic population structure demonstrated a “small wave” of development in the terms used by Uranov (1975).

Mass formation of antheridia was observed in the prothalli of all ontogenetic states when the proportion of cordiform gametophytes reached 20% in *Polypodium* and 40% in *Phyllitis*. Species-specific differences between the populations studied were revealed. For example, the male phase of development began three months earlier in *Phyllitis* than in *Polypodium*.

The results of these studies provided evidence that the methods of population biology are suitable for analyzing the populations of the sexual generation in ferns.

The question arises as to whether such differentiation of prothalli occurs in nature, as the natural reducers of biocenoses may neutralize the effect of antheridiogen-like exohormones and, thus, abolish the effects observed under laboratory conditions (Rabotnov, 1978). Some published data suggest a positive answer to this question. Thus, in natural habitats of *Platyzoma* in Australia, Tryon (1964) observed marked differences in gametophyte habitus, which ranged from filamentous in male to cordiform in female gametophytes. This fact was interpreted as a manifestation of the tendency toward heterospory. Tryon and Vitale (1977) mapped natural colonies of *Asplenium pimpinellifolium* and *Lygodium heterodoxum* gametophytes in Mexican forests. The distribution of gametophytes of these species relative to each other confirmed the concept of antheridiogen-mediated morphogenetic control: a few large female prothalli were surrounded by numerous filamentous male gametophytes.

In 1986 and 1987, I studied the age structure of *Athyrium filix-femina* and *Dryopteris carthusiana* gametophyte populations in a wood sorrel spruce forest in the Moscow region (Shorina, 1991). In the growing period, observations were carried out in the field; in winter, prothalli were studied in the laboratory using pieces of rotting wood (4 × 4 × 2 cm) on which gametophytes grew. The results showed that the age structure of gametophyte populations always remained complex. Its temporal variation in natural colonies proved to be less pronounced than under laboratory conditions. In *Dryopteris carthusiana*, the ontogenetic spectra remained unimodal, with the prevalence of young immature gametophytes (v), throughout the two-year observation period. In *Athyrium filix-femina*, the ontogenetic spectra changed from left-handed, with the prevalence of j, im, and v prothalli in spring, to right-handed, with the prevalence of definitive prothalli in autumn. The rejuvenation of pop-

ulations in winter months can be attributed to vegetative reproduction of gametophytes. It occurs in the form of the regeneration of j and im prothalli from marginal cells of dying definitive and senile gametophytes (Shorina, 1991).

These observations suggest that gametophyte colonies in nature can live for many years in the same place, maintaining themselves vegetatively. Such an assumption is also based on the data by Phillips (1919; cited from Miller, 1968), who noted the fact of the long-term existence of such colonies in nature. N.S. Barabanshchikova (personal communication) revealed the fact of overwintering of individual gametophytes during her observations over marked prothalli of *Athyrium filix-femina*.

It is noteworthy that, according to our data, the ontogenetic spectra of old (3- to 4-year-old) laboratory cultures, in which regenerated prothalli prevailed, remained complex and complete. Regenerates (i.e., gametophytes of vegetative origin) formed antheridia and archegonia, thus providing for the appearance of new sporophytes. It is quite probable that similar variants of the maintenance of gametophyte colonies take place in nature as well as in the laboratory.

CONCLUSIONS

(1) Gametophyte ontogeny can be subdivided into ontogenetic periods and states using the principles of discrete periodization of ontogeny proposed by Rabotnov and Uranov. The formation of archegonia is an important ontogenetic criterion. The formation of antheridia cannot be used as an age-related character because it is determined by intrapopulation interactions between gametophytes, rather than by their ontogenetic state.

(2) Biologically active substances secreted by prothalli into a substrate affect the course of gametophyte ontogeny. Antheridiogen is most important among such substances, as its action entails a multiplicity of ontogenetic variants associated with neoteny and accelerated antheridia formation.

(3) The discrete and polyvariant type of ontogeny leads to the formation of a complex sex and age structure of gametophyte populations, which can be studied by the methods of population biology.

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The Phenomenon of Pseudoviviparity in Alpine and Arctomontane Grasses (*Deschampsia* Beauv., *Festuca* L., and *Poa* L.)

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Abstract—It is known that pseudoviviparous plant taxa are most numerous in the Arctic and high mountain regions, where they sometimes account for a noticeable part of the local flora and play an important phyto-cenotic role. The complex of pseudoviviparous taxa is an interesting model for investigating the processes of hybridogenic speciation, as various mechanisms stabilizing the hybrid genetic systems proved to be effective in them. In particular, this concerns vast and taxonomically complex groups such as the genera *Deschampsia*, *Festuca*, and *Poa*. In this paper, published data on the taxonomy, chromosome numbers, and distribution of pseudoviviparous grasses in the Arctic regions and subarctic mountain systems are reviewed.

Key words: pseudoviviparity, evolution, *Deschampsia*, *Festuca*, *Poa*

Sexually propagating species appear to prevail in the Earth's biota, but various forms of asexual reproduction are widespread in all kingdoms of the organic world. Historically, it occurred that the basic principles of evolutionary theory were formulated and developed with regard to dioecious organisms (Timofeeff-Ressovsky *et al.*, 1969). Investigations of population processes in mainly agamous taxa are still at the initial stage (Grant, 1984).

This study is a brief review of the group of arctic and arctomontane grasses characterized by pseudoviviparity, i.e., the formation of vegetative diaspores in inflorescences, with the already developed flower parts undergoing proliferation and transformation into leaf-like structures (Pijl, 1969). True viviparity is the phenomenon of seed germination on the mother plant, as occurs in mangroves (Genkel', 1979).

Pseudoviviparity is known in plants belonging to many families (Alliaceae, Liliaceae, Agavaceae, Poaceae, Saxifragaceae, and Polygonaceae) and growing in the Arctic, high mountains of both hemispheres, and steppes and semideserts of Eurasia and Africa (Beetle, 1980; Elmqvist and Cox, 1996). This method of vegetative propagation is especially widespread in the Arctic regions and related mountain systems. In the local high-altitude floras, the proportion of pseudoviviparous species reaches 10% and, in special cases, even up to 25%: e.g., 9 out of 38 higher plant taxa in southern Spitsbergen, and 6 out of 57 taxa in the northernmost Russian area on Franz Josef Land (Safronova, 1983; Dubiel and Ziaja, 1993).

Why are pseudoviviparous plants so widely distributed in the Arctic regions? What is known about their

population structure and how large is their genetic diversity? What is the origin and evolutionary fate of such taxa? These questions are discussed in the present review, with an emphasis on the taxonomy, karyology, and geography of pseudoviviparous *Deschampsia*, *Poa*, and *Festuca*.

Genetic basis of pseudoviviparity. The normal or abortive development of flower parts and the induction of flowering are determined genetically, with the expression of these traits being influenced by external and internal factors. Indeed, in many grasses of the temperate zone, vegetative proliferation in the inflorescence may be caused by photoperiod shortening during differentiation of the generative growth cone (Nygren, 1949; Junttila, 1985). By modifying the conditions of *Festuca vivipara* cultivation, it is possible to change the ratio of normal flowers and vegetative diaspores and to increase pollen viability (Heide, 1988). The examples of induced proliferation demonstrate that there is a universal genetic mechanism responsible for the normal development of the flower and its metamorphosis, including the reversion to a vegetative sprout (Ma, 1994).

The capacity for induced proliferation, which is common in the family Poaceae, suggested to some specialists the conclusion that pseudoviviparity is an ecological phenomenon which largely depends on environmental influences. However it has been definitely shown that viviparity in certain species of the genera *Poa*, *Festuca*, etc., is determined genetically.

Hypotheses concerning the origin of pseudoviviparous taxa. There are two basic hypotheses explaining the origin of taxa consisting mostly or exclusively of pseudoviviparous plants. The hybridogenic hypothesis,

developed by Lindman, is based on the assumption that each pseudoviviparous taxon is the result of an individual interspecific or intersectional hybridization event; this implies its polytopic origin, and each pseudoviviparous clone (genotype) may be regarded as an independent hybrid. Thus, in terms of systematics, such taxa should be considered the aggregates of hybrid forms unified by their origin from the known parental species (cited from Lyngé, 1923).

According to the second hypothesis, the pseudoviviparous taxa are derivatives of the corresponding non-viviparous species in the rank of a variety or any other infraspecific unit. In this case, pseudoviviparity is an important morphophysiological trait used for discriminating between infraspecific taxa (Skvortsov, 1964; Tsvelev, 1964, 1974a, 1974b, 1976). It is assumed that hybridization could be involved in the formation of a pseudoviviparous taxon, along with other factors that have affected its survival and distribution (Scholander, 1934; Pils, 1985).

Both hypothesis acknowledge the role of hybridogenesis in evolution, which is quite natural in plant biology (Nannfeldt, 1937; Flovik, 1938; Muntzing, 1940; Grant, 1984). However, the first hypothesis postulates the continuous formation of hybrids, whereas the second postulates that a single hybridization event occurred in the evolutionary past.

The genus *Festuca* L. (fescue). Thus genus in the Northern Hemisphere includes pseudoviviparous taxa of various ranks (Table). On the one hand, there are "true" species related to *Festuca ovina*—*F. vivipara*, *F. viviparoidea*, and *F. chionobia*—with large continuous ranges, in which their morphological characters are rather stable. On the other hand, there are numerous hybrids, including those with one parental species being unknown (Turesson, 1930; Scholander, 1934; Siplivinskii, 1973).

Festuca vivipara is an amphiatlantic low-arctic species which is widespread in northwestern Europe and expands to the Arctic regions (Spitsbergen and Greenland). The relic populations of this species grow in most of the European mountain systems. However, some authors (e.g., Markgraf-Dannenberg, 1980) regard them as pseudoviviparous derivatives of other species, in particular, *F. airoides*.

In *F. vivipara* a series of chromosome numbers is known: 21, 28, 35, 42, and 49. Special investigations carried out in Great Britain and southern Norway revealed that triploid *F. vivipara* plants are the hybrids of *F. vivipara* \times *F. ovina* ($2n = 28$ and 14 respectively). They occur only in the areas (communities) where populations of the parental species are present (Watson, 1958; Salvesen, 1986). Compared to the tetraploid *F. vivipara* plants, pollen viability in these hybrids is much lower, the proportion of normal flowers is reduced, and seeds are virtually absent. Note that high-quality seeds have been found in *F. vivipara* and pollen

viability can be as high as 86% (Jenkin, 1922; Turesson, 1930; Salversen, 1986).

In Greenland populations of *F. vivipara*, differences in ploidy proved to correlate with some morphological characteristics (Frederiksen, 1974, 1981). Alekseev (1985) distinguished the Greenland type with 28 chromosomes as an individual species, *F. frederikseniae*. This species has also been collected in Scandinavia, so that it appears that morphologically similar tetraploid plants occurring there are not related by descent to the population from Greenland (Salvesen, 1986).

The Arctic part of the *F. viviparoidea* range extends from the Kanin Peninsula to the east, through the Arctic Urals and western Siberian tundra to the Taimyr Peninsula. This species has not been found in the Arctic part of East Siberia; it appears again in the Chukchi Peninsula and reaches the northeastern coast of Greenland. Similarly to *F. vivipara*, it spreads via mountain ranges far into southern Eurasia (table). The polyploid series (28, 49, 52, 56, and 63), compared to that of *F. vivipara*, consists of greater numbers. Western Canada is inhabited by the endemic subspecies *F. viviparoides* subsp. *krajina*, which also spreads far south (Pavlik, 1984).

Morphological differences between *F. viviparoidea* and *F. vivipara* are insignificant but stable. Taking into account its continuous range and greater chromosome numbers (mainly 49 and 56, while *F. vivipara* is mainly tetraploid), this taxon certainly deserves the rank of species (Holmen, 1964; Pavlik, 1984; Alekseev, 1985).

The third species, *F. chionobia*, grows in the mountain regions of eastern Siberia and the Far East, from Cisbaikalia in the west (where it was found in the same area as *F. viviparoidea*, in the Baikal Ridge) to northern Sikhote Alin and Karaginskii Island off East Kamchatka (Peshkova, 1973; Alekseev, 1982). This species is similar to *F. auriculata* in the anatomical structure of the leaf blades and, for some time, was regarded as a pseudoviviparous subspecies of the latter (Tsvelev, 1976). There is evidence that, in a few known localities in the Far East, *F. chionobia* occurs only together with *F. auriculata*, whereas on the Stanovoi Ridge it grows in ecologically extreme habitats where other *Festuca* species do not survive (Siplivinskii, 1973; Alekseev, 1982).

Three former *Festuca* species are related to *F. ovina*, whereas the *F. rubra* s.l. complex includes some hybrid forms in which one parental species is *F. rubra* and the other appears to differ in different parts of the range. An additional complication is that *F. rubra* is predisposed to spontaneous formation of pseudoviviparous plants: findings of proliferating sprouts, much more frequent than in other *Festuca* species, are known throughout the Holarctic area of its distribution (Aiken *et al.*, 1988; Rebristaya *et al.*, 1989).

Salvesen (1986) considered pseudoviviparous plants from Great Britain and Norway as a complex of hybrid *F. rubra* \times *F. vivipara* forms ($2n = 35$, 49, and ca. 63).

Names, synonyms, and known chromosome numbers of arctic and arctomontane pseudoviviparous taxa of *Festuca*, *Deschampsia*, and *Poa* from the Northern Hemisphere. Names are given according to Cherepanov (1995), *Flora Europea* (Clarke, 1980; Edmondson, 1980; Markgraf-Dannenberg, 1980), and recent reviews of individual groups (Pavlik, 1984; Olonova, 1998)

Name, synonyms	Range and known chromosome numbers
<i>Festuca chionobia</i> Egor. et Sipl. (<i>F. auriculata</i> Drob. subsp. <i>chionobia</i> (Egor. et Sipl.) Tzvel.).	Range: Baikal Ridge; Stanovoe Highland: Udokan, Kodar, Severo-Muiskii, Yuzhno-Muiskii, Ikatskii ridges (Peshkova, 1973); northern Amur region: Ezop, Dusse-Alin, Yam-Alin, and Badzhal ridges (Shlottgauer, 1986); Aldano-Uchurskii Ridge (Volo-tovskii and Kuznetsova, 1993); Aldan Highland (Volotovskii, 1991); Sikhote Alin (Vyshin, 1985); Karaginskii Island (Kharkevich <i>et al.</i> , 1979)
<i>F. viviparoidea</i> Krajina ex Pavlick subsp. <i>viviparoidea</i> Pavlick (<i>F. vivipara</i> (L.) Smith subsp. <i>glabra</i> Frederiksen) (Pavlick, 1984).	<i>2n</i> = 28 (Putoran Plateau; Krogulevich and Rostovtseva, 1984) <i>2n</i> = 49, 56, 63 (Alaska; Holmen, 1964; Johnson and Parker, 1968), <i>2n</i> = 49, 56 (Taimyr Peninsula and Greenland; Jorgensen <i>et al.</i> , 1958; Zhukova <i>et al.</i> , 1973) <i>2n</i> = 52 (Southern Chukchi Peninsula; Zhukova, 1980), <i>2n</i> = 28 and 56 (Wrangel Island; Petrovskii and Zhukova, 1981). Range: Yugor Peninsula, Vaigach and Novaya Zemlya islands, Arctic and Middle Urals (Mount Denezhkin Kamen'), Bol'shezemel'skaya tundra, Pai Khoi Ridge, Taz and Gydanskii peninsulas (Skvortsov, 1964; Tsvelev, 1976; Rebristaya, 1977; Morozov and Kuliev, 1994; Rebristaya and Khitun, 1994), Mount Byrranga, Putoran Plateau, and northwestern coast of Taimyr Peninsula (Andrulaitis <i>et al.</i> , 1976; Khodachek and Sokolova, 1989; Kozhevnikov, 1992), Western Sayan Mountains, Ergak-Targak-Taiga Ridge (Krasnoborov, 1976), Baikal and Eastern Sayan ridges (Siplivinskii, 1973), southern and eastern Chukchi Peninsula, northern Kamchatka (Alekseev, 1982; Korobkov and Sekretareva, 1997), Alaska and Yukon (Pavlik, 1984; Alekseev, 1985), Ellesmere Island, Canadian Arctic Archipelago (Aiken <i>et al.</i> , 1996), Greenland (Frederiksen, 1981).
<i>F. viviparoidea</i> Krajina ex Pavlick subsp. <i>krajina</i> Pavlick	Range: Canadian Cordilleras from the Yukon to southern Alberta (50° N) (Pavlik, 1984)
<i>F. vivipara</i> (L.) Smith (<i>F. ovina</i> L. var. <i>vivipara</i> L.).	<i>2n</i> = 21, 28, 42, 49 (Spitsbergen; Flovik, 1938), <i>2n</i> = 21, 28, 42 (Scandinavia and Iceland; Turesson, 1930; Love and Love, 1956), <i>2n</i> = 28 (Greenland; Bocher and Larsen, 1950), <i>2n</i> = 21, 28 (Great Britain and southern Norway; Hedberg, 1958; Watson, 1958; Salvesen, 1986), <i>2n</i> = 28, 35 (Tatra Mountains, Poland; Piotrowicz, 1954). Range ampiatlantic: Kola Peninsula, mountain and Arctic Scandinavia, Great Britain, Faeroes, Iceland, eastern Greenland, Spitsbergen (Markgraf-Dannenberg, 1980). Beyond the Arctic: Eastern Alps, Sudetes, Carpathians (Pils, 1985), Eastern Sayan and Baikal Mountains (Peshkova, 1973)
<i>F. frederikseniae</i> E. Alexeev (<i>F. vivipara</i> Smith var. <i>hirsuta</i> Scholander).	<i>2n</i> = 28 (Southern Greenland and Norway; Bocher and Larsen, 1950; Frederiksen, 1974; Salvesen, 1986). Range: Southern Greenland, Atlantic regions of the United States and Canada (Alekseev, 1985), Scandinavia (Salvesen, 1986)
<i>F. airoides</i> Lam. (<i>F. supina</i> Schur, <i>F. ovina</i> L. var. <i>supina</i> (Schur) Hackel).	<i>2n</i> = 28, 42 (Europe; Markgraf-Dannenberg, 1980). Range: European mountains from the Carpathians to the Alps; pseudoviviparous plants are occasionally found throughout the area (Markgraf-Dannenberg, 1980)
<i>F. prolifera</i> (Piper) Fern. (<i>F. rubra</i> L. subsp. <i>prolifera</i> Piper).	<i>2n</i> = ca. 70 (British Columbia; Taylor and Mulligan, 1968), <i>2n</i> = 50 (boreal zone of North America; Bowden, 1960). Range: northeastern United States and Canada, one locality in the mountains of British Columbia (Fernal, 1933; Alekseev, 1985)
<i>F. villosa-vivipara</i> (Rosenvinge) E. Alexeev (<i>F. rubra</i> L. var. <i>mutica</i> <i>f. prolifera</i> Hylander).	<i>2n</i> = 49 (Greenland; Frederiksen, 1981). Range: Greenland, sporadically in Norway
<i>F. rubra</i> L. × <i>F. vivipara</i> (L.) Smith agg. (Salvesen, 1986).	<i>2n</i> = 42 (northern Norway; Knaben and Engelskjon, 1967), <i>2n</i> = 49, 63 (United States and Canada; Love and Love, 1966), <i>2n</i> = 35, 49, ca. 63 (western Norway; Salvesen, 1986). Range: known from Scandinavia, Scotland, and Canada
<i>F. rubra</i> subsp. <i>rubra</i> f. <i>vivipara</i>	Found on Taz Peninsula (Rebristaya <i>et al.</i> , 1989); pseudoviviparous plants with characters typical of <i>F. rubra</i> repeatedly occurred in Yamal;

Table. (Contd.)

