

# Some Patterns of Spatial-Ontogenetic Structure in Populations of Tuber Orchids

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Received August 31, 2015; in final form, February 29, 2016

**Abstract**—Population dynamics, density, and aggregation size of tuberoid orchids have been identified based on mapping, electronic maps constructed with “point processes,” and Ripley function and pair-correlation function. Discrete and discrete-continuous types of spatial structure dominate in populations in optimal ecological conditions. The bounded aggregations of levels I (radius 0.45–0.75 m) and II (radius 1.2–2.5 m) are formed at 3 to 7.5 m<sup>2</sup>. The spatial pattern depends on generative specimens which are related with the “group effect.” The microloci have full ontogenetic structure and may be regarded as elemental populations. They form larger aggregations of levels III and IV with random spatial distribution and continuous bounds. Aggregations of higher level are not formed under worse ecological conditions. Random spatial distribution and incomplete ontogenetic spectrum of microloci are indicators of critical population status.

**Keywords:** Spatial–ontogenetic structure, microloci, aggregations, discrete and discrete–continuous types

**DOI:** 10.1134/S199542551605005X

## INTRODUCTION

One of the complex theoretical and practical problems of biodiversity conservation is the definition of “survival of the population of species in a state that ensures the preservation of its vitality and the possibility for the evolutionary formation of adaptations” (Soule, 1986). Assessing the stability of ecosystems based on a determination of the viability of “indicator,” or key, species that play the role of critical, limiting factors in ecosystems was proposed. According to Soule (1986), these species include environment-forming species determining the specifics of the composition and structure of ecosystems; mutualists species promoting the reproduction and expansion of other species; predators or parasites regulating the abundance of other species; species valuable for humans; and rare species, the diversity of which ensures the stable functioning of the community.

For the preservation of rare species of plants, one important aspect is determining the area within which the species can exist and develop long enough and a certain spatial pattern maintaining the stability of the population. However, the question about the patterns of the spatial structure of population is still poorly understood. The study of the spatial distribution of plants requires the use of special mathematical methods applied in foreign and domestic studies (Greig-Smith, 1961; Ripley, 1977; Galiano, 1982; Haase, 1995; Péliissier et al., 2001; Brzosko, 2002; Wiegand et al., 2007; Czarnecka, 2008; Dodd, 2011; Frey, 1967;

Vasilevich, 1969; Lyubarskii, 1976; Zaugolnova, 1994; Zhukov et al., 2006; Fardeeva et al., 2009).

Spatial distribution depends on external environmental conditions, but to a no less degree it also depends on the biological characteristics of the species (its propagation type, biomorph type, its size, nature and direction of shoot growth, vegetative mobility, etc.) and the status of the individuals (age and vitality) composing the population. Obviously, the spatial structure of populations of the species growing in different habitats differs in details, but it has the common specificity of species distribution in space, which is usually determined by the characteristics of its biomorph.

The concept of population patterns (mosaics) (Whittaker, Levin, 1977; *The mosaic-cycle...*, 1991) is based on a detailed study of the spatial structure of populations of plants and animals forming the spatial structure of communities. As Smirnova (2004) noted “unfortunately, in the publications devoted to population mosaics, there is no indication to the units of which rank this concept applies,” and she suggested that researchers consider population patterns as a characteristic trait of elemental populations. Elemental population, according to its definition, is the composition of many individuals of the same species that are required and sufficient for a steady stream of generations in the minimal possible space.

As we can see, the pattern of the spatial distribution of population elements, determined by endogenous

and exogenous environmental interactions (with different directions, intensities, and durations), offers the best retention and the use of the territory by the population, which is necessary for its relatively long existence in a particular biocoenosis. In this research we tried to answer several questions:

(i) what is the primary (or main) reason for the “pattern” of the spatial distribution of certain elements of the population—biological and ecological characteristics of the species and its life forms or ecological and phytocoenotic features of the habitat?

(ii) with which scale of the space will one or another reason dominate?

(iii) how will different ontogenetic groups be distributed in the space and which of them are the basis of the spatial “pattern”?

Consequently, the goal of this study was to identify common and specific features of the spatial ontogenetic structure of populations of tuberoid orchids for further monitoring. For this, the following issues were solved: (1) The features of the spatial distribution of individuals of different ontogenetic groups in different ecophytocoenotic and climatic conditions were analyzed; (2) patterns of the dynamics of the spatial structure of populations, their numbers, and density under the optimal, pessimal and critical growth conditions were determined; and (3) informative criteria of the state of tuberoid orchid populations based on identified patterns of spatial and ontogenetic structure were provided.