Name, synonyms	Range and known chromosome numbers
<i>Deschampsia alpina</i> (L.) Roem. et Schult. (<i>Aira alpina</i> L., <i>D. cespitosa</i> (L.) Beauv. subsp. <i>alpina</i> (L.) Tzvel.).	$2n = 35-39$ (Kolguev Island; Sokolovskaya and Strelkova, 1960), $2n = 39, 41$, and 49 (Spitsbergen; Flovik, 1938), $2n = 52$ (southwestern Greenland; Bocher and Larsen, 1950), $2n = 48, 52$, and 56 (Scandinavia; Hagerup, 1939; Nygren, 1949). Range amphiatlantic: northwestern Labrador, southern Baffin Island, Greenland (south of 70° N), Spitsbergen and Franz Josef Land, Scandinavia, mountains of Scotland, Khibiny Mountains, Kanin Peninsula, Novaya Zemlya (abundant on the northern island and rare in the southern island), Vaigach and Kolguev islands (Andreev, 1931; Mishin, 1953; Tsvelev, 1964; Clarke, 1980; Safronova, 1983, 1990)
<i>Poa arctica</i> R. Br. var. <i>vivipara</i> Hook.	$2n = 56$ (Peary Land, Greenland; Holmen, 1952; Fredskild, 1966). Range : Greenland, Scandinavia (Holmen, 1952; Tsvelev, 1964), Spitsbergen, Franz Josef Land and Novaya Zemlya (Scholander, 1934; Safronova, 1983; Khodachek, 1986), Taimyr Peninsula (Andrulaitis <i>et al.</i> , 1976; Khodachek and Sokolova, 1989; Pospelova <i>et al.</i> , 1977), Yakutia, Cape Svyatoi Nos (Safronova, 1982), southern and western Chukchi Peninsula, Wrangel Island (Petrovskii and Plieva, 1985; Katenin and Sekretareva, 1996; Korobkov and Sekretareva, 1997), Alaska (Hulten, 1942; Porsild, 1964).
<i>P. lindebergii</i> Tzvel. (<i>P. tolmatchewii</i> Roshev. var. <i>stricta</i> (Nannf.) Tzvel.).	Range : several occurrences in separate sites in Arctic regions: Novaya Zemlya (Khodachek, 1986); lower reaches of the Lena River, on the Tuora-Sis Ridge; and mountains in Norway, near Dovre (Tsvelev, 1976)
<i>P. alpina</i> subsp. <i>vivipara</i> (L.) Arcang. (<i>P. alpina</i> var. <i>vivipara</i> L., <i>P. alpina</i> subsp. <i>vivipara</i> (L.) Tzvel., <i>P. vivipara</i> Willd.).	$2n = 26, 33$, and 34 (Swiss Alps; Mutzing, 1940), $2n = 22, 23, 26$, and 28 on limestone and $2n = 33-35$ on granite (Tatra Mountains, Poland; Skalinska, 1950), $2n = 32-40, 44, 42 + 4ff, 43$, and 49 (Spitsbergen; Flovik, 1938; Engelsjon, 1979), $2n = 32-40, 43$, and 49 (Norway; Engelsjon, 1979). Range : Spitsbergen and Novaya Zemlya, Scandinavia, Scotland, Iceland; European mountains: the Carpathians, Tatra Mountains, Alps (Scholander, 1934; Tsvelev, 1964, 1976; Edmondson, 1980). One locality in nonarctic Siberia (western Altai): "in the upper part of slopes of the Chapchal'skii Ridge, stony tundra, $50^\circ 40' N$, $59^\circ 13' E$, 2600 m, no. 247, August 1, 1935, M.Kh." (Olonova, 1998). Another locality in the Kara tundra: "Nerusovei-yakha. The Kara River at its mouth, moist dolomite rock. Sukachev, July 16, 1909. L.E." Alaska (Hulten, 1942).
<i>P. smirnovii</i> subsp. <i>polozhinae</i> (Revjakina) Olon. (<i>P. alpina</i> var. <i>saposhnikovii</i> Serg., <i>P. smirnovii</i> Roshev. var. <i>vivipara</i> Malysch.).	Range : Altai, Katun and Kurkure ridges (Galanin <i>et al.</i> , 1979; Revushkin, 1988). Eastern Sayan Mountains, Kuznetskii Ala Tau (Malyshev, 1968), Tuva (Olonova, 1998)
<i>P. alpigena</i> \times <i>P. arctica</i> Lindm.	$2n = 56$ (eastern Chukchi Peninsula; Yurtsev and Zhukova, 1978). Range : Novaya Zemlya and Chukchi Peninsula (Lynge, 1923).
<i>P. alpina</i> \times <i>P. arctica</i> Lindm.	Range : sporadically occurs in Arctic Scandinavia and the Arctic Urals: "at foothills of Mount Shlem, Arctic Urals, August 8, 1965, Igoshina and Tsvelev, LE; Seida-Labotnangi, July 24, 1960, Mannik. LE" (Tsvelev, 1964)
<i>P. \times jemtlandica</i> (Almq.) K. Richter (<i>P. flexuosa</i> \times <i>P. alpina</i>).	$2n = 36$ and 37 (Europe; Love and Love, 1948; Edmondson, 1980). Range : mountain and Arctic Scandinavia, Scotland
<i>P. \times herjedalica</i> H. Sm. (<i>P. alpigena</i> \times <i>P. alpina</i> Lindm.).	$2n = 54$ and $47-80$ (Love and Love, 1948; Nygren, 1950). Range : Scandinavia, Novaya Zemlya (Lynge, 1923; Edmondson, 1980), lower reaches of the Pechora (Tsvelev, 1974b)
<i>P. \times nobilis</i> Skalinska (<i>P. granitica</i> \times <i>P. alpina</i>).	$2n = 80$ (Edmondson, 1980). Range : endemic to Southern Poland (the Tatra Mountains)
<i>P. granitica</i> subsp. <i>granitica</i> Br.-Bl.	$2n = 46-56, 64, 67, 71, 72, 80$, and 94 (Skalinska, 1950; Hadac and Haskova, 1956; Skalinska <i>et al.</i> , 1957). Range : endemic to the Western Carpathians (Edmondson, 1980)
<i>P. malacantha</i> Kom. (<i>P. hispidula</i> var. <i>vivipara</i> Hulten, <i>P. komarovii</i> var. <i>vivipara</i> Roshev.).	$2n = 62$ (the eastern Chukchi Peninsula; Yurtsev and Zhukova, 1978). Range : The Anadyr River basin and Providence Bay, Kamchatka, Alaska, and the Yukon, the Kuriles (Hulten, 1942; Tsvelev, 1964), on the Commander and Aleutian islands only the pseudoviviparous form (Probatova, 1971).

Table. (Contd.)

Name, synonyms	Range and known chromosome numbers
<i>P. platyantha</i> Kom. (<i>P. platyantha</i> f. <i>vivipara</i> Kom.).	Range: the seed form occurs throughout the nonarctic Far East; in Kamchatka, pseudoviviparous plants occur occasionally (Probatova, 1971)
<i>P. alpigena</i> subsp. <i>colpodea</i> (Th. Fries) Jurtz. et Petrovski (<i>P. pratensis</i> subsp. <i>colpodea</i> (Th. Fries) Tzvel., <i>P. alpigena</i> var. <i>vivipara</i> (Malmgr.) Scholander), <i>P. alpigena</i> var. <i>colpodea</i> (Th. Fries) Scholander, <i>P. rigens</i> C.Hartm. subsp. <i>colpodea</i> (Th. Fries) D.Love, <i>P. alpigena</i> f. <i>vivipara</i> Roshev.).	$2n = 37$ (Canadian Arctic Archipelago; Hedberg, 1967), $2n = 35$ (Peary Land, Greenland; Holmen, 1952), $2n = 35 + 3b$ (eastern Greenland; Jorgensen <i>et al.</i> , 1958), $2n = 42 + 4b, 51 + 5b$, and 61 (Spitsbergen; Flovik, 1938; Engelsjon, 1979), $2n = 56$ (basins of the Usa and Indgirkha rivers, Yamal and Chukchi peninsulas, Wrangel island; Zhukova, 1968; Sokolovskaya, 1970; Zhukova <i>et al.</i> , 1977; Sarapul'tsev, 1998), $2n = 42$ (Chukchi Peninsula and Wrangel Island; Petrovskii and Zhukova, 1978), $2n = 66, 71$, and 72 (Norway; Engelsjon, 1979), $2n = 38-80$ (northern Sweden; Nygren, 1950). Range: circumpolar high Arctic (up to the northern boundary of flowering plant distribution), without entering the forest-tundra zone (Holmen, 1952; Tsvelev, 1964; Safronova, 1983). Three localities in eastern Siberia, on the Barguzin and Yuzhn-Muiskii ridges (Siplivinskii, 1966)
<i>P. sublanata</i> subsp. <i>vivipara</i> (Tzvel.) Olon. (<i>P. sublanata</i> var. <i>vivipara</i> Tzvel.).	$2n = 42-49, 52$, and 54 (Yamal and Taz peninsulas; Sarapul'tsev, 1998). Range: Kolguev Island ("Kolguev Island, sand terrace in the Peschanaya River valley, between barns, September 9, 1936; A. Verlichenko. LE"); Bol'shezemel'skaya tundra ("the Korotaikha River basin, left bank, 3 km from the Yur-Yaga River mouth. Floodplain meadow with thin grass, August 28, 1931. Andreev and Savkina. LE"); Yamal, Taz, and Gydan peninsulas; lower reaches of the Yenisei, Bol'shaya Kheta, and Lena rivers (Tsvelev, 1964).
<i>P. beringiana</i> Probat. var. <i>vivipara</i> Probat. (<i>P. glauca</i> Vahl subsp. <i>beringiana</i> Probat.).	Range: one locality in Kamchatka, Elizovskii district (Probatova, 1984)
<i>P. vrangelica</i> Tzvel. (<i>P. hartzii</i> Gand. var. <i>vrangelica</i> (Tzvel.) Probat.).	$2n = 49$ and 56 (Wrangel Island; Petrovskii and Zhukova, 1978, 1981). Range: endemic to Wrangel Island (Tsvelev, 1976).
<i>P. pekulnejensis</i> Jurtz. et Tzvel. (<i>P. glauca</i> Vahl var. <i>pekulnejensis</i> (Jurtz. et Tzvel.) Probat.).	Range: endemic to southern Chukchi Peninsula: Pekul'nei Ridge and the Sokh River (Tsvelev and Yurtsev, 1980; Probatova, 1984; Korobkov and Sekretareva, 1997).

The same chromosome numbers were reported for this supposed hybrid from Iceland and North America (Love and Love, 1966); in northern Norway, one more number was estimated, $2n = 42$ (Knaben and Engelskjøn, 1967). In Europe and Greenland, such plants are fairly rare, but in the northeast of North America they are common and were described by Fernald as an independent species *F. prolifera* (Jenkin, 1922; Fernald, 1933; Scholander, 1934; Salvesen, 1986). A similar plant was found on Wrangel Island (Petrovskii and Zhukova, 1978); however, judging from its tetraploidy, this plant apparently represents *F. viviparoidea* and is listed in the table under this name.

Following the recent trend in taxonomy, Alekseev (1985) described the supposed hybrid *F. rubra* × *F. vivipara* under the name *F. villosa-vivipara* and attributed to it some plants from Greenland and Norway ($2n = 49$).

Investigations of the material from the entire *F. prolifera* range showed that this species is readily distinguishable from other pseudoviviparous *Festuca* species, but its intraspecific variation in many taxonomically important characteristics is enormous: for example, the length of an anther varies from 0.3 to 3.4 mm (Aitken

et al., 1988). Specialists regard *F. prolifera* as an aggregate of hybrid forms and nonhybrid derivatives of *F. rubra* belonging to the *F. rubra* s.l. complex.

In concluding the review of the genus *Festuca*, it may be noted that there is a certain variation of morphological and karyotypic characteristics in the complex of arctic pseudoviviparous *Festuca* species which provides the possibility of subdividing it into taxa of various ranks, including the species rank. The presence of hybrid forms is confirmed both by herbarium specimens and by direct observations in the field.

The genus *Deschampsia* Beauv. (hair grass). *Deschampsia alpina* is an example of a "true" species whose ancestral species is difficult to conjecture. Tsvelev (1964) regarded it as such a species, with the reservation that this taxon might be a pseudoviviparous variety of *D. brevifolia* R.Br. Later, its independence was questioned, and it was included in *D. caespitosa* (L.) Beauv. as a subspecies (Tsvelev, 1974b, 1976; Clarke, 1980). *Deschampsia alpina* differs from all the aforementioned taxa in having the most inhibited generative sphere: seeds were never found, and even flower formation is known as a very rare event (Scholander, 1934;

Mishin, 1953). A long series of known chromosome numbers comprises both euploid and aneuploid values (table), which is evidence for the instability of the developmental processes (Flovik, 1938).

The genus *Poa* L. (bluegrass). Pseudoviviparous *Poa* species are the largest and most taxonomically complex group of arctic pseudoviviparous grasses. In contrast to *Festuca* and *Deschampsia*, the genus *Poa* includes no well-defined species with pseudoviviparous propagation. As a rule, they are either supposed hybrids or intraspecific taxa of nonviviparous species. Most taxa (15 out of 17) belong to the type section of the genus; *P. pekulnejensis* belongs to the section *Stenopoa* Dum. and *P. vrangelica*, to *Abbreviatae* Nannf. (Tsvelev, 1974a). Pseudoviviparous *Poa* taxa belong to one of the largest and most dynamic intraspecific complexes in which active hybridization occurs and genetic interspecific barriers have not yet been formed. This is evidence for their hybrid origin (five out of 15 taxa are described as hybrids or hybridogenic species!).

Another important feature of the genus *Poa* is a relatively high frequency of various kinds of apomictic reproduction. This factor is responsible for a high karyotypic variation in such species as *P. pratensis*, *P. alpina*, or *P. alpigena* (table) (Nannfeldt, 1937; Muntzing, 1940; Nygren, 1950; Batygina and Mamet'eva, 1979).

The distribution of pseudoviviparous taxa related to *P. alpina* (*P. smirnovii* subsp. *polozhinae*, *P. granitica*, *P. × nobilis*, *P. × herjedalica*, *P. × jemtlandica*, *P. alpina* × *arctica*) is confined to the area of *P. alpina* s.l. Even the southern Siberian *P. smirnovii* makes no exception (Tsvelev, 1964; Edmondson, 1980). These are mainly endemic taxa growing in some mountain areas. They demonstrate no apparent hiatus by morphological characteristics and have high chromosome numbers. Probably, all of them are local varieties of the same species. The European *Poa alpina* subsp. *vivipara* proper is so diverse morphologically that attribution to it of the plants occasionally found in the Altai (Olonova, 1998) appears to be erroneous.

The Far Eastern species *P. malacantha* and *P. platyantha* are morphologically and ecologically close to *P. alpina*, but the level of their relationship remains unclear. No special investigations of the biology of these species were made. The origin of two fully pseudoviviparous endemic species *P. vrangelica* and *P. pekulnejensis* remains unknown: the former was found on Wrangel Island only, and the latter, in two localities of the Chukchi Peninsula. Some characteristics make them similar to *P. hartzii* and *P. glauca*, respectively. However, the most taxonomically important characteristics are those of glumes, and, hence, it is impossible to make any definite conclusions on the basis of morphology alone.

The situation with the taxa related to *P. pratensis*—*P. alpigena* subsp. *Colpodea* and *P. sublanata*—is different. They have wide ranges (the former species is circumpolar, the latter is Siberian), are widespread

within their limits, and play a major role in various phytocenoses of the tundra zone. According to my data, the populations of these taxa in western Siberian hypoarctic tundras comprise both seed and pseudoviviparous plants. The latter regularly produce high-quality seeds, and viviparity as a trait is inherited and manifests itself in a part of the first-generation seed progeny (Sara-pul'tsev, 1998). However, at the southern boundary of arctic tundras, the populations of the type taxon and the pseudoviviparous taxon become separated from each other: they occupy different habitats and begin to differ morphologically (in habitus); farther to the north, only plants with vegetative propagation remain. I agree with the opinion that it is correct to differentiate between the high-arctic *P. alpigena* subsp. *colpodea* (including the pseudoviviparous variety) and the arctomontane hypoarctic subspecies *P. alpigena* subsp. *alpigena* (Porsild, 1955).

Still more widespread, *P. arctica* also has a pseudoviviparous variety. It occurs rarely but in virtually all Arctic regions. Due to the continuum of morphological vegetative characters in *P. arctica* and *P. alpigena*, specimens of the latter or hybrids between these species (*P. lindebergii*, *P. alpigena* × *P. arctica*) were occasionally regarded as a pseudoviviparous variety of *P. arctica* (Scholander, 1934).

Thus, both *Poa* and *Festuca* comprise well-defined independent pseudoviviparous taxa (including those of the species rank), hybridogenic endemic taxa, and complex aggregates of hybrid forms, which are permanently supplied owing to hybridization in the areas cohabited by the ancestral species.

The population structure of pseudoviviparous grasses in the Arctic. At the northern boundary of flowering plant distribution, the existing climatic conditions are unfavorable for normal seed reproduction. Hence, it is not surprising that pseudoviviparous *P. alpigena* subsp. *colpoidea*, *D. alpina*, and *F. viviparoidea* could penetrate farther to the north (Holmen, 1952; Safronova, 1983; Aiken *et al.*, 1996). In the evolutionary aspect, the replacement of seed propagation by vegetative propagation is obviously a blind alley, as it leads to the loss of genetic diversity and fitness in the areas with less extreme environmental conditions.

Using the example of pseudoviviparous grasses, the processes of stabilization of the genetic system and of the return to sexual reproduction may be followed stage by stage. Initially, these plants are fully sterile hybrids; then, some flowers in the inflorescence begin to develop normally; the next stage is the appearance of fertile pollen, and the pseudoviviparous species assumes the role of male ancestor in hybridization; finally, the plants begin to form normal seeds. Such seeds are regularly formed in mixed panicles in *F. vivipara*, *P. granitica*, *P. sublanata*, and *P. alpigena*. In the latter two species, the seed germination rate in pseudoviviparous plants was shown to be even higher than in

jointly growing seed plants (Skalinska, 1950; Sarapul'tsev, 1996).

The evolutionary fate of a taxon is reflected in its population structure. The most evolutionarily advanced pseudoviviparous species have vast ranges, their populations are characterized by considerable genetic diversity, and their reproductive strategy implies balance between seed propagation and vegetative propagation.

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Phenes of Woody Plants: Identification, Scaling, and Use in Population Studies (An Example of *Pinus sylvestris* L.)

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Abstract—The methods of identification and scaling of phenes of forest plants are described. The phene identification consists of five stages. Specific features of studies at each stage are shown using identification of the phenes of seed color, cone color, and seed scale structure in Scotch pine (*Pinus sylvestris* L.) as examples. The method of phene scaling is based on the comparison of phene frequencies in a bog and in adjacent upland populations of pine. At the boundary between the bog and dry land, the frequencies of population-level phenes change, whereas those of superpopulation-level phenes remain unchanged.

Key words: phenetics, population, scaling, *Pinus sylvestris* L.

Phenetic methods are successfully used in studies on natural populations of animals and herbaceous plants. These methods are based on the notion of phenes as elementary, discrete variations of an organism's traits and characteristics. Phenets reflect certain genotypic features and mark, by their frequencies, genetic characteristics of groups of individuals (Yablokov, 1980, 1987; Yablokov and Larina, 1985). Today, these methods cannot be effectively applied to studying forest woody plants because of the insufficient number of phenes identified in them. Moreover, traits that do not comply with the definition of a phene are improperly used in population studies (Yablokov, 1980). According to our data, identification of individuals with the use of these phenes is difficult or impossible. Only a few phenes of woody plants are currently known because of the small number of elementary qualitative morphological variations of traits in populations of these plants (Abaturova, 1978). I believe that the phenes described are so few not only because of the specificity of woody plant biology, but also because woody plants have not been sufficiently studied in this respect.

We studied variation in some morphological traits of the generative organs in Scotch pine (*Pinus sylvestris* L.) and found several discrete variations that fit the definition of a phene. Identification of phenes consists of five stages. Consider the details of these stages using identification of the phenes of seed and cone color and the structure of the seed-scale apophysis.

Stage 1: Creation of the collection of cones and seeds. To begin identification of phenes, it is necessary to obtain a collection of cones and seeds. The collection should contain material from the entire species range or a considerable part of it. The sites of cone collection (test plots) should be evenly distributed in the geographic space. Cones are collected in pine forests with

the site conditions most typical of the given region. Cones from 100 trees (one cone per tree) are collected at each test plot and in each forest type within the same forest range. To study endogenous and temporal variation, 20–25 trees are selected. Forty to 50 cones are collected annually for three years. To study intracolonial variation, 15–20 clones are used. Ten cones are taken from each of ten ramets of each clone. Seeds and clones from each tree (ramet) are stored in special collection boxes. When developing the method for identifying the phenes, we used a collection of seeds and cones from 16600 trees from ten regions (oblasts and autonomous republics) of the eastern European part of Russia.

Stage 2: Testing the existing classifications of traits and determining the spectra of discrete variation of individual sets of traits. Literature is screened to find all existing classifications of the set of traits studied. Using each classification, multiple identification of the objects from several collection samples is performed by one researcher, which is followed by single identification by different researchers. If the results obtained are similar, the classification is considered objective and the variations of the traits studied are considered discrete. These variations should be further estimated to test whether they meet the criteria of a phene. If the results of classification are ambiguous, it is to be assumed that the individual variations found are not discrete but represent subjectively distinguished fragments of a homogenous distribution of the trait in the population. Thereafter, objects sampled from different populations are compared with respect to individual sets of traits (color, shape, structure of organs, etc.) in order to gain a general impression of the variation spectrum and the presence of discrete variations. Let us illustrate the course of studies at this stage by some examples.

According to published data, variants of seed color may represent phenes in woody plants (Mamaev and Semkina, 1977; Milyutin, 1990; Chernodubov, 1998). Seed color is especially variable in Scotch pine. It is known that the color of the seeds of this species is individual and stable in the course of ontogeny (Pravdin, 1964). There are several classifications of seed color, which are based on the same principle but differ in the number of variants distinguished. Classifications proposed by Pravdin (1964), Mamaev (1973), Kuz'mina (1978), and Cherepnin (1980) include 5, 5, 15, and 10 variants, respectively. Multiple identification of the same samples by different researchers using each of these classification and identification by the same researcher under different illumination conditions yielded different results. Thus, these classifications are subjective because they are based on the estimation of color of the predominant pigment and the ability to discern it depends only on the individual characteristics of the researcher. In addition, these variants of color are not discrete, as variations of the trait at the individual level are gradual and have many intermediate forms. The color of organs is known to be determined by the colors of the pigments and the presence of a pattern (Yablokov, 1980). We had no data on the presence of a pattern.

Estimation of cone color yielded similar results. It is known that cone color varies from light gray to dark brown (Pravdin, 1964; Mamaev, 1973; Kuz'mina, 1978; Pugach, 1982). Each researcher distinguishes a different number of color variants. For examples, Mamaev (1973) distinguishes gray, green-gray, sandy, and brown cones; whereas Kuz'mina (1978), gray, dapple gray, grayish brown, and dark brown cones. As with seeds, different researchers obtained different results when they identified the same samples of cones using these classifications. The only exception was the brown color, which was easily and unambiguously identified by all researchers. The estimation of cone color was subjective for the same reasons as in the case of seed color. The existing methodology based on determining the pigment prevailing in the organ does not allow the researcher to distinguish elementary discrete variants, since the trait varies continuously. No data have been published on a pattern (spots, dots, dashes, etc.) on the cones.

At the ends of the seed scales of Scotch pine, there usually are swellings, which form small protective covers (apophyses) (*Lesnaya entsiklopediya*, 1986). Variations in the height of the apophysis have mostly been studied. For example, Pravdin (1964) distinguishes cones with flat, tuberous, and hooked apophyses; Mamaev (1973), cones with flat, slightly tuberous, tuberous, prominent, and very long (usually bent) apophyses. Our data have demonstrated that, at the individual level, cones are characterized by a continuous variation in the length of the apophysis. Therefore, partitioning the variation range according to Pravdin's and Mamaev's classifications will inevitably be subjective,

which is confirmed by the different results of identification of the same cones by different researchers. It is impossible to distinguish discrete variants of the apophysis length.

It was reported (Pravdin, 1964) that the same population may contain trees with different types of hooked apophyses: in some trees, they are bent forward (to the top of cone), and in others, backward (to its base). The mechanisms of this phenomenon are unknown. These variants may be discrete; therefore, they should be tested for compliance with the criteria of a phene.

The comparison of large numbers of cones and seed with respect to color demonstrated that almost each tree has its own spectrum of colors and shades, scarcely discernible by the naked eye. This suggests that cone and seed colors in most pine trees are individual, specific, and unique. Along with the continuous variation of the trait at the individual level, this makes it impossible to detect discrete variants until simpler elements of the trait are identified. These elements are searched for at the next stage of the study.

Stage 3: Isolation of elementary traits; isolation and description of discrete variants. At this stage, complex traits are decomposed into simpler components. Among the simple (elementary) traits, discrete variants are detected. Then, these discrete variants are tested for objectivity of identification. Let us illustrate this by the following examples.

Studies on variation in the structure of seed color in different pine trees demonstrated that seed color is determined by three layers. The first (inner) layer is thin and dense; it homogeneously covers the seed coat. In different trees, it may contain either a gray or brown pigment.

The second (middle) pigment layer is relatively thick and can be rubbed off easily. It consists of granular structures containing only black pigment in all trees. Two types of seeds are distinguished according to the pattern of the distribution of these granular structures over the seed coat surface (Fig. 1): in some trees, granular structures homogeneously cover the seed coat, with their density varying from an almost continuous layer to single granules; in others, these structures form isolated spots. At the individual level, the number of spots varies from the maximum, when the spots adjoin each other to form a cellular pattern, to the minimum, when there are one or two small spots, often with a low degree of contrast.

The third (outer) pigment layer consists of a waxlike yellowish white substance covering the seed surface either almost entirely or only partly. The seeds of many trees lack the third pigment layer.

At the individual level, the gray and brown pigments of the first layer vary in shade from light to dark, whereas the pigments of the second and third layers are invariable. When identifying color phenes of animals, only the color of the pigment, but not its shade, is taken into account, since it is impossible to discern discrete

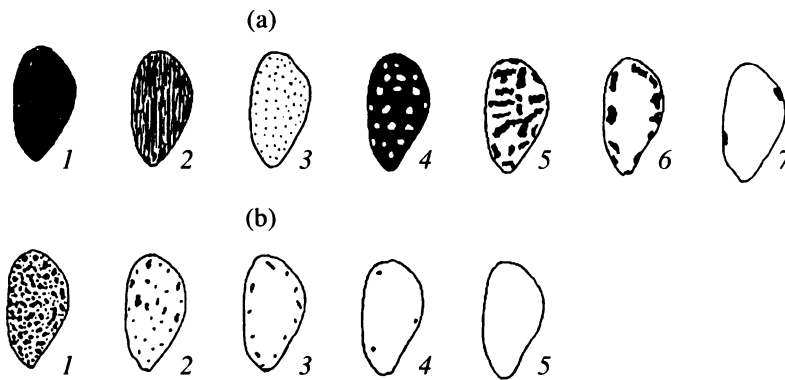


Fig. 1. Variation of Scotch pine seeds with respect to (a) the color of the second pigment layer (1–3, homogeneously colored; 4–7, spotted) and (b) the presence of the third pigment layer (1–4, seeds with the third layer; 5, seeds without the third layer).

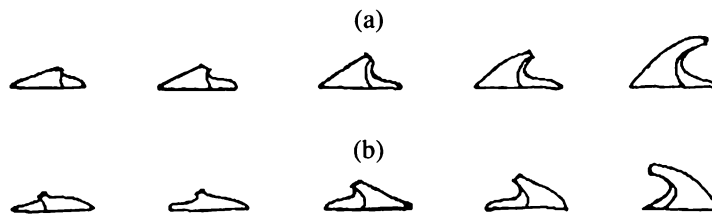


Fig. 2. Variation of Scotch pine cones with respect to the apophysis development type (ADT): (a) the posterior type (PADT); (b) the anterior type (AADT).

variants of the continuously varying trait (Yablokov, 1980, 1987). This applies to plants as well.

Thus, detection of elementary traits of seed color allows us to distinguish the following discrete variants: the gray, black, and brown variants of the first layer; the homogeneously pigmented and spotted variants of the second layer; and the presence and absence of the third layer.

We failed to decompose the cone color into elements. Cones of the same tree are colored by one layer of gray, green, or brown pigment. Most trees in the population have gray or green cones. In an individual tree, the gray or green cone color is actually a continuous range of shades of this color, from light to dark. Therefore, it is impossible to distinguish discrete variants of the gray-green cone color. The brown color, which is represented by a range of light to dark shades in each tree, is an exception. The brown and gray-green colors are contrasting. Therefore, the brown cones are easily identified irrespective of the shade of the pigment. Thus, two discrete variants of cone color, brown and gray-green, may be distinguished.

The apophyses of different cones were found to differ not only in height but also in the degree of development of the anterior and posterior parts. Two groups of cones (with predominant development of the anterior and posterior parts of apophyses, respectively) were distinguished in the population according to this trait. Thus, the apophysis development types (ADTs) were

distinguished. The variants with predominantly developed anterior and posterior parts of the apophysis were designated AADT and PADT, respectively. At the individual level, continuous variation with respect to the height of the best developed part of the apophysis was found in each variant (Fig. 2). A hook-shaped bend appeared on the best developed part of the apophysis as its height increased; this bend was directed toward the base and the top of the cone in AADT and PADT cones, respectively.

Different researchers obtained the same results when classifying the same samples with respect to the seed and cone colors and the ADT, which confirms that the traits were discrete.

Stage 4: Testing the identified variants for compliance with the criteria of a phene. We did not study the mode of inheritance of the detected discrete variants of the seed and cone colors and the ADT; nor did we find such data in the literature. However, this must not prevent the use of these traits in population studies because the important point is the very fact that the traits are genetically determined, rather than the precise mode of inheritance (including the number and location of the genes).

Petrov (1990) believes that the genetic determination of phenes can be estimated within one generation. According to Petrov, if a trait is stable in the tree crown, then it is independent of environmental conditions and its development is determined by the genotype. This

Table 1. Frequencies (%) of discrete variants of pine seed and cone colors in different forest types in the Nizhne-Ivkinskoe Forestry of the Kumenskii Forest Enterprise

Forest type	Variants of seed color						Brown cones
	first layer		second layer		third layer		
	black	brown	spotted	homogeneous	present	absent	
Cowberry pine forest	78.9	21.1	93.7	6.3	67.4	32.6	8.8
Wood sorrel pine forest	77.8	22.2	94.4	5.6	66.7	33.3	8.9
Bilberry pine forest	77.5	22.5	92.9	7.1	66.2	33.8	8.3

Table 2. Frequencies (%) of some phenes, indices, and countable traits in Scotch pine populations growing in bogs and dry areas of Kirov oblast

Population	Absence of the third pigment layer	AADT phene	Classes of the indices of cone shapes			Sprouts with the following numbers of cotyledons				
			≥0.455	0.456–0.546	≤0.546	4	5	6	7	8
Ivanovo Bog	69	19	45	55	0	3	23	55	16	3
Dry valley	54	0	43	57	0	2	24	56	16	2
Pishchal'skoe Bog	66	20	45	55	0	4	29	58	8	1
Dry valley	48	0	45	55	0	3	28	59	10	0

assumption was confirmed by the data on the pine population structure analyzed by means of index estimation of traits (Vidyakin, 1991a). In addition, stability of a trait in time and under different ecological (forest-typological) conditions within the same plantation (Vidyakin, 1991a, 1991b, 1995) or the same clone is also evidence in favor of its genetic determination.

Inspection of seeds and cones from individual trees during three seasons demonstrated that all of the aforementioned discrete variants of seed and cone colors and ADT were stable; they did not change within the tree crown and in different years. They were also identical in different ramets of the same clone. The microecological heterogeneity of growth conditions (or the forest type, which is an integrated characteristic of them) did not affect the frequencies of the variants detected. For example, the frequencies of the seed and cone colors were the same in different forest types (Table 1). This was also true for the ADT.

At the end of stage 4, the researcher should test whether the discrete variants are alternative. A phene is called alternative if each individual has only one variant of the trait (Yablokov, 1980, 1987). To determine whether a phene is alternative, trees from several dozens of samples from different geographic regions should be analyzed. The aforementioned discrete variants of the seed and cone colors and ADT were demonstrated to be alternative.

Stage 5: Estimation of the phene informativeness. If the spatial variation of the frequencies of phenetic variants is sufficiently large for differentiation of the species into groups within its range, the phene is considered informative. The greater the differences

between these groups, the more informative the phene. For example, the phene "absence of the third pigment layer of seeds" was more informative than the phene "brown color of the first layer." Their frequencies in different populations varied from 24 to 71% and from 15 to 30%, respectively.

Phenes of different ranks, from individual and familial to species, are distinguished (Yablokov, 1980, 1987; Yablokov and Larina, 1985). The ranks of phenes correspond to the hierarchical level of the species structure that is marked by specific stable frequencies of the phenes. For example, the population structure of Scotch pine includes three hierarchical levels: populations, groups of populations, and migration zones (Vidyakin, 1998). Correspondingly, Scotch pine has phenes of the population, population-group, and migration-zone levels.

Population is the basis of the structural organization of species (Timofeeff-Ressovsky *et al.*, 1973, 1977). Therefore, it is important to identify the population level of organization. For animals and herbaceous plants, dozens and sometimes hundreds of phenes are known, and their ranges are relatively small. Therefore, the population level can be identified in these species by means of phenogeographic studies on many phenes. The researchers distinguish intraspecific groups belonging to several hierarchically subordinate levels based on the estimated specificity and stability of phene frequencies in the geographic space within the range. Each level is marked by a certain set of phenes. The lowest of these levels is usually regarded as the population level. Each set of phenes is assigned the rank of the species organization level that is marked by these

Table 3. Frequencies (%) of the variants of seed color in two Scotch pine populations of Kirov oblast

No.	Sampling site: forest enterprise (forestry)	Phenes of seed color			
		first layer		third layer	
		black	brown	present	absent
The right bank of the Cheptsya River					
1	Peskovskoe (Kirsinskii)	82	18	69	31
2	Sezenevskoe (Zuevskii)	83	17	69	31
3	Tavolzhanskoe (Omutinskii)	84	16	69	31
4	Dubovitskoe (Zuevskii)	85	15	69	31
5	Tavolzhanskoe (Omutinskii)	82	18	67	33
The left bank of the Cheptsya River					
1	Mukhinskoe (Zuevskii)	70	30	46	54
2	Glazovskoe (Glazovskii)	70	30	45	55

phenes (phenes of the population level, the population-group level, etc.).

In the case of woody plants, with their large species ranges, such phenogeographic studies are inevitably labor- and time-consuming. In addition, phenogeographic studies on a limited number of phenes may not permit isolation of several intraspecific structural levels, and, if they have nevertheless been isolated, the lowest of them may not correspond to the population level. Therefore, the phenes of the population rank should be identified in woody plants before phenogeographic studies. I think that, in the case of Scotch pine, this methodical problem may be solved as follows.

Results of the numerous recent studies indicate that two different types of Scotch pine populations are formed under contrasting growth conditions in neighboring bog and upland areas (*Osobennosti formirovaniya...*, 1984; Petrova *et al.*, 1989; Petrova and San'nikov, 1996; Belokon' *et al.*, 1998). In this case, phene frequencies of one group should change at the boundary between a bog and dry land, whereas phene frequencies of another group should remain stable. The former and latter groups have the population and superpopulation ranks, respectively. The superpopulation group may include phenes of all levels of the population structure higher than population, up to the species level inclusive. Not only phenes but also other genotypically determined traits (e.g., indices and some countable traits) can be scaled in this way.

The data obtained on the variation of phenes, indices, and numbers of cotyledons in the bog and adjacent dry areas agreed with the aforementioned patterns of changes in the frequencies of these traits as one moves from one habitat to the other (Fig. 2). The phene frequencies of the third pigment layer of seeds and the type of apophysis statistically significantly change at the border between the bog and upland populations of Scotch pine. Therefore, these phenes should be assigned to the population rank. The indices of the

shape of cones and number of cotyledons are the same in both populations; therefore, they may serve as marker traits of superpopulation groups within the species.

Some phenes, indices, and countable traits have been found to be highly informative for studying the population structure of pine. For example, phenes of seed color allow the researcher to divide the species into populations (Table 3); indices of the shapes of cones and apophyses, into population groups (Vidyakin, 1991b; 1995); number of cotyledons, into migration zones (Vidyakin and Glotov, 1999).

The results of phenogeographic studies allowed us to construct the scheme of the population structure of pine in Kirov oblast. This scheme may serve as a basis for further research in microevolution, microphylogeny, taxonomy, gene pool conservation, and rational breeding and seed growing. It is probable that phenes of woody plants may be correlated with commercially important traits and properties, which can be used by breeders. Genetic control of the phenes detected should also be studied.

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Ontogeny and Population Structure of *Xanthoria parietina* (L.) Th. Fr. under Different Ecological Conditions

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Abstract—With regard to the concept of a discrete approach to the description of seed plant ontogeny, proposed by T.A. Rabotnov and A.A. Uranov, the ontogeny of apothecial foliose lichen *Xanthoria parietina* is described. Four periods and 13 ontogenetic states are distinguished by morphological and anatomical characters. In the urban environment, the thalli of *X. parietina* perish at early developmental stages (incomplete ontogeny); in general, their size and the number and size of apothecia decrease and the connection with substrates at the final ontogenetic stages becomes weaker. Adaptation of the *X. parietina* population to existence under adverse natural and anthropogenic conditions manifests itself in the retarded development of pregenerative individuals and elimination of the least tolerant generative individuals.

Key words: lichen, ontogeny, population, *Xanthoria parietina*

The state of populations may be estimated by comparing their development under optimum conditions and under ecological and anthropogenic stress. Such investigations are promising in both theoretical and applied aspects. The recorded characters of organisms and populations may be used for bioindication and monitoring, on the one hand, and for investigating the mechanisms of adaptation to varying environmental conditions, on the other. In the case of seed plants, this approach is based on well-developed population-ontogenetic methods based on the notion of the population as a complex biological system comprising individuals of different ontogenetic states, which are combined into age groups (Rabotnov, 1950; Uranov, 1975; *Tsenopopulatsii*, 1976, 1977, 1988; Zhukova, 1995).

Ontogenetic investigations are common in lichenology. However, most studies describe different variants of morphogenesis of the organs of sexual and asexual reproduction or the thallus. The description of thallus development is usually completed at the stage of formation of a life form characteristic of a certain lichen species and the development of fruit bodies or organs of vegetative reproduction (Jahns, H. *et al.*, 1979; Jahns, M. *et al.*, 1995; Lallemand, 1984; Ott, 1987a; Stocker-Wörgötter and Türk, 1988; Hill, 1994). Only a few studies deal with the development of the thallus from spore to death at final ontogenetic stages, or with “complete ontogeny” (Zhukova, 1983), and the dynamics of thallus degradation (Verseghy, 1983; McCarthy, 1989).

The problem of delimiting the boundaries of populations in lichens is more complicated than in other organisms. In lichens, the population is understood as a local group of thalli of the same species, which is spatially separated to some degree from other groups (Fah-

selt, 1996; Mikhailova and Vorobeichik, 1999). Probably, it is not quite correct to apply the term “population” to a symbiotic lichen thallus. The use of this term in lichenology is explained by the necessity of having a general system of notions applicable to different fields of biology. Many terms, including the notion of species, are used by analogy, although they have a special meaning in lichens.

In this study, the concept of a discrete approach to the description of higher plant ontogeny, proposed by T.A. Rabotnov and developed by A.A. Uranov and his followers, is applied to the description of ontogeny and population structure of the foliose apothecial lichen *Xanthoria parietina* (L.) Th. Fr. Its purpose is to reveal specific features of lichen ontogeny and the age structure of its populations in natural and anthropogenic habitats.

MATERIALS AND METHODS

This study was performed between 1994 and 1998 in the southern taiga subzone in two natural habitats—the Bol'shaya Kokshaga Nature Reserve and the Mari Chodra National Park—and in the city of Ioshkar Ola (the Republic of Mari El). Automobile exhaust is the principal source of pollution in the city, and the main pollutants are carbon oxide, hydrocarbons, and nitrogen oxides (*Gosudarstvennyi doklad*, 1998).

Xanthoria parietina was chosen for the study because it is a widespread lichen commonly occurring in the study region, its yellow-orange thalli are easily identifiable, and their boundaries are easy to determine. *Xanthoria parietina* propagates by spores, and its thalli form fruit bodies, lecanorous apothecia. An additional

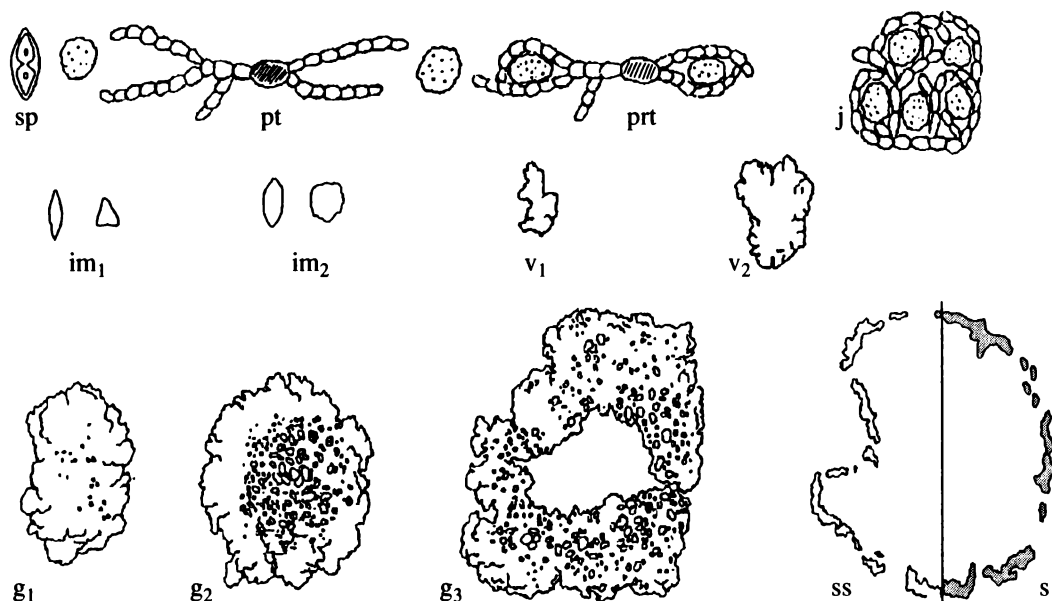


Fig. 1. Ontogeny of *X. parietina* (indices of ontogenetic states are explained in the table): sp, pt, prt (magnification 800×); j (600×); im₁, im₂ (25×); v₁ (10×); v₂, g₁ (2×); g₂, g₃, ss, s (natural size).

form of reproduction, by means of soralia, is known to appear when the thalli of *X. parietina* and *Physcia tenella* (Scop.) DC. In Lam. et DC are mixed (Ott, 1987a). There is an interesting adaptive mechanism characteristic of the *X. parietina* mycobiont, namely its temporary coexistence with “foreign” algae (e.g., those of the genus *Pleurococcus*) instead of *Trebouxia* or *Pseudotreboxia* that are necessary for true symbiosis. This mechanism facilitates the spread of the fungus over substrates (Ott, 1987a, 1987b).

For studies on lichen ontogeny, more than 400 samples were collected from separately standing aspen trees (*Populus tremula* L.) in the Bol’shaya Kokshaga Nature Reserve and from aspen and small-leaved linden (*Tilia cordata* Mill.) in the city of Ioshkar Ola, in the zone of moderate pollution. The ontogenetic states were determined by qualitative morphological and anatomical characters and some quantitative parameters that were used in previous studies (Suetina and Zhukova, 1997) for developing the criteria of ontogenetic states in this species. The initial ontogenetic stages—up to the formation of the crustose life form (the juvenile thallus)—were described taking into consideration the studies by Werner (1965), Shapiro (1971), Oksner (*Opredelitel*, 1974), Ott (1987a), and Hill (1994).

By analogy with seed plants, individuals in the ontogenetic states im₂–ss were studied with respect to the quantitative morphometric characters of vegetative structures (thallus area and thickness, the number of lobes, their length and width, the thickness of rhizines) and of generative structures (the number and width of apothecia, the width of the thallus edge of apothecia, the height of the hymenial layer, and spore size). To

estimate the relationship between thallus area and the number of apothecia in the g₁ and g₂ states, 100 “individuals” (thalli) in each state were studied.

The age structure of the *X. parietina* population on small-leaved linden was studied in a natural habitat, the Mari Chodra National Park (14 trees, sample size 173 specimens), and in Ioshkar Ola: in the zones of weak pollution (20 trees, 936 specimens), moderate pollution (20 trees, 239 specimens), and heavy pollution (32 trees, 300 specimens). In the national park, test trees were inside the stand, in the shaded area; in the city, these were separate trees. The zones of weak, moderate, and heavy pollution were delimited by means of lichenoidication (Suetina, 1999). On each tree, the number of individuals of each age group, beginning from immature, was counted at the trunk height of 1 to 1.8 m. Two immature states—im₁ and im₂—were difficult to differentiate in the field (they differ in thallus anatomy), and the immature state was recorded without subdivision in this part of the study.

The quantitative characters of individuals in different ontogenetic states were compared using the Student test, and the age structure of the population was analyzed with the aid of the chi-square test (contingency tables). Calculations were made using BIOMSTAT software (Rohlf and Slice, 1995; Rohlf and Sokal, 1995; Sokal and Rohlf, 1995).

RESULTS AND DISCUSSION

Ontogeny of X. parietina. Four periods and 13 ontogenetic states were identified (table, Fig. 1) (Suetina *et al.*, 1997). Three types of changes in the values of anatom-

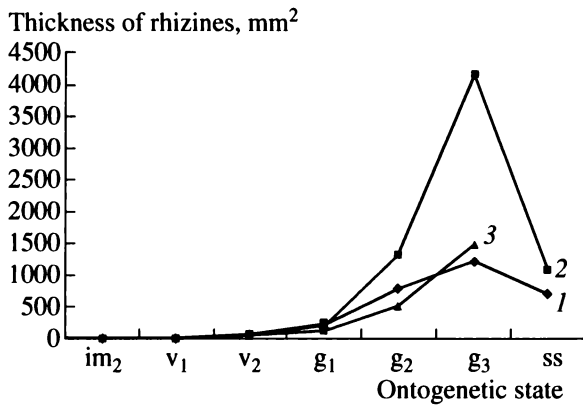


Fig. 2. Changes in the thickness of rhizines in the course of *X. parietina* ontogeny: (1) aspen, city; (2) aspen, nature reserve; (3) small-leaved linden, city.

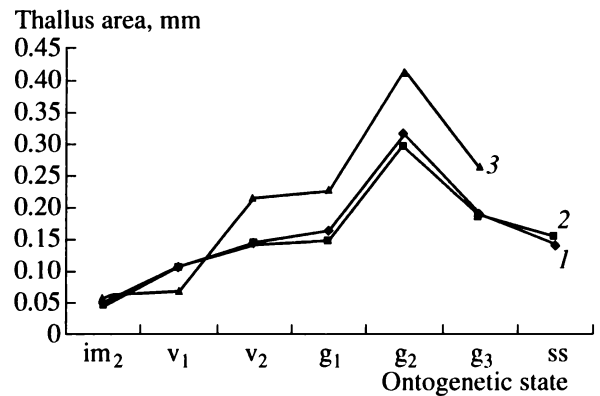


Fig. 3. Changes in the area of the thallus in the course of *X. parietina* ontogeny. For designations, see Fig. 2.

ical and morphological characters in the course of ontogeny were revealed. The thickness of rhizines (Fig. 2), the length and width of lobes, the width of the thallus edge of apothecia, and the size of spores reached the maximum in the g_2 state, with a subsequent decrease in the g_3 state (the values of vegetative characters decreased in the ss state as well). The thallus area (Fig. 3), the number of lobes, the diameter of the apothecia, and the height of the hymenial layer increased until the g_3 state, with a subsequent decrease in the values of vegetative characters in the ss state. The thallus thickness (Fig. 4)

sharply increased upon the transition from im_2 to v_1 , remained unchanged between v_1 and g_3 , and decreased in the ss state. The number of apothecia increased along with the thallus area in both g_1 and g_2 individuals: the Spearman rank correlation coefficients were 0.71 and 0.87, respectively ($p < 0.05$). The values of anatomical and morphological characters of thalli depended on the species of tree on which lichen grew; they were usually higher in lichens from aspen. More numerous apothecia and, hence, higher spore production provided evidence for more efficient self-maintenance of *X. parietina*.