In order to answer these questions and carry out the goals and objectives of the research, it was necessary to consider the spatial structure not only as a spatial arrangement of all individuals of the population, but also as a hierarchical system of spatial mosaics (patterns) of different ontogenetic groups. Indeed, in the course of ontogenesis and morphogenesis of the individual, new morphological traits appear: the size of the plant increases and the underground and aboveground organs are transformed; in this case, individuals begin to occupy a bigger space, increase in biomass, become more able to compete, and sometimes acquire capability for vegetatively reproducing and over-growth.

In this case it is advisable to consider the spatial structure of the *spatial-ontogenetic* (or spatial age), by which we mean a hierarchical system of spaces of distribution of different ontogenetic groups.

## MATERIALS AND METHODS

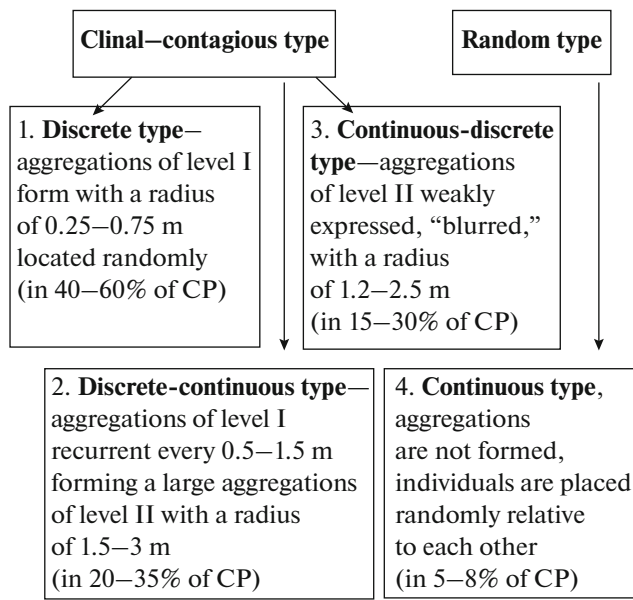
The algorithm of our research was as follows: the metapopulation was considered within the landscaped areas, the local population were determined within tracts, phytocoenotic population was determined within facies (Sochava 1979), and microloci or population loci were determined within microsite (microhabitat) (Naveh and Lieberman, 1984). The boundar-

ies of the local and phytocoenotic populations in vivo are continual and hardly definable, while population loci have small sizes of 1–10 m<sup>2</sup> and they can be identified and mapped. The scale of the dynamics of population loci is seasonal fluctuation, the scale of phytocoenotic and local populations is ontogenetic, and the scale of metapopulations is successive.

In the space occupied by the microlocus abiotic environment conditions, phyto-, zoo-, and anthropogenic factors remain more or less homogeneous and the spatial distribution of the species is determined mainly by endogenous factors, i.e., peculiarities of growth; reproduction; ontogenetic status of individuals; and, in general, by the life form of plant itself. The spatial-ontogenetic structure on a population locus level, within the boundaries of the microsite, is regarded as the microstructure, and the spatial structure of phytocoenotic populations or coenopopulations is regarded as the macrostructure of the population.

The study of spatial and ontogenetic structure of coenopopulations of tuberoid orchids was carried out based on the mapping of all ontogenetic groups of species within the boundaries of plots of 25–200 m<sup>2</sup>. The origin of coordinates for plots was selected as its southwest corner. From 1992 to 2012 more than 60 coenopopulations were studied. Cartographic and descriptive material was structured in the form of electronic population database (Fardeeva et al., 2013). For the characteristic of the point patterns of plant individuals and groups of plants with determined location, the Ripley K-function method of plotting was used (Ripley, 1977). Deviations of  $K(r)$  values calculated for the investigated point mosaics from  $K_{CSR}(r)$  values, anticipated for spatial randomness, allowed one to access the spatial clustering or regularity of the observed location of individuals for a given radius. The excess of  $K(r)$  function over  $K_{CSR}(r)$  indicates the determination of individuals to form clusters (aggregation); if the curve of the function  $K(r)$  is below  $K_{CSR}(r)$  values, it indicates the regularity of location of points or their sparsification. For the verification of the size of the clusters, the pair correlation function ( $PCF$ ), calculated based on Ripley  $K$ -function, was used (Wiegand and Moloney, 2004). Ripley  $K$  function and  $PCF$  were calculated in R medium using SPATSTAT package (Baddeley and Turner, 2005). The software used in the study was developed by N.A. Chizhikova at the Department of Ecological Systems Modeling of Institute of Ecology and Environmental Studies of Kazan Federal University.