Ontogenetic states of *X. parietina* and their marker characters

Period	Ontogenetic states and their indices	Characters
I. Latent	1. Fungal spore (sp)	Spore elliptic, bipolar, colorless
II. Pregenerative	2. Protothallus (pt)	Formation of fungal hyphae from the spore
	3. Proterothallus (prt)	Algal cells (<i>Trebouxia</i> , <i>Pseudotreboxia</i>) are surrounded by hyphae, primary thallus is formed
	4. Juvenile thallus (j)	Crustose thallus, homeomeric anatomical structure
	5. Immature 1 (im_1)	Thallus of foliose life form, homeomeric structure, the protective upper crust is formed
	6. Immature 2 (im_2)	Anatomically, the thallus is heteromeric and has a lower crust
III. Generative	7. Virginal 1 (v_1)	Irregular thallus, no increment in thickness
	8. Virginal 2 (v_2)	Thallus has the form of a regular round rosette typical of this species
	9. Young generative (g_1)	Sedentary apothecia appear separately, in the center of the thallus. The ratio of the thallus margin and apothecium disk is 1 : 2
	10. Middle-age generative (g_2)	Most apothecia are stalked, they are crowded in the central part of the thallus and present at its periphery. The ratio of the thallus margin and apothecium disk is 1 : 9
	11. Old generative (g_3)	Central part of the thallus dies off and is absent. The ratio of the thallus margin and apothecium disk is 1 : 16
IV. Postgenerative	12. Subsenile (ss)	The thallus consists of small disconnected fragments. The upper crust is absent from some areas, mainly on the side facing the lost central part of the thallus
	13. Senile (s)	The thallus consists of small disconnected fragments (as in ss), which become white because of necrotic processes

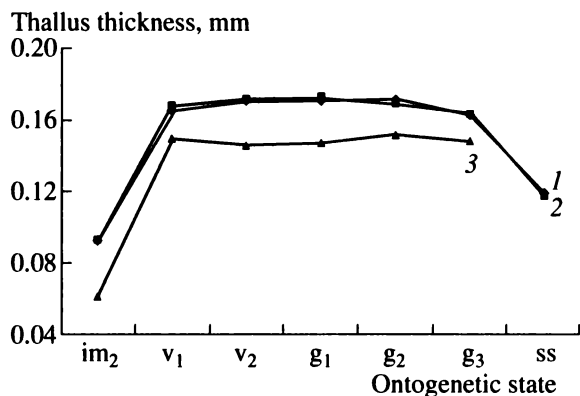


Fig. 4. Changes in the thickness of the thallus in the course of *X. parietina* ontogeny. For designations, see Fig. 2.

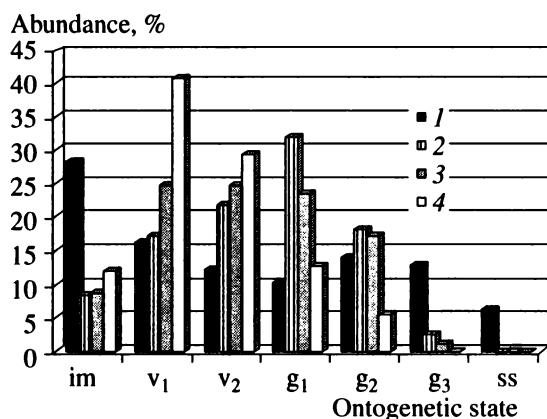


Fig. 5. Age spectra of *X. parietina* populations in a natural habitat and zones with different pollution levels in the city of Ioshkar Ola: (1) natural habitat; (2) the zone of weak pollution; (3) the zone of moderate pollution; (4) the zone of heavy pollution.

ina population on aspen. In v_2 – g_3 individuals, the thickness of rhizines was higher on linden, which provided for stronger attachment to the substrate. The rough surface of aspen bark apparently allowed sufficiently strong attachment without the development of strong rhizines.

The comparison of quantitative characters at different ontogenetic stages in lichens growing on aspen in the city and in the nature reserve demonstrated that the values of these characters are usually higher in clean habitats. This concerns the thallus area; the number and diameter of the apothecia; and the number, length, and width of lobes. Under conditions of pollution, a tendency toward the thinning of rhizines in ss individuals was revealed. As thalli with thin rhizines detach from the bark of trees more easily, subseile individuals occurred in the city more rarely; however, pollution did not cause any considerable changes in the thallus thickness and the internal structure of the apothecia. Thus, the state of *X. parietina* was better in natural habitats.

Age structure of the *X. parietina* population. The age spectra of populations from natural and urban habitats are shown in Fig. 5. Note that differences between all these distributions are statistically significant ($p < 0.025$ – 0.001). The population of the national park is characterized by the spectrum with the maximum at im individuals (28.3%). The frequencies of the two virginal and three generative groups are similar (10.4–16.2%). A relatively high frequency of g_3 individuals (12.7%) and the presence of ss individuals (6.4%) are noteworthy. On the one hand, the shift of the spectrum to the left and the prevalence of pregenerative individuals in the population indicate that the environmental conditions are not optimal (this may be explained by shading, as it was impossible to find separately standing linden trees in the national park). On the other hand, relatively high frequencies of g_3 individuals and the presence of ss individuals (not found in the urban environment) indicate that *X. parietina* growing in a clean habitat, even under conditions of shading, can complete its ontogeny: on fallen trees, some individuals in the s state were found.

Urban habitats were characterized by different pollution levels and good illumination. The age spectrum of the population from the zone of weak pollution proved to be unimodal, with a maximum in the group of young generative individuals. The accumulation of g_1 individuals in the population is accounted for by fairly rapid transition to this state, on the one hand, and by a considerable duration of the latter, on the other. In the zone of moderate pollution, the age spectrum is “transitional” between the spectra of populations from the zones of weak and strong pollution; v_1 , v_2 , and g_1 groups prevail, and their frequencies are almost equal: 24.7, 24.7, and 23.4%, respectively. The age spectrum in the zone of strong pollution becomes unimodal, with an obvious peak on the left, in the v_1 group (40.7%). The tendencies are the same as in the zone of moderate pollution but are more pronounced: the decrease in the number of generative individuals, the increase in the number of pregenerative individuals, and the decrease in population density.

All age spectra in urban habitats are incomplete and are characterized by a small proportion of old generative individuals: (1) they include no ss individuals, whereas the frequency of the latter in the natural population (6.4%) differs from zero with a high degree of significance ($p < 0.001$); (2) the frequency of g_3 individuals in the natural population is statistically more significant than in the urban populations ($p < 0.001$), while the urban populations do not differ from each other in this parameter ($p > 0.05$).

A considerable proportion of im and v_1 groups in the age spectrum of *X. parietina* populations may be explained by the fact that, according to Rabotnov (1964), the individual development of plants under unfavorable conditions can be retarded when they enter a certain ontogenetic state, primarily pregenerative. A

fairly high abundance of pregenerative individuals under conditions deviating from the ecological optimum of the species is explained by their relatively low requirements for resources, compared to adult plants (Rabotnov, 1950). In addition, the thalli growing in the polluted environment accumulate pollutants, which may retard the formation of the reproductive organs.

The analysis of age spectra showed that, of the four habitats studied, the optimum for *X. parietina* is in the zone of weak pollution in the city: the influence of pollution is as yet low, and good illumination favors the development of individuals. In the zones of moderate and strong pollution, the effect of airborne pollutants in lichens plays the key role. This is confirmed by the data on population density, namely, the number of thalli per tree: 12.4 in the natural population, 46.8 in the zone of weak pollution, 12.0 in the zone of moderate pollution, and 9.4 in the zone of strong pollution.

The results of this study fully agree with the data obtained in investigations of the populations of higher plants and the lichen *Hypogymnia physodes* (L.) Nyl. The observed pattern is similar to the situation described by Glotov *et al.* (1995) for *Trifolium repens* L. from oil-polluted and clean habitats. These authors obtained a seemingly paradoxical result: the plants from the polluted territory were in better condition. The explanation is simple. In clean areas, *T. repens* grows in a developed phytocenosis and has to compete with other species, whereas in the areas polluted with oil, which are free of vegetation, it plays the role of a pioneer species colonizing new territory. The retardation of development, observed in *X. parietina*, was described previously in perennial and paucennial plants exposed to the effects of both abiotic factors—change in climatic conditions (Zhukova, 1973) or increased pollution (Trubina and Makhnev, 1999)—and biotic factors, such as increased planting density (Zhukova, 1995). Such a “rejuvenation” of the population under environmental pollution was observed in the foliose sorediate lichen *H. physodes* (Mikhailova and Vorobeichik, 1999). The response of plant populations to pollution may also manifest itself in the prevalence of postgenerative individuals in their age spectra (Khantemirov, 1996), probably because of accelerated plant development. It is apparent that population response to stress depends on the life strategy of the species and on ecotope conditions.

CONCLUSION

The present study confirmed the possibility of applying the concept of a discrete description of plant ontogeny to apothecial lichens with a foliose thallus. In *X. parietina*, four periods and 13 ontogenetic states were distinguished using the criteria based on anatomical and morphological changes occurring in the course of thallus development. At the initial developmental stages, the processes of formation of new structures, complication of anatomical structure, and differentia-

tion of the thallus prevail; later, they are balanced by the processes of aging and deterioration of the thallus parts; and in the end of ontogeny, the destructive processes prevail.

Changes in the morphometric parameters of the *X. parietina* thallus depend on the substrate. Some of these parameters are higher in lichens growing on aspen than in lichens from linden. Although many researchers noted a high tolerance of *X. parietina* to air pollution, observations revealed the decrease in the thallus size, the number and size of the apothecia, and the strength of attachment to substrates at the final ontogenetic stages in the urban environment.

In the habitats with conditions favorable for *X. parietina*, young generative individuals prevail in the age spectrum and the population density is high. Under adverse conditions (strong pollution in the city and shading in forest ecosystems), the age spectra are characterized by the prevalence of pregenerative individuals and partial elimination of generative individuals and the population density decreases. The minimum number of generative individuals indicates the impairment of population self-maintenance. The greatest disturbances are caused by anthropogenic factors: under their effect, some age groups of the postgenerative and, partly, generative periods are eliminated. Such a reaction to stress in *X. parietina* manifests itself in retarded development and early destruction of the thalli, which may be regarded as the decrease of adaptation upon an increase in the level of environmental pollution. The trends in the dynamics of the age structure of *X. parietina* populations are an integrated reflection of changes in environmental conditions and may be used for making diagnosis of environmental quality.

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Morphophysiological and Population Adaptations of *Ajuga reptans* L. at the Northern Boundary of Its Range

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Abstract—The results of comprehensive morphophysiological and population studies on *Ajuga reptans* L., a species of the nemoral floristic complex, at the northern boundary of its range (in the middle taiga subzone of the Komi Republic) are reviewed. Adaptations at the cell, organism, and biocenotic levels are revealed. The maintenance and survival of the species at the boundary of its range are provided for by its physiological plasticity, resistance to low temperatures, and multiple variants of ontogeny. Prognosis of *Ajuga reptans* future status under conditions of global climate change and expansion of anthropogenically disturbed areas is favorable.

Key words: *Ajuga reptans* L., northern boundary of species range, adaptation, functional plasticity, ontogeny, cenopopulations, life strategy

The adaptation of organisms to a changing environment is achieved through the rearrangement of a combination of characters at all levels of biological organization. As applied to the genotype, the concept of adaptation implies phenotypic plasticity, i.e., the ability of an organism to take on more than one alternative form of the morphological and physiological state and/or behavior in response to environmental conditions (West-Eberhard, 1989; Getty, 1996). The combination of morphophysiological, behavioral, population, and other features of a species provides for its survival in a certain environment.

Ajuga reptans L. is a nemoral species whose range embraces a vast territory of Western Europe, the western part of the Mediterranean, European Russia, the Caucasus, and the Urals. In the northeast of European Russia, it belongs to the relicts of the Holocene thermal optimum (Martynenko, 1976). It occurs in herbaceous aspen and birch forests, mixed coniferous–small-leaved forests, and meadows. *Ajuga reptans* is a stolon-forming herbaceous polycarpic with monocarpic semirosette shoots and belongs to summer–wintergreen species (Serebryakov, 1952). It reproduces by seeds and incompletely rejuvenated vegetative diaspores (Smirnova, 1987). It is known as a medicinal ecdysteroid-containing plant (*Rastitel'nye resursy...*, 1991; Alekseeva *et al.*, 1998) and is used for landscaping as an ornamental soil-covering species.

The biology of *A. reptans* in the ecotopically favorable zone of broadleaved forests has been studied fairly comprehensively (Rysina, 1973; Mikhailovskaya and Kuz'micheva, 1974; Komarova, 1986; Smirnova, 1987). However, the data on its physiological parameters are far less abundant (Bachmann *et al.*, 1994; Bach-

mann and Keller, 1995; Luk'yanova *et al.*, 1986; Masarovicova, 1997).

One of the methods for revealing the adaptive responses of plants and assessing their plasticity is the comparison of morphophysiological, biochemical, and other indices in representatives of the species from different parts of its range. The purpose of this work was to reveal the adaptive properties of *A. reptans* under conditions of middle taiga communities, at the northern boundary of its range. To this end, the structural, functional, ontogenetic, and population features of the species were studied.

METHODS

Studies were performed in the middle taiga subzone of the Komi Republic (between 60° and 62° N), at the northern boundary of the species range. This region is characterized by elevated plains that have moderately rolling or, in some areas, dissected topography, with cover loams or sandy loams underlain with moraine and with green-moss middle-taiga spruce and fir–spruce forests on highly podzolic soils. In recent decades, the primary forests have been largely replaced by the secondary spruce–aspen and spruce–birch communities due to strong anthropogenic effects (Pruchkin *et al.*, 1999). The climate of the region is excessively humid and moderately warm.

Specific features of *A. reptans* growth and development were studied in 32 natural cenopopulations growing in white alder groves, herbaceous aspen forests, birch forests, and mixed coniferous–small-leaved communities, forest margins, grass–herb meadows, felling areas, and roadside banks. Studies were performed between 1995 and 1998 using conventional methods of

Morphophysiological parameters of plants and population parameters of *Ajuga reptans* in different parts of its range

Parameters	Broadleaved forest zone	Middle taiga subzone
Physiological characteristics		
Photosynthetic rate, mg CO ₂ /dm ² per hour	6.0–9.5**	2.5–4.5
Chlorophyll content, g/dm ²	4.40 ± 0.10***	2.15 ± 0.05
Soluble carbohydrate content, mg/g fresh weight	75–85**	20–30
Population parameters		
1. Cenopopulation element		
Biomass	3.0–3.5*	0.9–1.2
Height of assimilative surface, mm	150–200*	50–160
Root length, mm	40–80*	110–180
Vegetative growth rate, cm/year	30–50*	8–35
Potential annual production of vegetative primordia, pcs. per element	3–7*	0–4
Potential annual production of seed primordia, pcs. per element	100–250*	150–300
Duration of partial shoot ontogeny, years	2–3*	up to 6 and more
Duration of area retention, years	3–4*	2–6 and more
Developmental rate	Normal*	Cenopopulations
2. Cenopopulations		
Age spectrum	Generative age state dominates*	Immature age state dominates
Store of diaspores in the soil	Large	Small
Type of maintenance	Seed and vegetative*	Vegetative type is dominant, seed type manifests itself upon plant cover damage

Note: Data on the broadleaved forests zone are from studies by *Smirnova (1987), **Bachmann *et al.* (1994), and ***Masarovicova (1997).

cenopopulation research (*Tsenopulyatsii rastenii...*, 1976; Smirnova, 1987; Zhukova, 1995). As a unit of count, we used an individual *A. reptans* plant (before the onset of vegetative propagation) or a partial shoot (after the onset). To obtain the quantitative characteristics of age states, we measured the length of the largest leaf in the rosette part of a shoot, the number of plagiotropic shoots, and their lengths after rooting.

Morphophysiological studies were performed in nature, in a spruce-aspen herbaceous forest, and on cultivated plants in the experimental plot near Syktyvkar (62°52' N). Carbon dioxide exchange in mature summer- and wintergreen leaves was studied using an Infralit-4 infrared gas analyzer (Sivkov and Nazarov, 1990) at temperatures and illumination of 5–35°C and 4–500 W/m² of photosynthetically active radiation (PAR), respectively. The cardinal points of light and temperature curves of photosynthesis were determined as described by Garmash and Golovko (1997). The values presented in the paper are the averages of six to ten curves.

The chlorophyll and carotenoid contents in leaf blades were estimated spectrophotometrically (Shlyk, 1971), in five replications. Soluble hydrocarbons were analyzed

by HPLC with modifications proposed by Glyad (1999); free amino acids were determined in an AAA-T339M analyzer (Mikrotechna-Praha, Czechoslovakia), in three replications.

RESULTS AND DISCUSSION

Structural–functional level. The results of comparative analysis (table) showed that *A. reptans* at the northern boundary of its range, in the taiga subzone, is characterized by a decreased photosynthetic rate. With respect to the rate of CO₂ absorption, this species is much closer to the plants of the boreal floristic complex (Starostina, 1983) than to those typical of broadleaved forests (Mitina, 1981).

The low rate of photosynthesis correlated with a reduced green pigment content in *A. reptans* leaves. This result agrees with the concept that the amount of chlorophyll in shade-loving plants decreases at higher latitudes, which is explained by changes in the light spectrum. It appears that some other factors should also be taken into account. In particular, this concerns the deficiency of nitrogen (the element essential for chlorophyll synthesis), which is explained by soil poorness

and slow litter decomposition at low temperatures. At a low rate of CO_2 assimilation, *A. reptans* plants growing under the forest canopy in the middle taiga subzone accumulated approximately one-half less nonstructural hydrocarbons than plants from the central part of the range.

According to the parameters of light curves of photosynthesis (steepness and low values of adaptive radiation intensity and light compensation point) (Fig. 1) and the ratio of chlorophylls *a/b* < 3 in the pigment complex, *A. reptans* belongs to a group of shade-tolerant plants. Shade tolerance is determined genetically. This was confirmed in experiments with *A. reptans* plants from various ecotopes, which proved to be capable of adapting themselves to high illumination intensity (growth in culture) and retaining the properties of a shade-tolerant species (Dymova and Golovko, 1998a).

It should be noted that nemoral species in the broad-leaved forests zone can develop the properties of photophilic species and photosynthesize at a high rate in early spring, when the foliage of trees has not yet been formed completely (Mitina, 1981). We found that, under extreme conditions existing at the northern boundary of the *A. reptans* range, this nemoral species is incapable of absorbing CO_2 at a high rate in a light forest in spring. During the growing period, the rate of photosynthesis in leaves varied insignificantly (Fig. 2), which provided evidence for plant adaptation to the conditions of illumination in the middle taiga communities.

The photosynthetic apparatus of *A. reptans* is adapted to moderate temperatures of the middle taiga subzone and is capable of acclimating to weather changes during the growing period. During the season of 1997, with typical thermal conditions (average air temperature 11.6°C) but insufficient moistening (annual precipitation rate 260 mm), the range of temperatures optimal for photosynthesis was $8\text{--}16^\circ\text{C}$ (Fig. 3b). At a saturating illumination of about 50 W/m^2 and the optimum temperature, *A. reptans* leaves photosynthesized at a maximum rate, assimilating $6\text{--}8\text{ mg CO}_2/\text{dm}^2$ per hour. At a temperature of $6\text{--}7^\circ\text{C}$, this rate decreased by 20–40%; at temperatures exceeding 25°C , photosynthesis was strongly inhibited. The temperature optimum proved to change by $2\text{--}6^\circ\text{C}$ depending on thermal conditions and moistening. Thus, during the moist growing season of 1996 (total precipitation 375 mm) and the warm growing season of 1998 (average air temperature 12.9°C), this optimum shifted toward higher temperatures ($10\text{--}22^\circ\text{C}$) (Figs. 3c, 3d). Thus, the photosynthetic apparatus demonstrated functional plasticity and stability.

As in the central part of the area, the phenomenon of wintering with green leaves was clearly pronounced at the northern limit of *A. reptans* distribution. The leaves remained capable of photosynthesis in late autumn, after frosts, and in early spring, after wintering (Fig. 2). The overwintered leaves slightly differed from summer leaves in the rate and temperature dependence of pho-

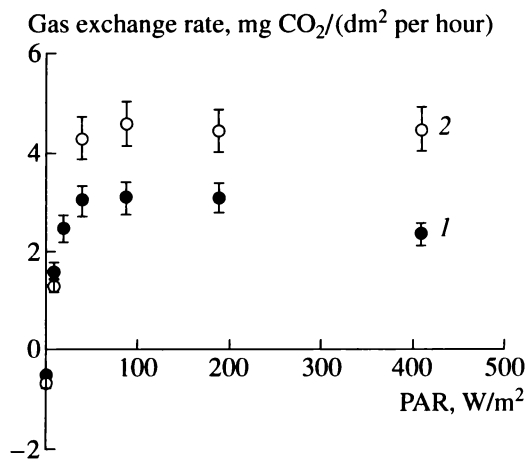


Fig. 1. Light dependence of photosynthesis in leaves of *Ajuga reptans* plants (1) growing under the forest canopy and (2) cultivated on a plot (June 1996, $n = 6\text{--}10$). PAR is photosynthetically active radiation.

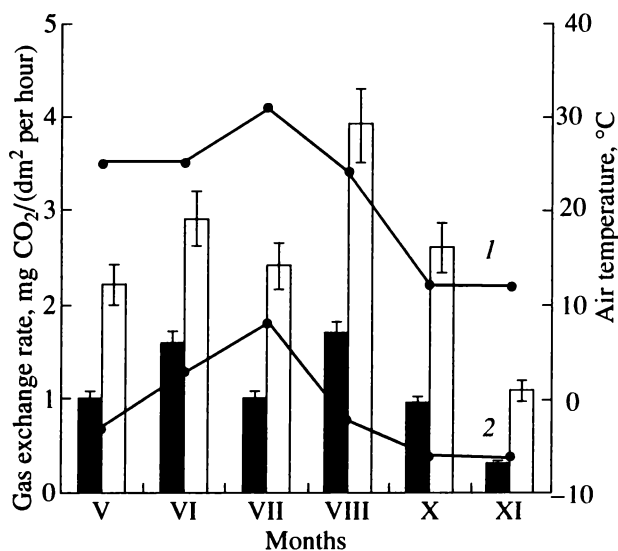


Fig. 2. Seasonal courses of photosynthesis in *Ajuga reptans* leaves and air temperature (1996, $n = 6\text{--}10$). Clear bars show the maximum rate of CO_2 absorption (P_{max}); filled bars show the rate of CO_2 absorption at adaptive radiation intensity (P_{ari}); curves show (1) maximum and (2) minimum monthly average air temperature.

tosynthesis (Figs. 3a, 3b). The assimilative apparatus remained functional at low temperatures, and this promoted the early onset of assimilative activity in the overwintered leaves. This adaptive strategy provided for plant growth in the spring–summer period (late May–early June).

Cold tolerance and the maintenance of the photosynthetic apparatus in autumn were promoted by the accumulation of soluble carbohydrates (up to 35 mg/g fresh weight) and free amino acids (up to 2 mg/g fresh weight). In this period, the photosynthetic apparatus

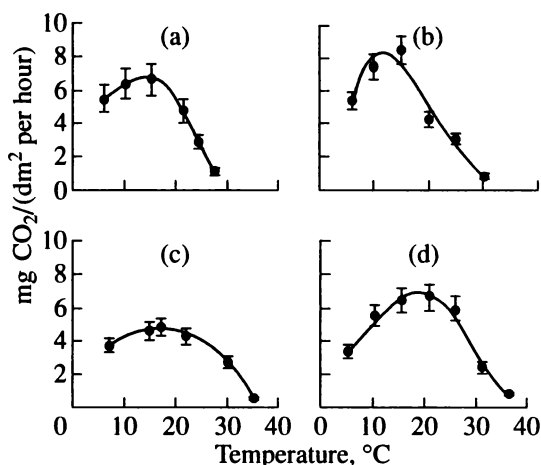


Fig. 3. Photosynthesis in *Ajuga reptans* leaves as a function of temperature in different years and growing seasons: (a) June 1997, wintergreen leaves; (b) June 1997, summer leaves; (c) July 1996; (d) August 1998 ($n = 6-10$).

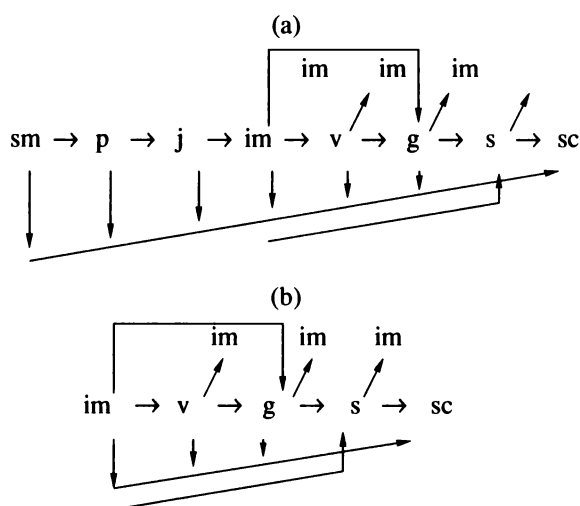


Fig. 4. Scheme of multivariant ontogeny of (a) *A. reptans* plant and (b) partial shoot in the middle taiga subzone. Age states: (sm) seeds, (p) sprouts and seedlings, (j) juvenile, (im) immature, (v) virginal, (g) generative, (s) senile, (sc) dying.

underwent some structural–functional rearrangements manifested in a decrease in the number of grains in thylacoids (less than 10) and the size of chloroplasts, starch hydrolysis, and partial degradation of chlorophylls and carotenoids (by 25–30%). The fact that *A. reptans* grows in the ground layer, where it is protected by the snow cover and litter, is very important for the survival of its wintergreen leaves. Species adaptation to subzero temperatures allows it to endure autumn frosts and winter cold.

Despite the low rates of photosynthesis (4–8 mg CO₂/dm² per hour), the assimilative organs of *A. reptans* were characterized by a relatively high respiration rate (1–3 mg CO₂/g per hour) during vegetation.

Such rates are characteristic of many plants cultivated in the North (Golovko, 1999). The high respiratory capacity of these plants provide them with the amounts of energy necessary for growth in a cold climate.

Thus, the study of *A. reptans* at the functional level revealed its physiological plasticity, resistance to unfavorable environmental conditions, and high shade tolerance, which provide for the growth and survival of this nemoral species in the middle taiga subzone.

Organism level. As compared with southern plants, northern plants of *A. reptans* had smaller dimensional parameters (leaf length, the area of foliage surface, the number of stolons per partial shoot) and biomass (table). It is known that the distribution of resources in living organisms is aimed at improving their adaptation. The observed decrease in plant size and the number of growing vegetative structures may be regarded as an adaptive response to unfavorable ecotopic conditions, which promotes species survival in the North.

The study of *A. reptans* ontogeny at the northern boundary allowed us to distinguish four periods subdivided into eight age states: latent (seeds), pregenerative (seedlings, juvenile, immature, virginal), generative (generative state), and postgenerative (senile and dying states). A specific feature of the species is that the immature age state is prominent: the partial shoot in the form of leaf rosette with underdeveloped axillary buds exists for several years (Tetryuk, 1996).

Figure 4 shows the schemes of *A. reptans* ontogeny and the partial shoot. We observed the following variants: progression through all ontogenetic states in consecutive order, omission of one or several states, and plant death at different developmental stages. In addition, temporal variants (dynamic multivariability) of plant ontogeny were revealed, which were accounted for by dicyclic and polycyclic development of generative ramets. Analysis with regard to their actual age indicated that the partial shoot may develop at the normal rate or demonstrate dicyclic development, with flowering in the second year of life (Fig. 5). This is typical of plants from the central part of the range. In the study area, dicyclic development took place rarely, only under the most favorable ecotopic conditions. Most ramets developed slowly, with a delay in the immature and virginal age states; genets demonstrated a delay in the juvenile, immature, and virginal states. Flowering occurred in the third year of life or later. Similar changes of developmental cycles in different parts of the species range were described in *Poa annua* L., *Cochlearia arctica* Schlecht. Ex DC, and *Androsace septentrionalis* L. (Goryshina, 1979).

It is considered (Zhukova, 1995) that the existence of multiple variants of ontogeny increases the adaptive potential of species. The decreased vital activity of northern plants and unfavorable edaphic conditions of their natural habitats in the middle taiga subzone cannot provide for a sufficiently high rate of biomass accumulation and may be responsible for a delayed devel-

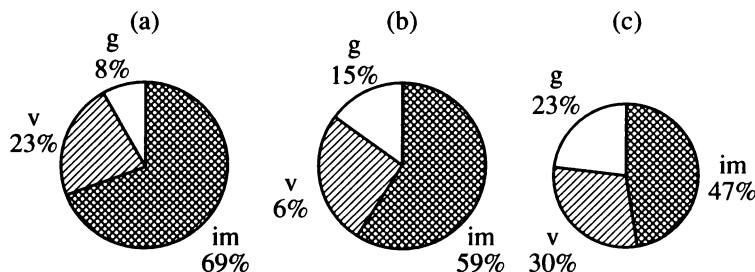


Fig. 5. Rates of development of *Ajuga reptans* partial shoots in the middle taiga subzone: (a) ramets in the second year of life, (b) third year of life, and (c) of conventional age over three years.

opment of the species. The polycyclic development of most ramets and genets, the prominence of the immature age state, and their multivariant ontogeny, which involves different rates of progression through the age states, may be regarded as an ontogenetic adaptation of the species to conditions of the North.

Population level. Our studies provided data on the *A. reptans* age spectrum in the middle taiga subzone (Fig. 6). This basic spectrum is shifted to the left due to the prevalence of the immature age group, as most of the partial shoots demonstrate polycyclic development. It differs from that obtained in the subzone of broadleaved forests, where generative plants prevailed (Smirnova, 1987). This fact reflects general trends in the development of a species at the boundary of its range.

The age spectrum provided evidence that the change of *A. reptans* generations in the middle taiga subzone is retarded, the activity of seed and vegetative reproduction is decreased, and their relative significance for the maintenance of species cenopopulations has changed in favor of vegetative reproduction. In white alder groves, small-leaved forests, and mixed coniferous–small-leaved communities, we revealed a relatively high proportion of virginal plants with the maximum possible number of stolons (two to four in the study area), whereas genets occurred very rarely.

Seed reproduction plays no significant role in maintaining the density of species populations at the boundary of its range, but it allows the species to form a reserve of viable diaspores, colonize new remote areas, and survive in critical situations (*Tsenopopulyatsii rastenii...*, 1988). The most favorable ecophytocenotic conditions for the maintenance of *A. reptans* cenopopulations by seed reproduction exist in anthropogenically disturbed areas, such as hayfields, felling areas, and roadside banks. In the age spectra of such cenopopulations, the generative age group accounted for up to 35%, and seedlings and juvenile individuals were present.

Thus, our studies provided evidence for a change in the basic age spectrum of the species at the boundary of its range and a decrease in the activity of seed and vegetative reproduction. The leading role in the maintenance of cenopopulations proved to belong to vegeta-

tive reproduction, which is more energy-efficient and provides for higher survival in the progeny.

Biocenotic level. One of the aspects of species adaptation to the environment is its “behavior,” or life strategy. There are several classifications of the types of plant behavior (Ramenskii, 1971; Grime, 1979; Mirkin, 1985; Smirnova, 1987). They are based on three main types of strategy: competitiveness, tolerance, and reactivity.

In the zone of broadleaved forests with ecotopically favorable conditions for the model species, special and general (phytocenotically significant) characteristics of behavior were determined (Smirnova, 1987). *Ajuga reptans* belongs to species with the reactive life strategy, which are characterized by the minimum period of growth confined to a certain territory (area retention), active reproduction, and a high rate of expansion to new habitats. In the middle taiga subzone, we observed a decrease in the biomass of cenopopulation components, the height of their assimilative surface, and the rates of their development, accompanied by an increase in the period of area retention by ramets (table). The rate of expansion to new habitats was lower than in the central part of the range. This is evidence that the life strategy of *A. reptans* at the northern boundary of its distribution became less reactive and more tolerant under the effect of unfavorable ecological and phytocenotic conditions. The signs of species tolerance manifested themselves more strongly in mature aspen

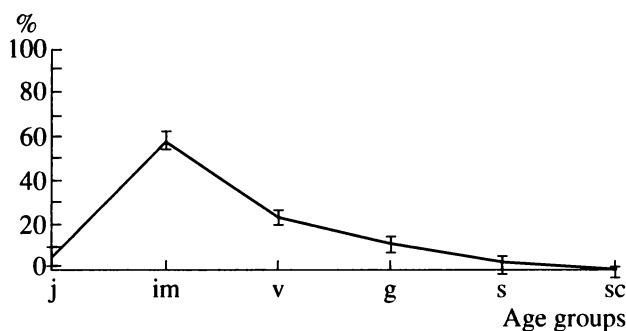


Fig. 6. Basic age spectrum of *Ajuga reptans* cenopopulations in the middle taiga subzone.

groves, birch forests, and mixed coniferous–small-leaved communities and less strongly in disturbed communities, such as those on roadside banks and in felling areas.

CONCLUSION

The maintenance and survival of the nemoral species *A. reptans* at the northern boundary of its range were promoted by adaptations on the cell, organism, population, and biocenotic levels. The species became adapted to conditions of the North due to its physiological plasticity, acclimation of the photosynthetic apparatus to conditions existing in middle taiga forests, and cold tolerance. Its multivariant ontogeny and a long period of growth in the pregenerative state allow *A. reptans* to maintain its abundance in the environment where metabolic processes cannot provide for biomass accumulation at a high rate, which leads to a decrease in plant size, the number of vegetative structures, and the intensity of seed and vegetative reproduction. Morphophysiological and population characteristics of the species at the boundary of its range affected its life strategy.

Studies on cultivated *A. reptans* showed that this species is capable of an accelerated development in the middle taiga subzone on conditions of high illumination intensity and the lack of competition for environmental factors (Dymova and Golovko, 1998b). This indicates that relatively low temperatures and a short growing season are not the main factors limiting the growth, development, and expansion of the species. Specific features of *A. reptans* development in its natural habitats are probably accounted for by the combination of unfavorable edaphic conditions (poor podzolic soils) and interspecific competition for nutrients.

The results of this research indicate probable trends in the development of *A. reptans* as a species under conditions of global climate change. It is expected that temperatures at northern latitudes will increase by 3–7°C and the CO₂ concentration in the atmosphere will become two times higher. On the basis of morphophysiological characteristics and physiological plasticity of *A. reptans*, it may be assumed that the expected changes will be favorable for the photosynthetic function and, hence, the growth and development of plants. The ever-increasing size of anthropogenically disturbed areas will also be favorable for the expansion of this species, which is characterized by the reactive life strategy, beyond the present-day boundaries of its range.

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Cytogenetic Variation in Populations of Scotch Pine

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Abstract—Cytogenetic variation was analyzed in daughter populations of Scotch pine from the Voronezh Forestry. The dependence of the variation on the method of seed collection (the commercial method; the population method, when seeds from a group of phenotypically normal trees in the center of the forest are collected; or the individual method, when seeds from plus trees are collected) and on the ecological situation at the sampling site (ecologically safe conditions or chemical or physical pollution) was studied. The parameters of the mitotic rate and mitotic pathology were estimated at 7–9% and up to 5%, respectively. These parameters may be considered as normal when estimating the quality of seed progeny in pine and when pine is used as a test object in cytogenetic monitoring. The limits of variation and the spectra of cytogenetic characteristics allowing the pine populations to maintain their homeostasis were also determined.

Key words: micronuclei, mitotic index, pathological mitoses, population, radioactive contamination, Scotch pine, nucleolar activity

Studies on the population structure in forest woody plants are important for developing an appropriate strategy of breeding and rational use of forest resources. Genetic differentiation of population structure allows the efficient use of the environment and provides the possibility of adaptation to changing environmental conditions (Kaidanov, 1996). This differentiation manifests itself in the existence of intrapopulation groups differing from one another in genotypic and, hence, morphological, physiological, biochemical, and cytological characteristics.

Stability of the cytogenetic characteristics at the most important ontogenetic stages is an indicator of an organism's developmental homeostasis. This is especially true for characteristics of mitosis—a fundamental ontogenetic process—such as mitotic activity (the proportion of proliferating cells) and the rate and spectrum of mitotic disturbances, or pathologies (MPs). These characteristics determine the organism's growth and play the most important role at the early ontogenetic stages and during tissue differentiation. All mitotic events are genetically determined (Inge-Vechtomov, 1989). They are coupled with numerous biochemical, biophysical, and physiological processes in the cell (Mitrofanov, 1969); therefore, disturbances in the mitotic cycle inevitably cause alterations in the vital activity of cells, which may trigger pathological processes in the organism.

We studied the variations of the aforementioned cytological characteristics of mitosis in the seed progeny of Scotch pine, assuming that the seed progeny determines the structure of daughter populations. The dependence of these variations on the method of seed collection (the commercial method; the population

method, when seeds from a group of phenotypically normal trees in the center of the forest are collected; or the individual method, when seeds from plus trees are collected) and on the environmental situation in the habitat of the mother population was studied. We chose Scotch pine (*Pinus sylvestris* L.) as the object of the study because it is among the main forest-forming species in Russia and is important in terms of both its commercial use and environment protection. Therefore, the current generation of forestry specialists should be concerned about the quality of future forests of this species.

The quality of forests can be predicted based on the results of cytogenetic analysis of seeds (Butorina, 1989). The routine silvicultural estimates of seed quality, including the weight of 1000 seeds, seed vigor, germination rate in the field and in the laboratory, and the seed origin, are sometimes incorrect. Seed weight may be increased due to polyembryony (Selivanov, 1983), and seeds can sometimes germinate irrespective of severe cytological abnormalities. For example, ring and dicentric chromosomes (Isakov *et al.*, 1977; Butorina *et al.*, 1979a, 1979b; Suntsov, 1982; Kozubov and Muratova, 1986; Muratova 1991, 1992), accessory chromosomes (Butorina *et al.*, 1979a, 1979b; Shafikova, 1999), and somatic chromosome reduction (Butorina *et al.*, 1984) were found in developing seedlings.

Testing in cultures, including geographic cultures, is a direct and most accurate method for estimating the quality of progeny. However, this method is expensive, time-consuming, and laborious. Preliminary cytogenetic assessment makes it possible to decrease the cost of the tests, because this allows the researchers to detect mutant forms and to isolate mother plants (or populations) producing the progeny that grows rapidly at early

ontogenetic stages. This assessment should begin with analysis of the cytological variation spectrum and the frequencies of pathological mitoses in the offspring of pines from a high-quality natural forest growing under favorable environmental conditions (in a clean area). These characteristics reflect the spontaneous mutation rate and the organisms' adaptability. They may be used as reference parameters for estimating the quality of pine progeny obtained from seeds collected in polluted forests (from individual trees with different genotypes and during commercial collection of seeds).

MATERIALS AND METHODS

All studies were conducted on Scotch pine seeds obtained by means of free pollination. The seeds were collected in the Voronezh Forestry in the autumn and winter of 1998. Seeds from the ecologically clean territory of the Venevitinovo Training and Research Center (Voronezh State University) served as a control group. According to Shchetinkin *et al.* (1992), the contamination of plant material with radionuclides and chemicals in this area did not exceed maximum allowable concentrations (MACs), the background γ -radiation was 10–12 $\mu\text{R/h}$; the content of ^{137}Cs in the soil in the period of the study was no more than 0.1 Ci/km^2 . Seeds were collected from a group of phenotypically normal trees (20 plants aged about 70 years) in the depth of a natural forest. The seeds of the plus trees ES-12 and VZ-16, which also grew in the clean area, were collected separately. These seeds and the seeds obtained during commercial collection were kindly supplied by A.I. Chernodubov.

The content of ^{137}Cs in the soil was measured by specialists from the Department of Nuclear Physics (Voronezh State University) using the standard method (GOST (State Standard) 30108-94: *Materials and Products: Determination of the Specific Effective Activity of Natural Radionuclides*); MED was measured using an RKSB-104 device.

We collected seeds in the following polluted zones: (1) a "radioactive spot" in the Voronezh State Reserve (VSR) (soil ^{137}Cs contamination 0.45 Ci/km^2 , background γ -radiation 17–20 $\mu\text{R/h}$); (2) two points in Voronezh oblast exposed to radiation after the Chernobyl accident, Verkhnyaya Toida (two trees) and Rep'evka (three trees) (soil ^{137}Cs contamination 0.19 and 0.41 Ci/km^2 , background γ -radiation 15–18 and 16–20 $\mu\text{R/h}$, respectively); (3) the 1-km zone of the Novovoronezhskaya Nuclear Power Plant (28 trees), where heavy metals were presumably the main pollutants and where synergistic effects of radioactive noble gases discharged from the nuclear power plant (^{222}Rn , ^{220}Rn , ^{219}Rn , and ^{85}Kr) and other pollutants were possible (background γ -radiation 12–14 $\mu\text{R/h}$); and (4) pine plantations along Yuzhno-Moravskaya Street (the Southwest district of Voronezh), which was characterized by heavy traffic (seeds were collected from five trees). The latter zone

was studied because of the increasing contribution of automobile exhaust to environmental pollution and the considerable recreational load on city parks. Exhaust gases are the main pollutant in this district of the city (*Doklad o sostoyanii...*, 1999). The samples of pine seed progeny were mixtures of all seeds collected in these areas, without identification of individual mother trees.

Freshly collected seeds germinated on moist filter paper in Petri dishes at a constant temperature of 25°C. Seedlings with 0.5- to 1-cm rootlets were fixed by acetic alcohol (a 1 : 3 mixture of glacial acetic acid and 96% ethyl alcohol). To study the circadian dynamics of mitotic activity, the material was fixed every 2 h for one day. We estimated the circadian rhythms of mitotic activity in seedlings obtained from the seeds collected in the Venevitinovo Training and Research Center and seeds obtained by means of commercial collection in the Usmanskii pine forest. Seedlings that developed from seeds collected in all other zones were fixed at 9 a.m. (winter time). Microscopic preparations made as described earlier (Butorina and Evstratov, 1996) were examined under a Laboval-4 microscope (Carl Zeiss, Jena, Germany).

We studied the following cytogenetic characteristics of the seedlings: mitotic activity (MA), the frequency and spectrum of MPs, and nucleolar activity (NA). Mitotic activity was estimated using the mitotic index (MI), i.e., the proportion (percentage) of dividing cells among all meristematic cells examined. The proportion of MPs was calculated as the proportion (%) of cells with disturbed mitoses in the total pool of dividing cells; MPs were classified according to Alov (1965). We estimated the NA as the ratio between the numbers of cells with 1, 2, 3, ..., n nucleoli in the sample studied; the percentage of cells with n nucleoli was calculated as the ratio of the number of cells with n nucleoli to the total number of interphase cells. The proportion of cells with micronuclei was calculated as the ratio between the number of cells with micronuclei and the total number of interphase cells (expressed in percents).

The data was processed using the STADIA statistical software package.

RESULTS AND DISCUSSION

The figure shows the circadian cycle of rootlet meristem cells in Scotch pine seedlings. As is seen from the figure, we observed two peaks of MA, at 9 a.m. and 9 p.m. Therefore, Scotch pine has two synchronized pools of dividing cells. The MA determines the energy of growth. This parameter is genetically determined; however, it is also considerably affected by environmental factors. For example, radiation and chemical mutagens stimulate MA at low doses (Butorina *et al.*, 1991; Narimanov and Korystov, 1997) and inhibit it at high doses (Mitrofanov, 1969). The table shows the cytological characteristics of mitosis in pine seed prog-

Cytogenetic characteristics of Scotch pine seeds collected at different sites in 1998

Sampling site	Number of specimens examined	Number of cells examined	MI, %	MP rate, %	Frequency of micronuclei, %
Venevitinovo	20	20351	9.4 ± 0.6	3.2 ± 0.4	0
ES-12	10	13990	6.8 ± 0.3	1.6 ± 0.4	0
VSR (the plus tree VZ-16)	17	49771	7.6 ± 0.4	1.2 ± 0.2	0.01 ± 0.01
Usmanskii pine forest (commercial collection)	11	20511	5.3 ± 0.4	7.7 ± 1.6	0.02 ± 0.01
Southwest district of Voronezh	11	20787	4.9 ± 0.4	6.9 ± 1.2	0.01 ± 0.01
Radioactively contaminated zones in the VSR	8	14632	7.1 ± 0.5	5.4 ± 0.9	0.13 ± 0.06
Verkhnyaya Toida	6	6092	10.2 ± 0.4	3.0 ± 0.7	0.17 ± 0.05
Rep'evka	7	7092	12.1 ± 0.6	2.8 ± 0.7	0.10 ± 0.04
1-km zone of the Novovoronezhskaya Nuclear Plant	50	60000	8.1 ± 3.5	3.1 ± 3.0	0.02 ± 0.01

eny as related to the method of seed collection and the ecological situation at the sampling sites.