Tuberous plants make up a combined group including herbaceous plants with aboveground and underground tubers on the stem, roots, stolons, and rhizomes (Zhmylev et al., 2005). The species that we studied—*Orchis militaris* L., *Neottianthe cucullata* (L.) Schlechter, *Platanthera bifolia* (L.) Rich., *Dactylorhiza incarnata* (L.) Soó, *Dactylorhiza fuchsii* (Druce) Soó,



**Fig. 1.** Types of spatial structure of populations of tuberoid orchids.

*Dactylorhiza maculata* (L.) Soó, and *Gymnadenia conopsea* (L.) R. Br.—have tubers of caulorrhizous origin: tuberooids (named by Dressler (1981)). The life form of such orchid species is defined as a geophyte (Raunkiaer, 1934), a tuberous rosellate perennial plant (Smirnov, 1990), and a vegetative annual plant with caulorrhizous tuberoid (Tatarenko, 1996; Vakhrameeva et al., 2008).

Original features of ontogenesis of orchids include the underground germination of seeds, their subsequent development into contact with the mycorrhizal fungus, and the formation of an underground shoot called a protocorm that develops underground for 2–4 years (Burgeff, 1932). Since seed reproduction is predominant in tuberoid orchids, their populations contain mainly genets. The specifics of the development of spatial organization of the vegetative body of tuberoid orchids has a monocentric type. Monocentric lifeforms include vegetative immobile and low vegetative mobile species—taproot plants, alliaceous and tuberous herbs, and most trees and caespitose plants characterized by one definite center of impact on the environment: the concentration of roots, shoots and reproduction buds resume (Smirnova et al., 1976).

Ontogenetic groups of orchids are defined mainly based on morphological traits: the size and number of leaves, number of veins, tuber size, the number of roots, the number of flowers and fruits, etc. There are the following ontogenetic groups: the prereproductive age group, juvenile (*j*), immature (*im*), and virginile (*v*); generative (*g*), subdivided into young (*g1*), mature (*g2*), and old *g3*; postgenerative, senile (*s*), which are extremely rare, since many orchids die immediately after the last flowering (Vakhrameeva et al., 2008).

The biological feature of tuberoid orchids is a “pendulum” type of shoot growth (Blinova, 1996, 2008). With the pendulum growth mechanism, a new shoot occupies the space of the former shoot after 2 years; i.e., the development of the whole system is associated with the same place in the plant community, practically unchanged during ontogeny. According to the assessment of resistance of plants to various anthropogenic factors, the investigated orchid species are sensitive (Vakhrameeva et al., 1997); according to the type of life strategy, they belong to stress-tolerant species and, sometimes, when competition become weaker, to stress-tolerant—reactive species.

## RESULTS AND DISCUSSION

Initially, for the analysis of the common patterns of spatial and ontogenetic structure of populations of *N. cucullata*, *D. incarnata*, *D. fuchsii*, *P. bifolia*, and *O. militaris*, once and multiple times mapped under different environmental conditions, the Ripley  $K(r)$  function was used. Ontogenetic (age) coenopopulations spectra (CP) of different species of tuberoid orchids were of the same type, with a high proportion of prereproductive individuals; their age structure included all age groups. This allowed to one perform a spatial analysis of different ontogenetic groups; their spatial arrangement relative to each other was considered: *j-im*; *j-v*; *j-g1*; *j-g2*; *j-s*; *im-v*; *im-g1*; *im-g2*; *im-s*; *v-g1*; *v-g2*; *g1-g2*.

A common feature of the spatial distribution of tuberoid orchids in the size of population of loci is the formation of expressed clusters: discrete microloci of level I with the radius of 0.2–1.2 m. Sometimes smaller discrete clusters of plants randomly distributed within the radius of 0.5–1.5 m formed large discrete aggregation of levels II–III with a radius of 1.5–3 (5) m. All possible combinations of prereproductive age groups in 100% cases form clusters, generative individuals, as well as the totality of individuals in 90% of cases have a *contagious* type of spatial structure. The spatial macrostructure of populations of tuberoid orchids generally have a *clinal-contagious* type, with an increase in the density of individuals upon a gradient of one or another environmental factor (humidity, lighting, etc.); random distribution was rarely observed and the microstructure of microloci has discrete, continuous–discrete, and discrete–continuous types (and rarely a continuum type) (Fig. 1).