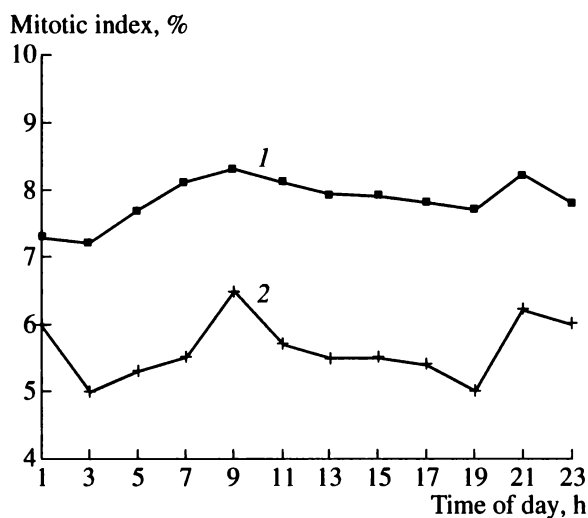
The data obtained indicate that the variation of MI (from 5.8 to 13.3%; on average, 9.4%) in the seed progeny of pine trees from the Venevitinovo Training and Research Center (fixation at 9 a.m.) is sufficient for ensuring population stability. The limits of this variation in the plus tree ES-12 were 5.0 and 8.4% (on average, 6.8%); therefore, the progeny of this tree was adapted to a narrower range of environmental conditions and possibly has a shifted peak of mitotic activity. The seedlings obtained from the seeds of the plus tree VZ-16 had approximately the same range of MI variation as the control trees (5.5–11.1%; on average, 7.6%). In trees from the "radioactive spot" in VSR, the MI varied from 4.8 to 8.7%, averaging 7.1%. The MI was decreased in seedlings obtained from the seeds collected

by the commercial method (1.8–7.0%; on average, 5.3%) and the seeds collected in the Southwest district of Voronezh (3.2–7.5%; on average, 4.9%). Depression of MA in seedlings growing from the seeds that were obtained during commercial collection may be explained by the fact that it was easier to collect the seeds from short trees. These were so-called minus trees, which either were mutant or grew under unfavorable conditions.

In practice, seeds are often collected at forest margins, where trees experience the strongest anthropogenic stress. In the city, this stress is even stronger and is further strengthened by the effect of traffic exhaust, which leads to the suppression of proliferative activity and growth. In seedlings obtained from the seeds collected in Verkhnyaya Toida and Rep'evka, the MI was higher than in other variants. The average MP rates in the seedlings studied were low (3 and 2.8%); however, it varied fourfold (from 1.1 to 5.8%) within a sample. We may assume that the pine offspring contained radioresistant forms, because the MI and MP rate in 1 out of 13 seedlings fell within the control range. The pine seed progeny from the VSR exhibited a considerable variation with respect to the MP rate (from 1.9 to 9.5%). This agrees with the suggestion that this sample contained seeds of radiosensitive and radioresistant plants.

In the offspring of pine trees from the 1-km zone of the Novovoronezhskaya Nuclear Power Plant, the MI considerably varied (from 8.1 to 14.0%), which suggests an unfavorable environmental situation near the enterprise. This is confirmed by the high MP rate (17.0%).

The range of the MP rate was the greatest (from 1.6 to 17.4%) in the seedlings grown from the seeds obtained during commercial collection; however, the minimum MP rate corresponded to the minimum MI. In the sample from the Southwest district, the MP rate variation was the smallest (from 3.2 to 14.6%); however, the general situation was approximately the same as in the preceding sample. An MP may lead to



Circadian dynamics of mitotic activity in the seed progenies of phenotypically normal pine trees from (1) the Venevitinovo Training and Research Center and (2) Usmanskii pine forest (commercial seed collection).

genomic mutations and chromosome aberrations (Alov, 1965). The rate of mitotic disturbances may serve as a measure of the mutation rate in the organism's cell populations, whereas the spectrum of MPs reflects the degree of damage of the genetic material, i.e., the compatibility of the lesions with life.

MPs occur in proliferating tissues of all organisms; they are usually caused by intracellular metabolites. The metabolic processes determine the rate of spontaneous mutations, which are usually eliminated by repair systems. This mutation rate may be somewhat increased due to random fluctuations of external factors, which, however, do not go beyond the normal limits. Our data suggest that an MP rate lower than 5% should be considered normal for Scotch pine. In general, the spectra of MPs were the same in all samples studied. These were mostly disturbances related to chromosome damage: metakinesis and anaphase lags, as well as simple and complex anaphase and telophase bridges with or without fragments. However, the seed offspring sampled near the Novovoronezhskaya Nuclear Power Plant exhibited an increased proportion of bridges and a decreased number of aberrations accompanied by chromosome fragments. Some researchers (Simakov, 1983) believe that this reflects an increased capacity for repair and, probably, adaptation of the trees to stress (irradiation).

The formation of micronuclei results from chromosome lagging during mitosis and from multipolar mitoses. Therefore, micronuclei reflect disturbances in the genetic apparatus. In our study, the rate of micronuclei was the highest in the seedlings grown from the seeds collected in radioactively contaminated zones; in samples from other areas, we sometimes observed single micronuclei. The NA is highly variable in pine. Pine cells may contain 1 to 12 nucleoli; their number is higher under extreme conditions, e.g., in a pine growing in a bog (Butorina *et al.*, 1979a, 1979b; Sedel'nikova, 1997). Cells with four to eight nucleoli, which corresponded to two to four chromosome pairs with functioning nucleolar organizers, prevailed in all the samples studied.

The variation of cytogenetic parameters in the progeny of plus trees suggests that, unless the composition of pollinators changes, it will show good hereditary quality and will be homogeneous with respect to growth parameters. However, the results of testing the seven-year-old progenies of the ES-12 and VZ-16 trees (Ievlev and Isakov, 1988) demonstrated that the progeny of the ES-12 tree grew faster, whereas its MI at 9 a.m. was lower than this value for VZ-16. Therefore, we may suppose that ES-12 had a genetically determined shift of the MA peak. Thus, it is necessary to determine the circadian rhythms of MA and use these data for a preliminary cytogenetic assessment of the progenies of individual trees.

The pattern of cytogenetic variation in the seed sample obtained using the population collection method

suggests that the guidelines for seed collection were not complied with and that cytological control of these seeds would be important for ensuring the high quality of artificial populations obtained from them. The pattern of variation of cytogenetic characteristics in the offspring of pine trees from polluted zones indicates that these seeds should not be used for creating artificial forest stands.

The data obtained demonstrate that Scotch pine has a wide spectrum of variation of cytogenetic characteristics, which determines adaptation of this species to various ecological conditions. In the case of heavy contamination (e.g., acute irradiation of woody plants in the 30-km zone around the Chernobyl Nuclear Power Plant in 1986), the cytogenetic variation spectrum may be narrower than under normal conditions due to the death of cells with lethal aberrations (Butorina *et al.*, 1997). In the present study, the aberration spectrum in the plants from polluted areas was wider than in the control group, which may be explained by relatively low pollution in the areas studied. The variation of cytogenetic parameters in seed progeny largely depends on the genotype of mother plants (plus, normal, or minus) and may be either higher or lower than the average population level; the latter should be regarded as a reference value when estimating the quality of pine seed offspring. In general, this agrees with the data on the seed germination rate, which was high (90%) in the population sample of phenotypically normal trees and low (60%) in the sample obtained during commercial collection of seeds.

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A Method for Evaluating the Morphological Diversity of Strawberry Leaves in Natural Populations

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Abstract—A method for comparing polymorphic characters is proposed. As an example, the morphological diversity of strawberry leaves is evaluated. Initially, the factors determining leaf shape and the main directions of its variation are identified. These directions are used as coordinates outlining the space of possible realizations of the character. The polymorphic sets of real leaves from individual populations differ in being located in different parts of this space.

Key words: strawberry, leaf, morphology, morphogenesis

Ternate leaves are most typical for strawberry (*Fragaria vesca* L.), but studies on the series of “age states” (Rabotnov, 1950; Uranov, 1960; Zhukova, 1995) shows that this leaf form is not the only one in this species. The first leaves of a seedling are always simple, then follow lobed leaves, and the typical ternate leaf form is observed beginning from approximately the fifth leaf. Within this form, structural deviants with four and five leaflets are observed. The question arises as to whether it is possible to compare different plant populations with respect to the features of the leaf structure if the character studied represents a polymorphic set.

We answer in advance that such a comparison is possible if (a) the factors controlling leaf form and, hence, determining the main directions of its variation are identified; (b) the space of possible realizations of these factors is plotted; and (c) the frequencies of morphotypes actually occurring in a certain population are determined. The space of possible realizations represents a topographic map, and the frequencies of morphotypes serve as additional information about the actual “differences in elevation.” Eventually, we obtain the “response surface” of a certain configuration. This surface is the desired operational form of a polymorphic character, as its configuration will change upon transition from one population to another. The plotting and analysis of response surfaces is an adequate technique for studying population variability. We shall demonstrate the application of this technique to the analysis of morphological diversity of strawberry leaves in regard to the first two tasks.

Let us identify two main factors determining the concrete form of a leaf, namely, the structural and geometrical factors. Assume that the former determines the axial structure of a leaf and the latter determines the shape of its contour. In the axial system, we shall distinguish the central axis and the lateral axes branching

from it. This system is morphologically reflected in leaf venation. The central axis of a strawberry leaf is represented by the leafstalk and its continuation, the main vein (midrib) of the upper leaflet. All veins branching from the midrib, including the main veins of lateral leaflets, are regarded as lateral.

As there are one central axis and several lateral axes, only the latter will be ranked and numbered (beginning from the leaf base). The main veins of lateral leaflets are regarded as the first pair of first-order lateral axes; all the veins branching from the first-order lateral veins are the second-order lateral axes. Thus, in a typical ternate leaf, the lateral veins of its upper leaflet are first-order lateral axes and the lateral veins of lateral leaflets are second-order lateral axes. The uniform nomenclature of axes makes it possible to arrange all the forms of strawberry leaves, simple and complex, into a unified structural series (Korona, 1987).

The first members of this series are presented in Fig. 1. For clarity, only symmetrical structural variants are shown, although real leaves are more or less asymmetrical. The leaves are arranged in order of increase in the number of pairs of first-order lateral axes. The scheme shows that the initial structural series of strawberry leaves is subsequently subdivided into two morphotypical series. The beginning of the series is represented by simple dentate leaves. These are the first leaves of strawberry; they are small and have one, two, or three pairs of first-order lateral axes, each ending in a denticle. Later, as the number of lateral axes increases, the leaf blade either remains simple or is gradually dissected. In rare cases when it remains simple, one-leaflet forms appear. More often, leaf blade dissection begins at the fourth or fifth stage of the development of the axial structure (the appearance of a new pair of first-order lateral axes is regarded as one stage): the first,

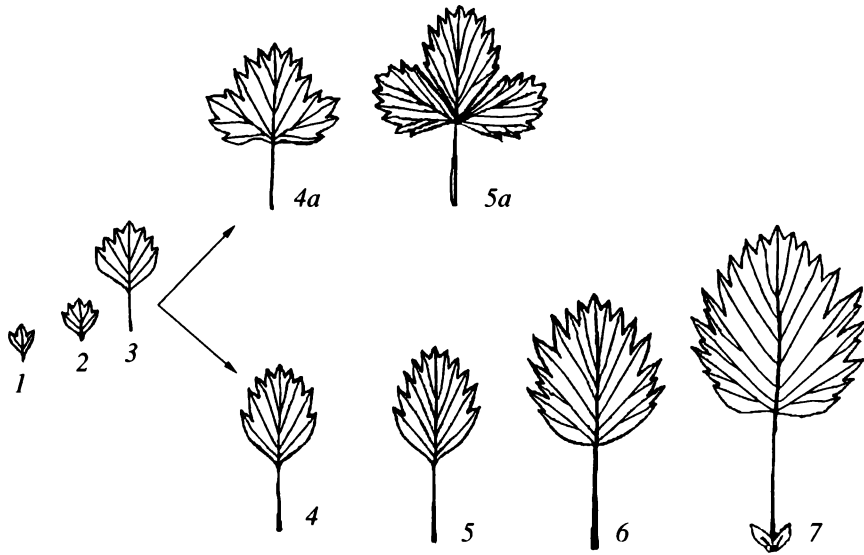


Fig. 1. Consecutive complication of the axial structure of strawberry leaves in a series of structural types. The type number corresponds to the number of pairs of first-order lateral axes.

lower pair of lateral axes becomes separated from others. This means that the second (geometrical) morphogenetic factor, which changes the shape of the leaf, is at work. Thus, a simple dentate leaf becomes trilobate. At the following stages, the depth of dissection increases and a typical ternate strawberry leaf appears.

Taking into consideration that the structural and geometrical morphogenetic factors are relatively independent and their action is "gradual" (i.e., they can be expressed through the number of stages of axial structure complication or through the depth of leaf blade dissection), we can formally use them as an orthogonal system of coordinates outlining a certain plane. Each concrete leaf will correspond to a certain point in this plane, with the corresponding numerical values of morphogenesis factors being the coordinates of this point. The coordinate plane is the space of possible realizations, i.e., of all potentially possible forms of the strawberry leaf.

The notion "the space of possible realizations" is conceptually similar to the notion of "epigenetic landscape" and related ideas of programmed morphogenesis (Bonner, 1967) and the existence of stable morphogenetic trajectories (Waddington, 1970). We do not propose any radically new ideas but only adapt known ideas to the purposes of studies on plant populations. Although the concept of creod was formulated more than twenty-five years ago, the fact that any "point" character of an organism is a "landscape" character in a population (i.e., the form of its distribution reflects not so much random deviations from the mean value as the structure of the response surface) has not yet become trivial. Hence, the task of concretizing the ideas about the space of possible realizations of a character as a component of the epigenetic landscape of a population is still important.

As a first approximation, the diversity of strawberry leaf forms can be described by the system of two variables. This system outlines the two-dimensional space of possible realizations, in which movement along one coordinate axis is morphologically manifested as a change in the degree of leaf structural complexity of a leaf, and that along the other axis, as a change in the depth of leaf blade dissection. It is logical to regard these orthogonal movements along the coordinate plane as the principal directions of morphological variation, as all other directions are formally their derivatives.

In what way are the typical strawberry leaves formed? The directional change of morphotype (the transformation of simple leaves to ternate ones as the axial structure becomes more complex) suggests that they shift from one morphogenetic trajectory to another in the course of individual development. The initial direction leads to the formation of a simple dentate leaf, but progression along this trajectory ceases at the third step; at the fourth step, the developing system shifts to another trajectory and makes five to six additional steps along it. As the result, a typical strawberry leaf contains, on average, eight to nine pairs of first-order lateral axes.

The real morphogenetic mechanisms of this shift are unknown, and we can only assume that, as in other related cases, we observe the response of a system to the exceeded critical (threshold) value of some morphogenetic parameter. In our case, this critical value is the degree of structural complexity of a leaf, which is numerically equal to three pairs of first-order lateral axes. When this value is exceeded, the process of leaf blade dissection is switched on, which separates the "extra" (the first, lowest) pair of lateral axes from those formed later.

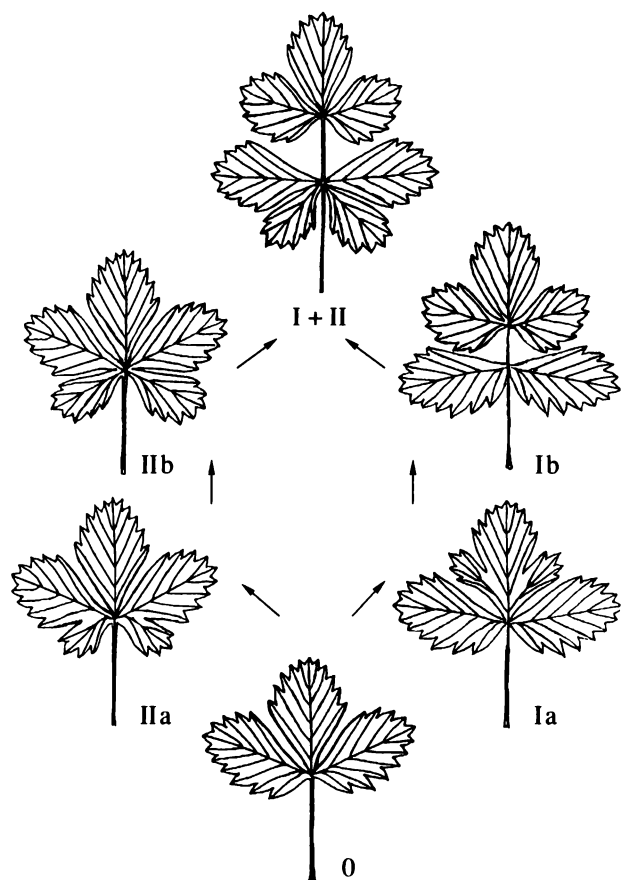


Fig. 2. Morphotypes of strawberry leaves emerging upon the second symmetrical dissection of a typical ternate form: (I, II) variants of consecutive dissection; (a, b) conventional intermediate stages of dissection.

If the ability for threshold response is lost for some reason, a simple leaf is formed, which may reach the same degree of complexity as typical ternate forms. If this ability is retained, the repeated (second) dissection of leaf blade occurs, giving rise to aberrant morphological variants.

The second dissection follows the same pattern: the lowest lateral axis separates and subsequently transforms into an independent leaflet. In a typical ternate leaf, this process can occur in two ways: (a) through separation of the lower pair of lateral axes in the upper leaflet, which results in the formation of an imparipinnate five-lobed leaf, and (b) through separation of the pairs of lower lateral axes in lateral leaflets, which also leads to the formation of a five-lobed leaf but of a slightly different shape. Figure 2 shows the schemes of both these directions of development and their "intersection," which gives rise to a hypothetical seven-lobed leaf form.

In natural strawberry populations, quaternate leaves are sometimes found. They result from dissection of a lateral leaflet or asymmetrical (right- or left-handed)

dissection of the upper leaflet in a ternate leaf. Quinate forms occur even more rarely. To date, we have found no septenate leaves, which may appear upon simultaneous symmetrical dissection of the upper and lateral leaflets in a ternate leaf. Hopefully, this form will be found in the future, as its existence was predicted by extrapolating the actual trends in leaf development. It should be emphasized that all the true (idealized) morphotypes of strawberry leaves shown in Fig. 2 are variants of the same structural type, which has six pairs of first-order lateral axes. The diversity of morphotypes in this case arises owing to variation in the multiplicity of dissection against the background of constant structural complexity.

Thus, plant leaves are not only single independent objects comprising a polymorphic set, but also the components of an integrated system reflecting the features of their individual development. Hence, prior to analyzing the frequency distribution of such objects in a population, it is necessary to construct the space of realizations for this system. The analysis of leaf diversity in natural strawberry populations shows that, as a first approximation, variation in the leaf form can be formally described with the aid of two morphogenetic factors: the structural factor, which defines the complexity of the axial structure, and the geometrical factor, which determines the depth of one-fold dissection of the leaf blade. The space of possible realizations in this case takes the form of a two-dimensional surface in the Cartesian system of coordinates. The second leaf dissection transforms it into a three-dimensional space by adding the second, parallel plane. Coordinates of each point on each of these planes correspond to a potentially possible leaf morphotype. The typical leaves of strawberry occupy a relatively small central part of this space, whereas juvenile and aberrant forms are in its immediate vicinity.

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Variability of the Flower Structure in European Starflower (*Trientalis europaea* L.) in Natural Populations

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Abstract—Flower variability was studied in natural populations of European starflower (*Trientalis europaea* L.). The results showed that the flower structure in this species is determined by two parameters: the multiplicity of primordia of flower components and the uniformity of flower meristem development. The frequencies of non-uniformly developing flowers differs depending on the habitat. It appears that both parameters are largely determined by random fluctuations.

Key words: flower structure, variability, European starflower, *Trientalis europaea* L.

It is generally accepted that intraspecific variability is determined by variation in several factors, including the genotype, the stage of organism development, and the environment (Korochkin, 1999; Lutova *et al.*, 2000). The role of each factor can be accurately singled out only in artificial, controlled model systems. The analysis of variability in nature is much more difficult because of the impossibility of strictly controlling the genotype and the aggregate of environmental effects. Hence, concrete factors responsible for natural variability remain poorly studied in most species. However, if an organism forms several structures of the same kind, such as flowers (they have the same genotype and, hence, are analogous to monozygotic twins), the character of their variability can be revealed even in natural conditions. For example, a high degree of similarity between these structures is evidence for strict genetic control of their development; conversely, their significant heterogeneity suggests that their variability is not hereditary. This approach proved to be successful in studies on many characters of both animals and plants (Woolf, 1995; Kerstetter and Poethig, 1998).

This work deals with the regularities of flower variability in the populations of the European starflower (*Trientalis europaea* L.).

MATERIALS AND METHODS

Object. European starflower is a pseudo-annual herbaceous plant widespread in the boreal zone of the northern hemisphere (Charlier, 1913; Hiirsalmi, 1969; Gryzlova and Vakhrameeva, 1990). This plant vegetates only in summer and remains in the form of a resting tuber for the rest of the year. A short aboveground shoot develops from the maternal tuber in June and finishes flowering by early July. In August, the maternal plant produces one or several underground stolons, which give rise to a series of filial tubers (Warming, 1918;

Golubev, 1956). Seed reproduction apparently plays a secondary role in the biology of this species (Hegi, 1908; Gryzlova and Vakhrameeva, 1990).

One or several actinomorphic flowers are formed on the adult plant. Every flower has sepals, petals, and stamens (their numbers are usually equal or similar, ranging from five to nine) and one pistil. Seven-membered flowers are most common (Charlier, 1913; Matthews and Roger, 1941; Hiirsalmi, 1969). The structure of the flower can vary even within the same clone (Charlier, 1913; Hiirsalmi, 1969), which suggests that variation in this character is not hereditary. However, any regularities of this phenomenon were unknown by the beginning of our work.

Study area. The work was carried out on Konevets Island (Lake Ladoga). This island combines loamy and sandy deposits in its geomorphological structure and is characterized by a great diversity of plant communities. Different types of pine and spruce forests, birch forests, and white alder groves grow on this island. European starflower is found in all forest types except dry (lichen–green moss) pine forests and strongly shaded spruce forests. In addition, plants of this species successfully populate open sites adjoining the forest.

This work was carried out using five communities located along the gently sloping southern shore (for two of them, similar communities from the inner area of the island were studied as a control):

(1) Bilberry–green moss pine forest I growing on the southwestern steep slope of the island, approximately 8 m above the lake level. The stand consists of adult and young Scotch pine (*Pinus sylvestris* L.) trees, with European mountain ash (*Sorbus aucuparia* L.) undergrowth. The herbaceous–dwarf shrub layer includes bilberry (*Vaccinium myrtillus* L.), cowberry (*V. vitis-idaea* L.), and Scotch heather (*Calluna vulgaris* (L.) Hill). In the moss cover, *Pleurosium schreberi* (Brid.) Mitt. and *Dicranum polysetum* Sw. prevail.