For determining the patterns of spatial-age structure of CP, their habitats were subdivided into three groups: (1) *optimal*, where, due to the sparseness of vegetation, interspecific competition is reduced (low grass, sometimes alkaline meadows, forest edges and clearings, edges of swamps, and rarely calcareous slopes and areas after ground fire); (2) *pessimial*, where, due to demutational successions (forest and meadow restoration), competition of orchids with forest or meadow grasses increased, or habitats subjected

to periodic and minor human impacts (rare cattle driving, slope processes, etc.); and (3) *critical*, where ecocoenotic conditions radically changed as a result of the intensification of anthropogenic influences (grazing, recreation, soil erosion, haying, etc.). Pair-correlation function PCF was used for a more accurate assessment of sizes of aggregation of individuals in the CP of tuberoid orchids (Fig. 2).

Under optimal conditions, the studied species formed aggregates of different radii: from 0.45 to 0.75 m, with a maximal abundance in clusters up to 17–40 individuals (the average number was 4.3–19.5 individuals). Aggregations of level I may be recurrent every 0.5–1.5 m; they were randomly distributed in space and formed aggregations of level II with a radius reaching 2.5 m. This type of microstructure of population loci is defined as a discrete-continuum. If single individuals were present between aggregations, then undefined or “blurred” aggregations of level II were formed; this type of microstructure is characterized as continuous-discrete (Fig. 2).

Under pessimal conditions, sizes of aggregations of level I fell to 0.25–0.35 m, while the maximum number of plants reaches 4–8 individuals (the average number was 2.5–3.4 individuals). Aggregations of level II under pessimal conditions were formed rarely; discrete spatial microstructure prevails. In the total distribution of all the individuals of CP of *O. militaris*, *P. bifolia*, *D. fuchsia*, *D. incarnata*, and *N. cucullata*, low-density population loci (0.5–2.3 ind./m<sup>2</sup>) with a spatial structure characterized by a random type of distribution were rarely formed. It was noted in secondary communities, along forest edges, paths, clearings and traffic dumps and during years with unfavorable weather conditions, when a decrease in the abundance and the density of plants occurred and, probably, most individuals entered the secondary dormancy state.

The spatial distribution of prereproductive and reproductive age groups of individuals and their relative positions and the dynamics of their abundance and density under pessimal and optimal conditions are presented in more detail using *O. militaris* and *D. incarnate* as an example (Figs. 3 and 4).

Under critical conditions, in CP of *O. militaris* (during recreation or cattle driving, Fig. 3) and in CP of *D. incarnata* (upon constant grazing or haying, Fig. 4), there is a sharp decrease in sizes of aggregations of level I. Prereproductive age *O. militaris* individuals form aggregation with the radius of 0.2–0.3 m; for *D. incarnata* it is 0.25 m. Loci with low density with a radius reaching 2.5–3 m formed between aggregations of level I; i.e., microloci where either individuals were not present or single and distribution of small aggregations was random or sparse. Generative individuals in the CP of both species, due to the reduction of number and density, had random spatial distribution. The analysis of the mutual arrangement of the

reproductive and prereproductive age groups revealed a decrease in the size of the plant aggregations up to 0.2–0.5 m and the formation of discrete spatial microstructure. Large aggregations of level II were not formed.

Similar patterns of spatial–ontogenetic CP structures were identified for all the studied species.

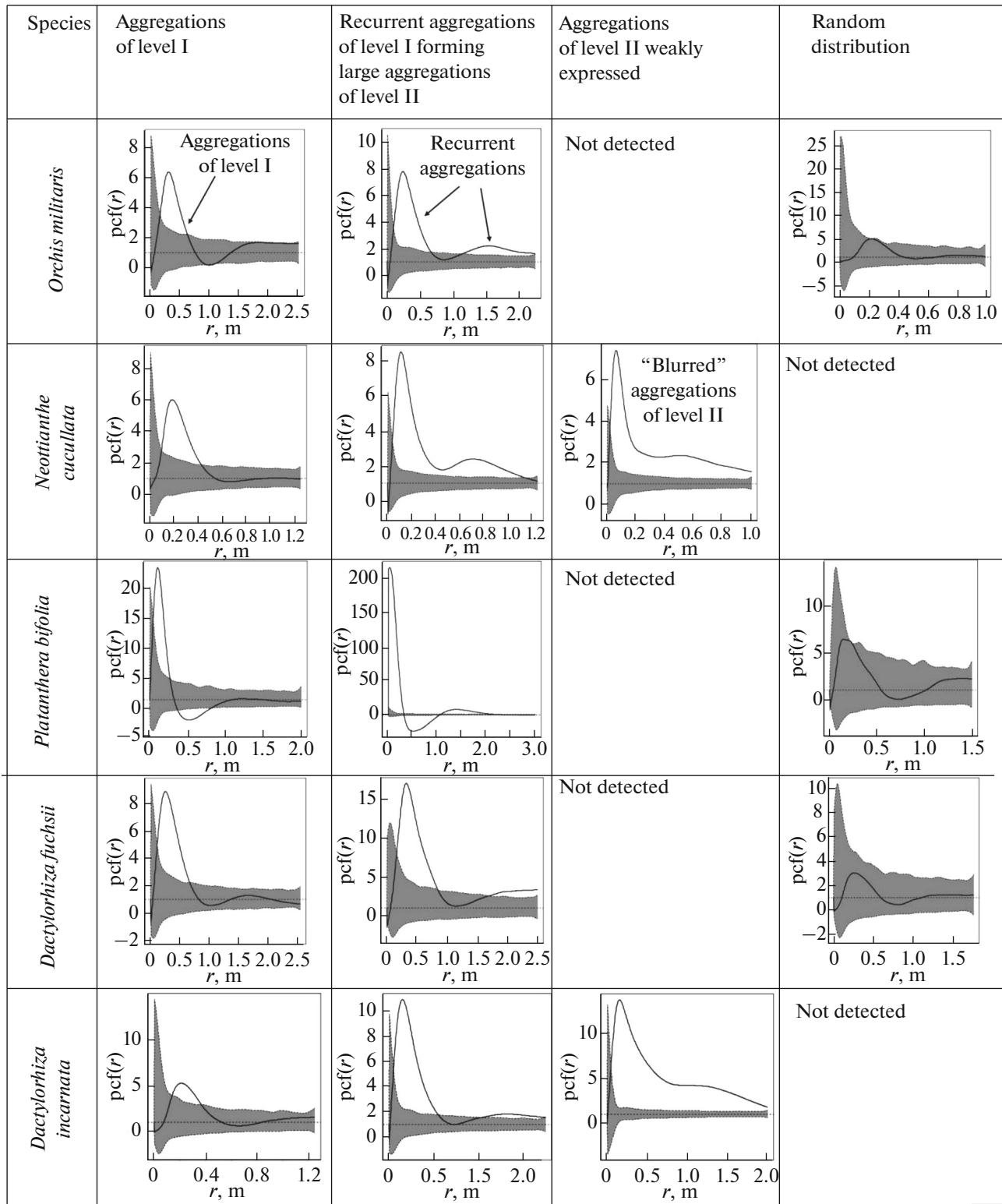
Studying the spatial–ontogenetic structure of CP of plants is impossible without an analysis of the density of individuals. While fluctuations of the abundance and density of populations of different species of orchids are significant, the nature of the oscillations are specific to one species biomorph and type of propagation. The type of spatial–ontogenetic structure (size, shape, and degree of discreteness or continuity of microloci) reflects the efficiency of resource utilization by plants under different ecological and phyto-cenotic, edaphic, and climatic conditions and contributes to the achievement of optimal abundance and density by the population under these conditions.

The average values of abundance are associated with an area of microloci of different radii by linear dependence: with increasing radius of the area, the abundance naturally increases; the abundance curve has smooth character. Maximal values of abundance abruptly increased; when the radius of the area increased the abundance curve was consecutive (Fig. 5).