(2) Bilberry–green moss pine forest II growing in the inner part of the island, 400 m away from pine forest I (10 m above the lake level). This community was closely similar to pine forest I and, hence, served as the corresponding control.

(3) Bilberry–green moss pine forest with an admixture of spruce, growing on the southern bank of the island, approximately 6 m above the lake level. Along with pine, the stand includes individual adult trees and abundant undergrowth of Norway spruce (*Picea abies* (L.) Karst.) and European mountain ash. Scotch heather is absent from the herbaceous–dwarf-shrub layer, but there are May lily (*Maianthemum bifolium* (L.) F.W. Schmidt), club moss (*Lycopodium clavatum* L.), and stone bramble (*Rubus saxatilis* L.). In the moss cover, *P. schreberi*, *Pohlia nutans* (Hedw.) Lindb., and *D. polysetum* prevail.

(4) Bilberry–green moss spruce forest with an admixture of pine. This community is situated on the southeastern bank, approximately 4 m above the lake level. Adult pine and European mountain ash trees occur in the stand along with spruce; pine is absent from the undergrowth. Bilberry and reed grass (*Calamagrostis arundinacea* (L.) Roth) are dominant in the herbaceous–dwarf-shrub layer; bracken (*Pteridium aquilinum* (L.) Kunh. ex Decken) also occurs there. In the moss cover, *P. schreberi* and *P. nutans* prevail.

(5) Herbaceous–bilberry birch forest growing in the periodically flooded southeastern part of the island, approximately 1.5 m above the lake level. European white birch (*Betula pendula* Roth), white alder (*Alnus incana* (L.) Moench), and European aspen (*Populus tremula* L.) dominate in the stand. The species prevailing in the herbaceous layer include reed grass, bilberry, stone bramble, wood sorrel (*Oxalis acetosella* L.), lady fern (*Athyrium filix-femina* (L.) Roth), and wood fern (*Dryopteris expansa* (C. Presl.) Fraser-Jenkins et Jermy).

(6) Trembling bog on the low eastern bank of the island. Being in the immediate vicinity of the lake, this community is often flooded. The tree stand is sparse and low and consists of pine. The floating mat is mainly formed of sphagnum mosses, marsh cinquefoil (*Comarum palustre* L.), purple lythrum (*Lythrum salicaria* L.), and sedges (*Carex lasiocarpa* Ehrh. and *C. cespitosa* L.).

(7) The peripheral part of a raised bog. This community is in the inner part of the island, at the boundary between a bilberry–green moss spruce forest and a raised sedge–sphagnum bog with the prevalence of star-headed sedge (*Carex echinata* Murr.) and few-flowered sedge (*C. pauciflora* Lightf.). This community was chosen as a control for the trembling bog on the bank.

In each community, a uniform plot of about 400 m² in area was studied.

Analysis of flowers. In each community, 100–200 undamaged flowers of European starflower were analyzed. The distance between the plants studied was no less than 1 m. In each flower, the numbers of sepals (K), petals (C), and stamens (A) were determined to devise

the formula $K_xC_yA_z$. The number of carpels was not analyzed. Any partially bifurcated component was regarded as a single component. The flowers with equal numbers of components (for example $K_6C_6A_6$, $K_7C_7A_7$, etc.) were named uniform (R). The flowers of all other types ($K_7C_6A_6$, $K_7C_8A_6$, etc.) were regarded as nonuniform (N). The frequency of nonuniform flowers (F_N) was used as the quantitative index of flower variability in a given community. Its values were compared using the chi-square test (Sokal and Rohlf, 1995).

Another approach consisted in the analysis of European starflower plants bearing two open intact flowers. The total sample of such plants was divided into three groups consisting of plants with two uniform (RR), two nonuniform (NN), and one uniform and one nonuniform (RN) flowers. In order to estimate the contribution of random events to the development of these flowers, the observed ratio of RR, RN, and NN plants was compared with that expected on the basis of binomial distribution (Sokal and Rohlf, 1995).

RESULTS

Variability of *Trientalis europaea* flowers on Kon-evets Island. The uniform flowers $K_7C_7A_7$, subsequently referred to as R_7 , were most abundant among the 2616 flowers studied between 1995 and 1998 (Table 1). In addition, we found other classes of uniform flowers: $K_5C_5A_5$ (R_5), $K_6C_6A_6$ (R_6), and $K_8C_8A_8$ (R_8). The remaining flowers were nonuniform (N); they formed a wide range of classes.

Most N-type flowers (462 out of 491) differed from uniform flowers by the absence of one component (–1) or by the presence of an additional component (+1). Judging from these data, the N-type flowers appeared because of local anomalies of the flower meristem. Each anomaly usually affects only one primordium and either prevents its development or promotes the formation of an additional primordium.

The total number of N-type flowers studied (491) was significantly smaller than the number of R_6 flowers (618). Hence, the formation of R_6 flowers appeared to be based not on a series of independent local anomalies, but rather on the principally different mechanism that has changed the multiplicity of all primordia of flower components from 7 to 6. We assumed that analogous changes of multiplicity are the cause of formation of R_5 and R_8 flowers.

Based on this assumption, we reconstructed the origin of the nonuniform flowers studied. For example, a $K_6C_7A_7$ flower is the variant of abnormal R_7 meristem development resulting from a defect in one of the seven sepal primordia. Similarly, a $K_6C_7A_6$ flower is formed via the development of one extra petal primordium in the initial R_6 meristem. Because of this, nonuniform flowers of $K_6C_7A_7$ and $K_6C_7A_6$ types will be subsequently referred to as N_{7-1K} , N_{6+1C} , etc. Only 29 nonuni-

Table 1. Variability of *Trientalis europaea* flowers on Konevets Island

Type of initial meristem	Uniform flowers	Nonuniform flowers							
		+1 K	-1 K	+1 C	-1 C	+1 A	-1 A	double*	total
R5	2	4	0	0	0	2	0	0	8
R6	618	37	16	24	5	35	22	6	763
R7	1478	2	114	13	37	31	96	18	1789
R8	27	0	10	1	3	0	10	5	56
Total	2125	43	140	38	45	68	128	29	2616

* Nonuniform flowers formed as the result of two independent developmental anomalies. We found the following types of such flowers: $K_4C_6A_6(N_6-2K)-1$, $K_6C_6A_4(N_6-2A)-1$, $K_5C_6A_7(N_6-1K+1A)-1$, $K_8C_6A_6(N_6+2K)-2$, $K_6C_6A_8(N_6+2A)-1$, $K_5C_7A_7(N_7-2K)-5$, $K_7C_7A_5(N_7-2A)-7$, $K_6C_8A_7(N_7-1K+1C)-1$, $K_7C_6A_8(N_7-1C+1A)-1$, $K_7C_8A_6(N_7+1C-1A)-1$, $K_8C_6A_7(N_7+1K-1C)-1$, $K_8C_7A_6(N_7+1K-1A)-1$, $K_9C_7A_7(N_7+2K)-1$, $K_6C_8A_8(N_8-2K)-3$, $K_8C_6A_8(N_8-2C)-1$, $K_8C_8A_6(N_8-2A)-3$.

Table 2. Variability of *Trientalis europaea* flowers in different communities of Konevets Island

Community	Number of flowers	Uniform flowers	Nonuniform flowers		
			+1/-1*	double**	total, %
Spruce forest with pine	164	156	8	0	8 (4.9)
Floating mat	170	157	13	0	13 (7.6)
Edge of raised bog	116	105	11	0	11 (9.5)
Birch forest (10.5)	200	179	19	2	21 (10.5)
Pine forest with spruce	161	135	24	2	26 (16.1)
Pine forest I (18.0)	150	123	26	1	27 (18.0)
Pine forest II (19.1)	199	161	36	2	38 (19.1)

* Nonuniform flowers formed as the result of one developmental anomaly.

** Nonuniform flowers formed as the result of two independent developmental anomalies.

form flowers were of a more complex origin: in each of these cases, the initial meristem apparently had two independent anomalies (Table 1).

Thus, in the sample of 2616 flowers, the number of sepals varied from 4 to 9, the number of petals varied from 5 to 9, and the number of stamens varied from 4 to 8. These flowers were divided into three groups: (1) uniform flowers R₅, R₆, R₇, and R₈; (2) nonuniform flowers formed as the result of one anomaly; and (3) nonuniform flowers formed as the result of two anomalies.

Effect of the environment on the frequency of nonuniform flowers. We studied the frequency of nonuniform *T. europaea* flowers (F_N) in different communities of Konevets Island in June 1996 (Table 2). The values of this index in similar communities chosen as mutual controls proved to be closely similar. The differences between the value for the spruce forest with an admixture of pine (the lowest F_N value) and the values for pine forests were significant ($P < 0.001$).

Analysis of biflorate plants. We studied 160 biflorate plants of European starflower in two different communities of Konevets Island in June 1997: 100 plants in the pine forest with an admixture of spruce and 60 plants

in the birch forest. The number of plants studied was small because the first and second flowers rarely open in the same period (this circumstance did not allow us to perform the study in 1998 and 1999). We found three types of biflorate European starflower plants in each community: (1) plants with two uniform flowers, (2) plants with two nonuniform flowers, and (3) plants with one uniform and one nonuniform flower (Table 3). It should be emphasized that the plants of the third type were fairly abundant in both communities. Judging from these data, European starflower is characterized by high nonhereditary variation in the character "uniformity of flower development." Moreover, the ratios between different types of biflorate plants in the two communities did not differ significantly from those expected assuming that the flowers develop independently. Thus, uniform or nonuniform development of a certain flower in *T. europaea* is determined by some random events, rather than by the genotype.

The method of assessment used in this work made it possible to reconstruct the origin of the flowers studied, and each flower was described with respect to both the character "uniformity of development" and the multiplicity of primordia of its components. When the latter char-

Table 3. Analysis of biflorate *Trientalis europaea* plants

Community	Ratio	Ratio of biflorate plants*	
		RR : RN** : NN	7-7 : 7-6** : 6-6
Birch forest	Observed	47 : 12 : 1	7 : 20 : 33
	Expected	46.82 : 12.31 : 0.87	4.82 : 24.36 : 30.82
		$\chi^2 = 0.028$; $P = 0.87$	$\chi^2 = 1.921$; $P = 0.17$
Pine forest with spruce	Observed	43 : 52 : 5	15 : 49 : 36
	Expected	47.61 : 42.78 : 9.61	15.60 : 47.80 : 36.60
		$\chi^2 = 4.645$; $P > 0.05^{***}$	$\chi^2 = 0.063$; $P = 0.80$

* Designations of biflorate plants: (RR) with two uniform flowers, (RN) with one uniform and one nonuniform flower, (NN) with two nonuniform flowers, (7-7) with two 7-membered flowers, (7-6) with one 7-membered and one 6-membered flower, (6-6) with two 6-membered flowers. Some errors could have been made while analyzing the character "multiplicity of primordia of flower components." Thus, a concrete $K_6C_7A_7$ flower could be formed from a meristem initially containing six- rather than seven-membered sets of primordia ($N_6 + 1C + 1A$). However, as the frequency of double developmental anomalies is low, such situations could not have any strong effect on the observed ratios.

** In some plants of this class, the nonuniform (or 6-membered) flower was situated in the axil of the lower leaf, relative to the uniform (or 7-membered) flower; in other plants, an inverse picture was observed.

*** Taking into account the Shidaka correction for two independent comparisons (Rohlf and Sokal, 1995).

acter was taken into account, the entire sample of biflorate plants was subdivided into three groups: (1) plants with two initially seven-membered flowers, (2) plants with two initially six-membered flowers, and (3) flowers with one seven-membered and one six-membered flower. It was found that nonhereditary variation resulting from random events is typical of this character as well (Table 3).

DISCUSSION

The number of flower components is usually determined by the size of the flower meristem, as was demonstrated in studies on *Arabidopsis thaliana* mutants (Clark *et al.*, 1993; Running *et al.*, 1998). We consider that flower variability in *T. europaea* is also based on variation in the size of the flower meristem.

As follows from our data (Table 1), the R_7 flowers are most typical of this species and the diversity of flowers is apparently connected with two types of accidental events. On the one hand, a certain flower meristem can be greater or smaller than the normal meristem, with the proportion between all its "rings" remaining normal; in this case, the multiplicity of primordia of flower components will change from 7 to 8, 6, or 5. On the other hand, the initially uniform meristem can acquire a local anomaly affecting the size of only one "ring"; in this case, a nonuniform flower will develop.

What are the possible mechanisms of such accidental events? It is probable that they are based on the insufficiently coordinated expression of genes that control the structure of the flower meristem. The possibility of such situations was demonstrated in studies on *fasciata*, *clavata*, and *wiggum* mutants in *Arabidopsis thaliana* (Leyser and Furner, 1992; Clark *et al.*, 1993; Run-

ning *et al.*, 1998). On the other hand, these events may be the consequence of a high plasticity of the flower meristem under the effect of locally fluctuating external factors. Such environmental effects are especially important at the critical stages of flower morphogenesis, when the choice between several alternative development programs can take place. As different flowers of the same plant are not formed simultaneously, they are exposed to different environmental effects and, hence, can acquire some structural differences (Table 3).

In our opinion, environmental factors are responsible for different frequencies of nonuniform flowers (F_N) in different plant communities. Note that lower and higher F_N values are typical of moist and dry communities, respectively (Table 2). Hence, soil moisture appears to be among the key environmental factors determining F_N in European starflower. However, it should be taken into account that the lowest F_N value was observed in the spruce forest with an admixture of pine, rather than in the moistest communities at the periphery of the raised bog and the floating mat. These data suggest that not only soil moisture but other environmental factors (e.g., illumination) determine F_N in European starflower. This conclusion agrees with the fact that many genes controlling flower development in *Arabidopsis thaliana* are regulated by environmental factors, temperature and light in particular (Amasino, 1996).

In this work, we obtained no evidence that the flower structure in European starflower is controlled by the plant genotype. This can be explained in two ways. On the one hand, the plants studied could be the vegetative descendants of the same ancestor (the plant that was the first to appear on Konevets Island) and, hence, could have the same genotype. On the other hand, some genetic differences between individual plants could

level off owing to a high ploidy of this species ($2n = 160$: Löve and Löve, 1961; Krogulevich, 1978). In any of these situations, flower variability in European starflower should be mainly determined by factors other than genotype, including random factors.

Using the example of flower development in *T. europaea*, we demonstrated that the random choice of alternative programs of development is among the mechanisms of intraspecific variability in nature. Note that the environment does not specify a certain program but only affects the probability of its choice. These data make it possible to gain a new insight into the role of the environment in phenotype determination: in our opinion, the main role belongs to local fluctuations of environmental factors at critical stages of organism development, rather than to average environmental influences.

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Survival Under Conditions of Environmental Stress: Variability of Brain Morphology and Behavior in the House Mouse

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Abstract—Two populations of laboratory mice lived outdoors in open pens for two years. Thereafter, some of them were bred in the laboratory. Morphometric analysis showed that the size of the synaptic projection area of mossy fibers (in the CA3 region of the hippocampus), which has an important functional role, and some behavioral traits of the open-pen mouse progeny had significant genetically determined differences from those in the initial population. This was attributed to differential breeding accounted for by the influence of severe environmental factors. Under environmental stress, selection occurred in the population and the mice with behavioral and neuromorphological characteristics differing from those of the control group proved to be better adapted to such conditions.

Key words: behavioral genetics, genetic variation, adaptation, natural selection, exploratory behavior, anxiety, aggressiveness, hippocampus, mossy fiber, morphometry

Differences between inbred mouse lines commonly used in genetic studies concern not only their behavior (learning, memory, locomotion, emotionality, stress reactivity, etc.) but also neuroanatomical characteristics (Lipp *et al.*, 1987, 1989). It was found that randombred mice with a smaller hippocampus size are more successful in passive avoidance learning in response to an electric shock (Wimer *et al.*, 1971). This is consistent with the results of “invasive” experiments on the destruction of the hippocampus (e.g., Means *et al.*, 1971).

The hippocampus, the so-called paleocortex of the mammalian forebrain (see scheme in Fig. 1), is known to play a key role in spatial cognitive behavior and memory (Olton, 1983; Crusio *et al.*, 1987) and several “nonspatial” forms of behavior (Sluyter *et al.*, 1994).

The analysis of hippocampal synaptic connections with other brain areas—the neocortex, basal ganglia, and diencephalon (thalamic nuclei)—and of the inter-strain variability of hippocampal regions (Schwegler and Lipp, 1983) suggested that one of the synaptic areas of the hippocampus serves as a kind of command center in the rodent forebrain. This is the projection area of mossy fibers—axons of granular neurons of the dentate fascia—on basal dendrites of pyramidal neurons of the CA3 region (Fig. 1), which is called the intra- and infrapyramidal area (iip-MF). Hence, variation in the size of this area can significantly affect the behavior of mice. Experiments confirming this assumption were performed with rats selected for a high or low ability for active avoidance learning, several inbred mouse strains, F2 hybrids of DBA/2J and C3H mice

sharply differing in the size of iip-MF, and on several other models. A significant negative correlation between iip-MF size and success in avoidance learning was revealed (Lipp *et al.*, 1989). Later, it was shown that the size of iip-MF positively correlates with spatial learning success in radial and water mazes (Schopke *et al.*, 1991; Crusio *et al.*, 1987) and with the level of exploratory activity (Crusio and Schwegler, 1987, Hausheer-Zarmakupi *et al.*, 1996).

It remained unclear whether this relationship has any general biological significance and whether it will persist in a mouse population breeding in a large open pen. According to Lipp and Wolfer (1995), if the size of iip-MF correlates with individual or population adaptability, experiments with animals kept in a quasi-natural environment for a long time may reveal some changes of this morphological index in the surviving progeny, compared to the initial population. Thus, the question was as follows: will the size of iip-MF change, and in what way, in animals that will manage to survive and breed under living conditions drastically different from those in the laboratory?

The search for an answers to this question was the purpose of joint studies of the Laboratory of Physiology and Genetics of Behavior (Biological Faculty, Moscow State University) and the Institute of Anatomy (University of Zurich, Switzerland), which were conducted at the Chisty Les Biological Station (Director V.S. Pazhetnov, Doctor of Biology) of the State Central-Forest Biosphere Reserve, Tver oblast.

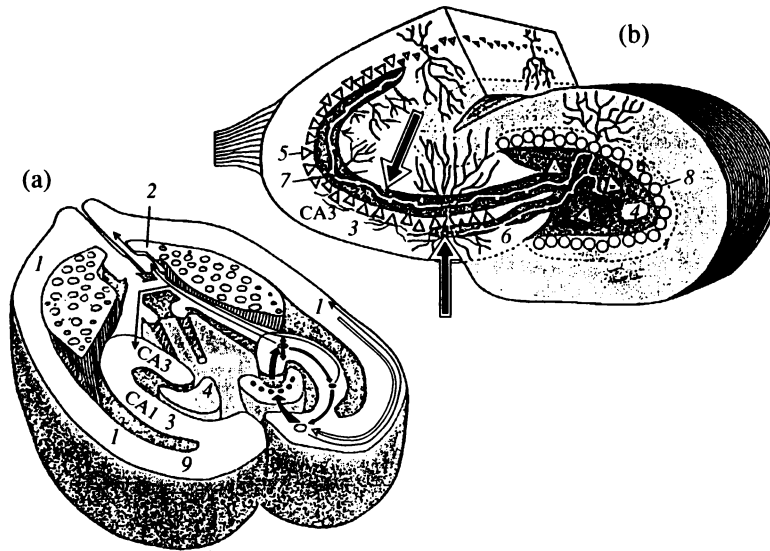


Fig. 1. Scheme of the hippocampus: (a) mouse forebrain, horizontal section; (b) structural scheme of the hippocampus and dentate fascia; (1) neocortex, (2) corpus striatum, (3) hippocampus with CA3 field, (4) dentate fascia, (5) layer of pyramidal cells, (6) layer of their basal dendrites (arrow indicates iip-MF area), (7) layer of apical dendrites (arrow indicates sp-MF area), (8) granular cells of dentate fascia, (9) entorhinal cortex.

METHODS

Experimental animals. Two groups (36 mice each) of reciprocal mouse hybrids (strains DBA/2, 57B1/6J, NZB, C3H) were released into two large open pens (19 × 19 m). These mice were protected from terrestrial predators (cats, weasels, etc.) but not against birds of prey, which were abundant in the study area. The mice were exposed to daily and annual changes in temperature and humidity, which normally occur in the region. They had free access to water and food and could find shelter in straw-packed "houses" constructed in the center of each pen. Hybrids of the control group were randomly bred under laboratory conditions in Moscow.

All mice in each pen were trapped at least once each summer, and groups of 18–20 animals were taken for neuroanatomical analysis. The proportions of males and females of certain age and coat color in these samples corresponded to those in the entire group. The total number of mice in each pen varied from year to year between 75 and 90.

In August 1997, five pairs of mice from each pen were taken for breeding in the laboratory. Below, the progenies of animals from pens 1 and 2 are referred to as BUB1 and BUB2 (from Bubonitsy, the village where the pens were situated). The F4–F7 progenies of these mice were investigated. The control population (F14–F17), which was bred in the laboratory from the beginning of the experiment, is subsequently designated MC (Moscow control). The BUB1 and BUB2 groups consisted of 15 males, and the MC group, of 18 males.

Behavioral testing. The "open field" test. Locomotor activity and emotional reactivity were estimated in two "open field" sets of different sizes. One was a plat-

form (1 m in diameter) surrounded by a plastic wall 35 cm in height, with a rectangular grid (10 × 10-cm squares) drawn on the floor. The experiment was carried under usual electric light (not bright). The noise level was 30–40 dB. The test was performed for 2 min to estimate the numbers of squares crossed (each minute separately) and episodes of rearing (standing upright), defecation, urination, and grooming episodes. The other open field set was a cylindrical box 36 cm in diameter, with 20 holes in the floor. The number of "hole-poke" reactions (looks into the holes) was recorded.

Aggressiveness of males was estimated in 20-minute encounters with a "standard opponent," a CBARb male of equal body weight. Males were kept in isolation for 5 days before testing. Five tests (once a day) were performed. Both animals were put into a plastic cage (20 × 40 × 20 cm) with fresh bedding. The number of forced grooming episodes (demonstration of weak aggressive reaction), the latent period before the first attack, and the total number of attacks were recorded.

Extrapolation ability. The ability to extrapolate the direction of stimulus movement was estimated by a technique described earlier (Krushinsky *et al.*, 1986). A mouse deprived of food and water for 20 h was placed in a special box with three small openings in the wall and was offered milk in a small cup placed behind the central opening. In a few seconds, the cup was moved to the right or left opening, out of the animal's sight. The animal's movement toward the same or opposite opening was regarded as correct or incorrect performance, respectively. If the mouse did not move to either opening within 120 s, this was considered "zero performance," and if the animal did not approach the

central opening (so that it was impossible to begin the test), it was considered as refusal to perform the task. Two days before testing, the mice were given a habituation session. For this purpose, animals kept in the same cage and previously deprived of food and water were placed into the box and were given an opportunity to receive some milk through the central opening. During feeding, the cup was moved from side to side for 0.5 cm in order to habituate the mice to the onset of its movement. On the day of testing, such a session was repeated for 12–15 min. The animals were tested individually, and each test was performed 18 times (three series of six presentations).

Morphological analysis of the brain. To prepare histological sections, the brain was fixed using transcardial perfusion with 1.17% Na₂S and 3.0% glutaraldehyde solutions under Nembutal anesthesia. Horizontal sections of the frozen brain (40 μ m) were cut using an American Optical cryostat and stained by Timm's method (Schwegler and Lipp, 1983) to detect the zinc-containing synaptic endings of the mossy fibers. The size of these areas was determined using an automated device (Megaplug CCD + Zeiss Axioplan) with standard AdobeTM Photoshop and NIH Image 1.61 software.

Experimental data were processed statistically with the aid of the Statistica program package, using the Wilcoxon test (open field and aggressiveness), the Fisher alternate proportions method (extrapolation test), and ANOVA (sizes of mossy fiber projections). Differences with $p < 0.05$ were considered significant.

RESULTS AND DISCUSSION

The open field test. The locomotor activity of mice from the three groups was of approximately the same level. The frequency of defecation in the open field test is often used as an index of fear and autonomic reactivity in rodents (Archer, 1975). In both versions of the open field test, this frequency was significantly higher in BUB1 and BUB2 groups than in MC (Fig. 2). In other words, the progeny of pen mice demonstrated higher reactivity.

In the first test, the exploratory activity of mice (species-specific rearing and hole-poke reactions) was similar in all three groups (Fig. 3). In the second and third experiments, however, this parameter became significantly lower in the BUB1 and BUB2 groups than in the MC group. Thus, the BUB1 and BUB2 mice adapted themselves to new conditions more rapidly than the control mice, which could be attributed to a higher "efficiency" of their behavior in collecting information about the environment (Crusio and Schwegler, 1987). Thus, the responses of both BUB groups to new conditions were different from that of the MC group. Differential reactivity to novelty, which correlated with inter-strain differences in the size of iip-MF in rats, was described earlier (Lipp *et al.*, 1987).

Number of droppings

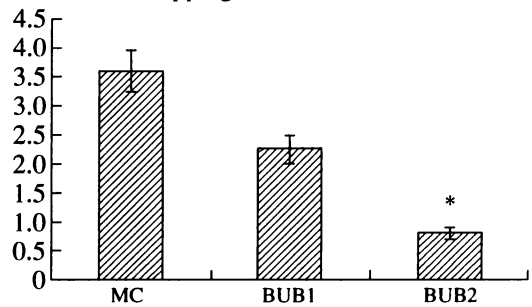


Fig. 2. Defecation frequencies in mice of MC, BUB1, and BUB2 groups in the open field test; (*) differences from MC and BUB1 are significant at $p < 0.05$.

Number of squares crossed

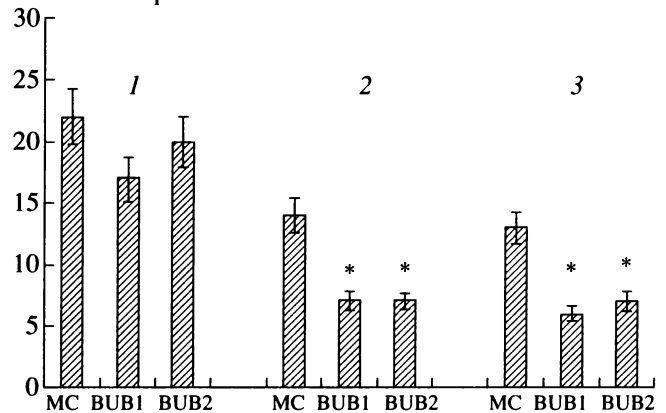


Fig. 3. Exploratory activity of mice in three consecutive open field tests (1, 2, 3); (*) differences from MC are significant at $p < 0.05$.

Aggressiveness. The average number of behavioral acts belonging to the aggressive behavior repertoire (forced grooming and attacks) was relatively small in all three groups (one to four during a 5-min test), and the mean latency of their manifestation was about 400 s. The MC mice were slightly more aggressive, but the difference was not significant. Thus, aggressiveness in the progeny of pen mice was not increased, although experiments on other strains revealed the dependence between the latency of the first attack and the size of iip-MF (Sluyter *et al.*, 1994).

Extrapolation test. Laboratory mice are generally incapable of performing this task, but such capacity has been found in mice carrying the Robertsonian translocation Rb(8.17)1Iem and in feral mice (Krushinskii *et al.*, 1986). In our experiments, the initial proportions of correct solutions in all three groups of mice were about 50%, i.e., at the level characteristic of random performance. However, after repeated testing (a total of 18 presentations), these proportions in both BUB groups significantly exceeded the random level (60.3 and 68.8%, $p < 0.01$), whereas that in the MC group remained virtually unchanged (54.2%).

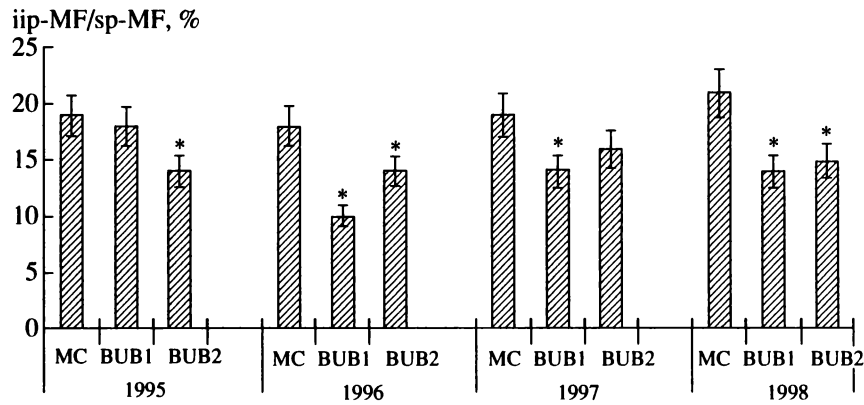


Fig. 4. Relative sizes of the iip-MF area of CA3 hippocampal region in mice of MC, BUB1, and BUB2 groups in consecutive seasons of the long-term experiment; (*) differences are significant at $p < 0.05$.

After being placed in the experimental box, the mouse first explores the environment (remember that animals were habituated to the box) and then begins to drink milk from the cup. This means that it is possible to begin testing. However, timid animals approach the feeder very cautiously or even avoid it and begin to eat only on the second or third day of the experiment.

In the BUB1 and BUB2 groups, ten mice in each group (58.8 and 66.7%, respectively) demonstrated such refusals, compared to only four mice (23.5%) in the MC group; the difference is significant at $p < 0.01$. The frequency of zero solutions—cases when the animal failed to make a choice within 2 min—was also higher in the BUB mice (13.4 and 17.9% vs. 7.5% in the MC group; $p < 0.01$).

It is impossible to explain these facts by differences in the level of food motivation because refusals and zero solutions were often displayed before correct performance; moreover, the frequency of correct performance in the progeny of pen mice exceeded the random level (see above). A more probable explanation is that the BUB1 and BUB2 mice were hyperreactive in a new environment. The situation of motivational conflict (hunger and fear) was making them passive, which was manifested in zero solutions and refusals. An obvious

fear of the test environment in these mice was expressed in their attempts to climb out of the box and in freezing reactions and jumps. The suggestion about hyperreactivity of the progeny of pen mice, compared to animals bred only in cages, agrees with the conclusions drawn from the open field data.

Morphological analysis. Measurements of the size of iip-MF (relative to that of the suprapyramidal mossy fiber area, sp-MF) size) were made throughout the experimental period. After two years, the relative iip-MF size in both pen populations decreased significantly (Fig. 4), initially in the BUB2 group and, in the next year, in the BUB1 group. By the fourth year of the experiment, this morphological index increased slightly but remained significantly different from that in the MC group (Fig. 4).

As is shown in Fig. 5, the iip-MF/sp-MF size ratio in the pen mouse progeny bred in cages for five generations was equal to that in pen populations in the year when the parent mice were trapped. Therefore, the change of this ratio, which occurred after two years of living in pens, persisted in the progeny of these mice during breeding in cages.

Thus, the appearance of fine but statistically significant changes in the brain morphology (the size of the mossy fiber projection area in the hippocampus) and behavior of pen mouse progeny was observed for the first time. Since these differences were inherent to both the mice kept in pens and their progeny bred in cages, they were determined genetically. Although the behavioral differences were small in absolute values (as the differences in hippocampal morphology, they were identical in sign in both BUB groups), it was impossible to explain them by random changes in the genetic structure of populations (i.e., by genetic drift). More probably, these differences were accounted for by changes that occurred in the experimental populations as the consequence of their life and breeding under stress in open pens.

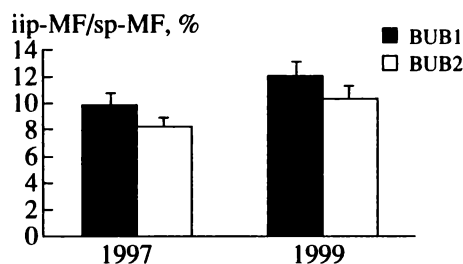


Fig. 5. Relative sizes of the iip-MF area of the CA3 area of the hippocampal region in the progenies of mice kept in two pens (BUB1 and BUB2) in the year of trapping (1997) and two years later (1999).

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Aging and Longevity as Indicators of Ecological Health of the Environment

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Abstract—The analysis of the demographic situation in the Republic of Mari El over ten years revealed the phenomenon of population aging with an increase in the number of elderly people. The phenomenon is regarded as an ecological indicator of the improvement of environmental quality; however, it poses some new problems in population gerontology.

Key words: demographic situation, aging, environment

As is known, the proportion of long-lived individuals in the human population is a criterion for estimating the state of its health and the health of the environment. According to Chebotarev (1984), a traditional territorial model of natural population aging with respect to the proportion of long-livers is the Caucasus, the region famous for the longevity of its residents. According to recent data (Gogoberidze, 2000), long-livers comprise 0.3% of the entire Georgian population, and the longevity index in 1996 comprised 22.1%; i.e., it exceeded the average index for Russia by a factor of more than 2 (Nikitin and Tatarinova, 1998). This is mainly accounted for by climatogeographic and other ecological factors promoting the maintenance of stable population ranges even among people of the extreme age group (over 100 years).

The purpose of our research was to study specific features of population aging in the Republic of Mari El in the ecological aspect and to make some population forecasting. According to official reports, the study area is comparatively safe, as the level of discharges and emissions to the environment has been decreasing over the past decade due to the restructuring of the industrial complex, nature conservation measures, and activation of the system of environmental protection (*O sostoyanii okruzhayushchei sredy...*, 1997; *Ob ekologicheskoi obstanovke...*, 1998). At the same time, climatogeographic characteristics of the republic are typical of the temperate zone of Russia and especially of the Volga region, where population aging is most pronounced (Zdravomyslova *et al.*, 1999; Lazebnik, 1999). Note that, until recently, no data on the demographic situation on this territory were available to the State Committee on Statistics of the Russian Federation (*Ob osnovnykh tendentsiyakh...*, 1997).

MATERIALS AND METHODS

We performed the analysis of selected statistical data (obtained from the State Committee on Statistics

of the Republic of Mari El) using conventional methods for studying the dynamics of aging (Safarova, 1997). Based on the initial data on human population size and composition, secondary indices were determined. To analyze aging, the following population groups were distinguished: children or young people under working age (0–15), people of working age (16–59), people beyond working age (60 years and older), and long-livers (90 years and older). The dynamics of indices in the first three groups were compared over ten years (1987–1996), and the indices of the group of long-livers were analyzed over five years (1995–1999).

RESULTS AND DISCUSSION

During the observation period, the total population was increasing. Its dynamics, without regard to the proportion of urban and rural components, is shown in the table. It is seen that for the ten-year period the resident population has increased by 20600 ind. However, it should be noted that, in 1994, the population growth stopped, and in the subsequent three years, there was a decrease in the total population size (negative increment of the population). We revealed the following factors that led to this decrease: (1) increasing mortality (Fig. 1), (2) a considerable decline in the birth rate (Fig. 2), and (3) decrease of the total birth rate coefficient (average number of children born by a woman in her life) (Fig. 3).

The data obtained suggest that the present demographic situation in the republic is characterized by “aging from the bottom,” i.e., a decrease in the population of children due to a decline in the birth rate. The dynamics of the decrease of the population of children exceeds the dynamics of the increase in mortality that indirectly accounts for “aging from the top”—a relative increase of the population of elderly age groups. Hence, the population is at the stage of the so-called

Changes in total population in the period from 1987 to 1996, thousand ind.

Sex	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996
Men	345.1	348.5	351.6	354.1	356.4	358.1	358.5	359.8	359.9	359.4
Women	399	400.8	402.2	403.8	405.4	406	406.1	406.3	406.3	405.3
Total	744.1	749.3	753.8	757.9	761.8	764.1	764.6	766.1	766.2	764.7

demographic transition, a phenomenon of population aging characteristic of most European countries and described earlier (Rosset, 1968; Kirilova, 1998). Further, we established that, on the unfavorable background of the natural reproduction of the population, the absolute number of people beyond the working age increased during the last decade (Fig. 4).

Comparison of these results with the index of the population increment for the analyzed period (20600 ind., table) demonstrates convincingly that the increment of the population in the republic occurred mainly due to persons of elderly age groups, i.e., that it is a clearly pronounced phenomenon of "aging from the top." However, if we use the conventional standard of the United Nations (65 years and older), the elderly population in 1987 comprised 61300 ind. and in 1996, 86700 ind. Hence, the absolute increment of the age sixty-five and older category comprised 25400 ind., which still further emphasizes the aging of the population.

To compare our data with the literature, we calculated the primary demographic indices for the determination of the proportion of people over the working age—coefficients $W_{60}(W_{65})$ —with the subsequent data assessment according to the scale proposed by Rosset (1968):

$$W_{60} = P_{60}/P \times 100\% \text{ or } W_{65} = P_{65}/P \times 100\%,$$

where P_{60} (P_{65}) is the number of people older than 60 (65) years; P is the total population of the republic.

As is customary in the literature, when interpreting results, it was considered that if the magnitude W_{60} is smaller than 8%, the population is considered to be "young," if it is greater than 12%, the population is considered to be "old," and for W_{65} , 4% and 7%, respectively. Our calculations showed that W_{60} for the period of 1987 to 1996 changed from 16% to 19%, and W_{65} , from 8% to 11%.

By comparison, we point out that the analogous index for all of Russia equaled 17.6% in 1998 (Zdravomyslova *et al.*, 1999); in the Volga-Vyatka region, over 23% (Lazebnik, 1999); and according to the data of world demography for 1993 with a historically "old population" in Sweden, 22.4%; in Norway, 20.6%; in Japan, 18.7%; in Georgia, 17.5%; and in Canada, 16.0% (cited according to Gogoberidze, 2000).

Thus, our data unambiguously indicate that by the beginning of the analyzed period, the population of the republic was "old" according to both criteria, and by

1996, the proportion of elderly people further increased. To support this conclusion we calculated the aging index (AI) of the population:

$$AI = \frac{P_{60}}{P_{(0-15)}} \times 100\%,$$

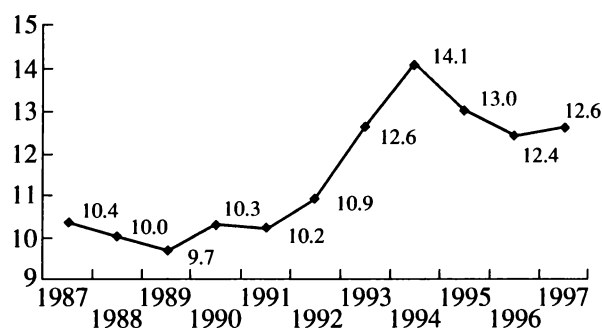


Fig. 1. Mortality dynamics (per 1000 ind.) between 1987 and 1996.

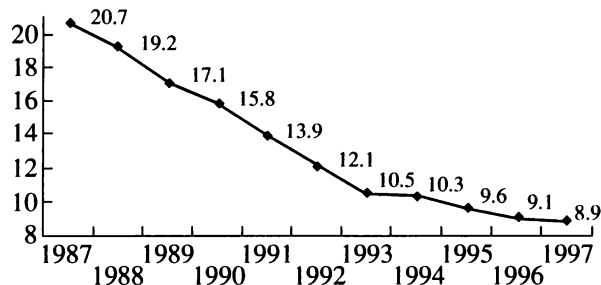


Fig. 2. Birth rate dynamics (per 1000 ind.) between 1987 and 1996.

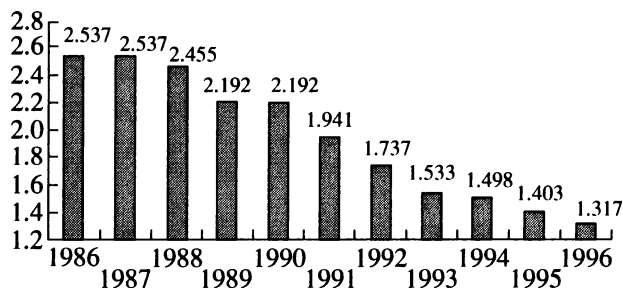


Fig. 3. Dynamics of the birth rate coefficient between 1987 and 1996.

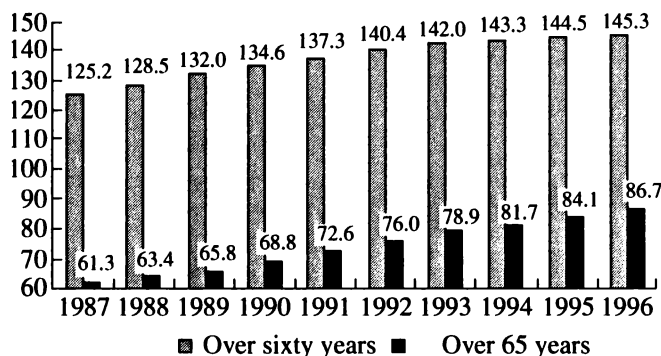


Fig. 4. Dynamics of the population (thousand ind.) beyond the working age (60 and 65 years) in the Republic of Mari El.

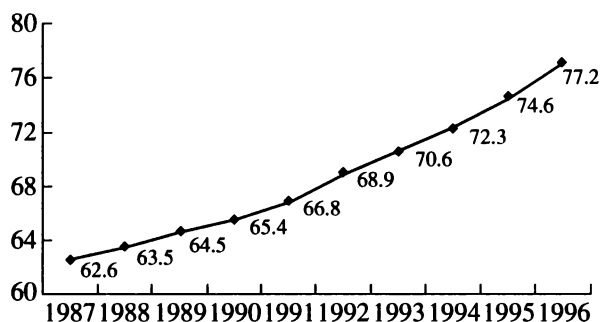


Fig. 5. Dynamics of AI between 1987 and 1996.

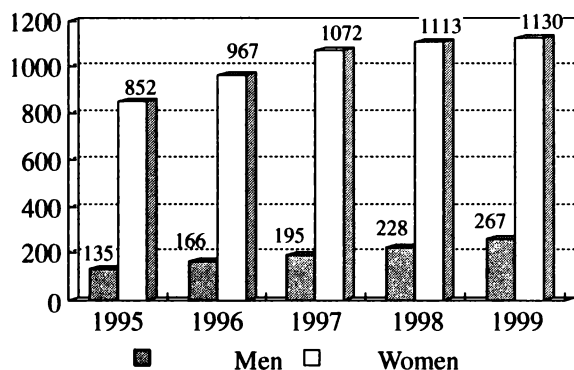


Fig. 6. Dynamics of the long-lived population in the Republic of Mari El over five years.

where $P_{(0-15)}$ is the number of children.

These calculations also show that the population "becomes old progressively" (Fig. 5). Finally, we obtained indices of growth of the long-lived population for the last five years (Fig. 6) and selectively determined the index of longevity (Nikitin and Tatarinova, 1998).

$LI = (\text{Number of people ninety years old and over} / \text{Number of people sixty years old and over}) \times 1000\%$.

To make our results comparable with the published data, we performed calculations using statistical material for 1995 and 1996. When numerical values were

substituted into the formula, we obtained LI values to 6.8 and 7.8%, respectively. On average, LI in different Russian regions varies from 6.1% to 10.2% (Nikitin and Tatarinova, 1998).

We determined the proportion of people whose age was over ninety years. For the territory of the republic, with a total population of 764 700 ind. and a long-lived population of 1133 ind., the value of this magnitude by 1996 comprised 0.15%, i.e., half of that in Georgia.

During recent decades, we have witnessed the unprecedented phenomenon of global population aging. Persons who live to an age of over 60 years comprise the most rapidly increasing population group. For a negligibly small evolutionary period, the average human life expectancy also increased. According to the UN data, the absolute number of elderly people has increased to 570 million by the year 2001 and will exceed 1100 million people (i.e., will increase almost two times) by 2025 (cited from Zdravomyslova *et al.*, 1999).

At first glance, this biological phenomenon contradicts traditional concepts and socially is regarded as a "demographic disaster." At the same time, Academician A.M. Ugolev (1985) justly noted: "Can we complain about Nature solely for the fact that it does not always follow the rules invented for it by the mind of scientists and prefers its own logic?" The perspectives of development of gerontology indicate that in the immediate future its advances will actually increase the species duration of human life (Anisimov, 2000). Hence, the group of long-lived individuals (people older than ninety years) will increase. This suggestion is supported by our studies on the territory of Republic of Mari El. They indicate that the dynamics of "population aging" in the abovementioned region has, in general, the same quantitative characteristics as in other historically "aged" countries. Therefore, it has become urgent to accumulate knowledge about population aging in large groups, i.e., on the population level.

In our opinion, it is expedient to study in a long-range perspective the stability of the existence of the elderly group in several aspects: (1) the population of elderly people (separately, of long-lived individuals) as an indicator of environmental health and an index of the stability of species (*Homo sapiens*) existence; (2) levels and specific features of the self-protective and nature-protective behavior of elderly people; (3) life quality of elderly people and possibilities for optimizing organization of their life activity; (4) morbidity of elderly people as an indicator of "pathology" of the environment and an index of the level of preventive health care and development of medical-diagnostic technologies in geriatrics; and (5) specific features of the reproductive behavior of elderly people and the extent of the risk of transfer of genetic disturbances from the aging organism to the progeny.

This list of problems is sufficient to acknowledge that the group of elderly people as a biological system

can be an object for ecological–population studies and a source for new concepts concerning the essence of aging as a global phenomenon.

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