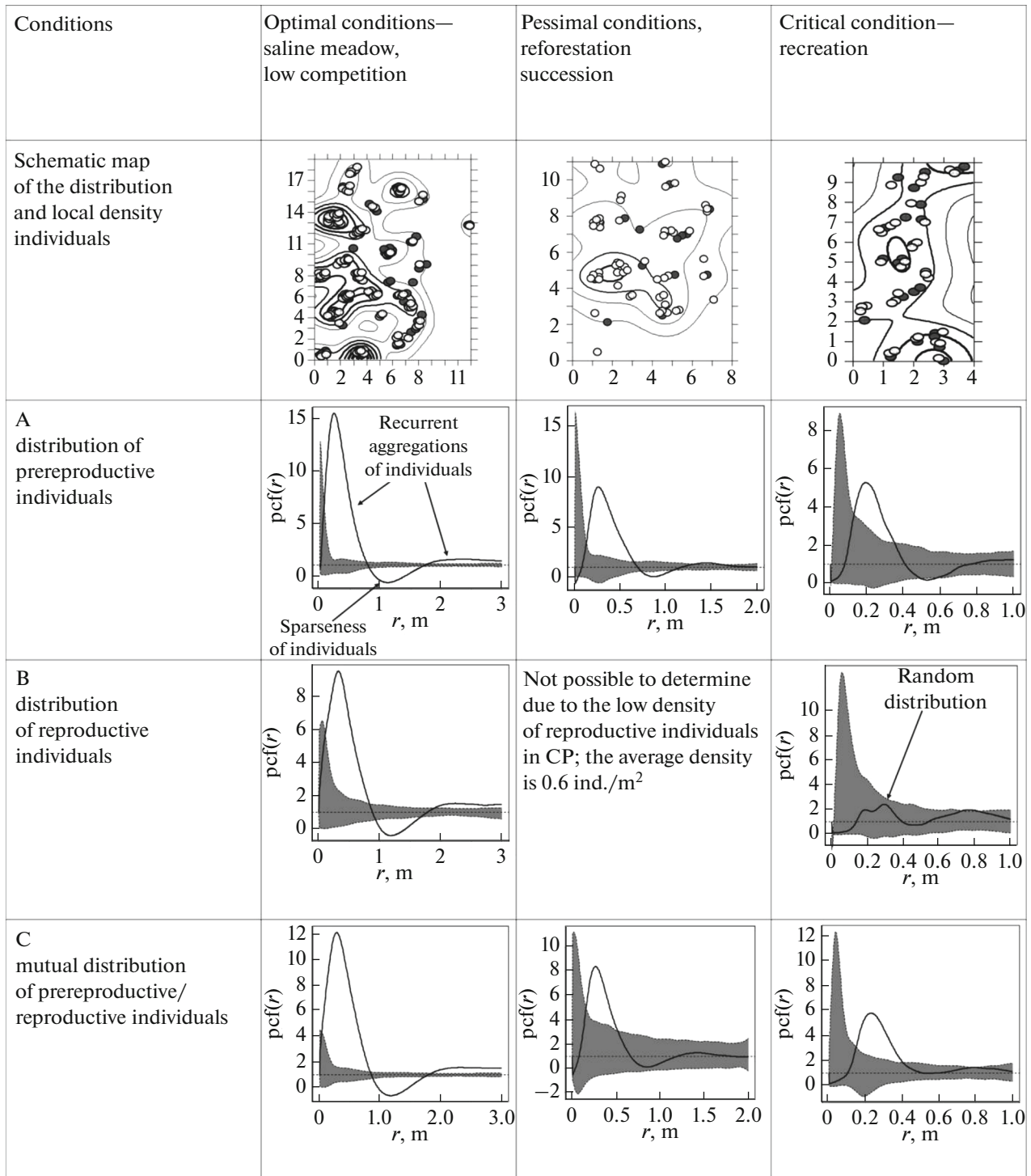
More precisely, the localization of plants, which is reflected by Ripley function and pair-correlation function, manifested when indicators of individual density was used. For areas with different radii, the difference of absolute density values was more significant than the difference of the absolute abundance values. Density values were inversely proportional to the radius of the area.

On the growth curve of maximal abundance shown in Fig. 5, structures with stable abundance, “steps,” correspond to microloci with low density, where the distribution of plants (the totality of individuals or different ontogenetic groups) was random (density varied from 0 to 3.5 ind./1 m<sup>2</sup>). On the other hand, the sharp “increases” in the abundance curve corresponded to the formation of local densities–aggregations. In comparison with microloci, where the distribution of individuals was random, in aggregations on the small area (0.2–1.77 m<sup>2</sup>, radius 0.25–0.75 m), the density increased 3–10 times (from 4.5 to 63.1 ind./1 m<sup>2</sup>). These areas of the local density with small radii formed discrete clusters, which were randomly placed and formed discrete-continuous spatial structure.

Under growth conditions optimal for the CP of orchids, the abundance and density of plants was 2–5 times higher than under pessimal and critical conditions (differences were significant at  $t_{\text{observ}} > 2.0$ ; level of significance was 0.90). Under optimal conditions, high density even in loci with a small radius was often determined by juvenile individuals, the irruption



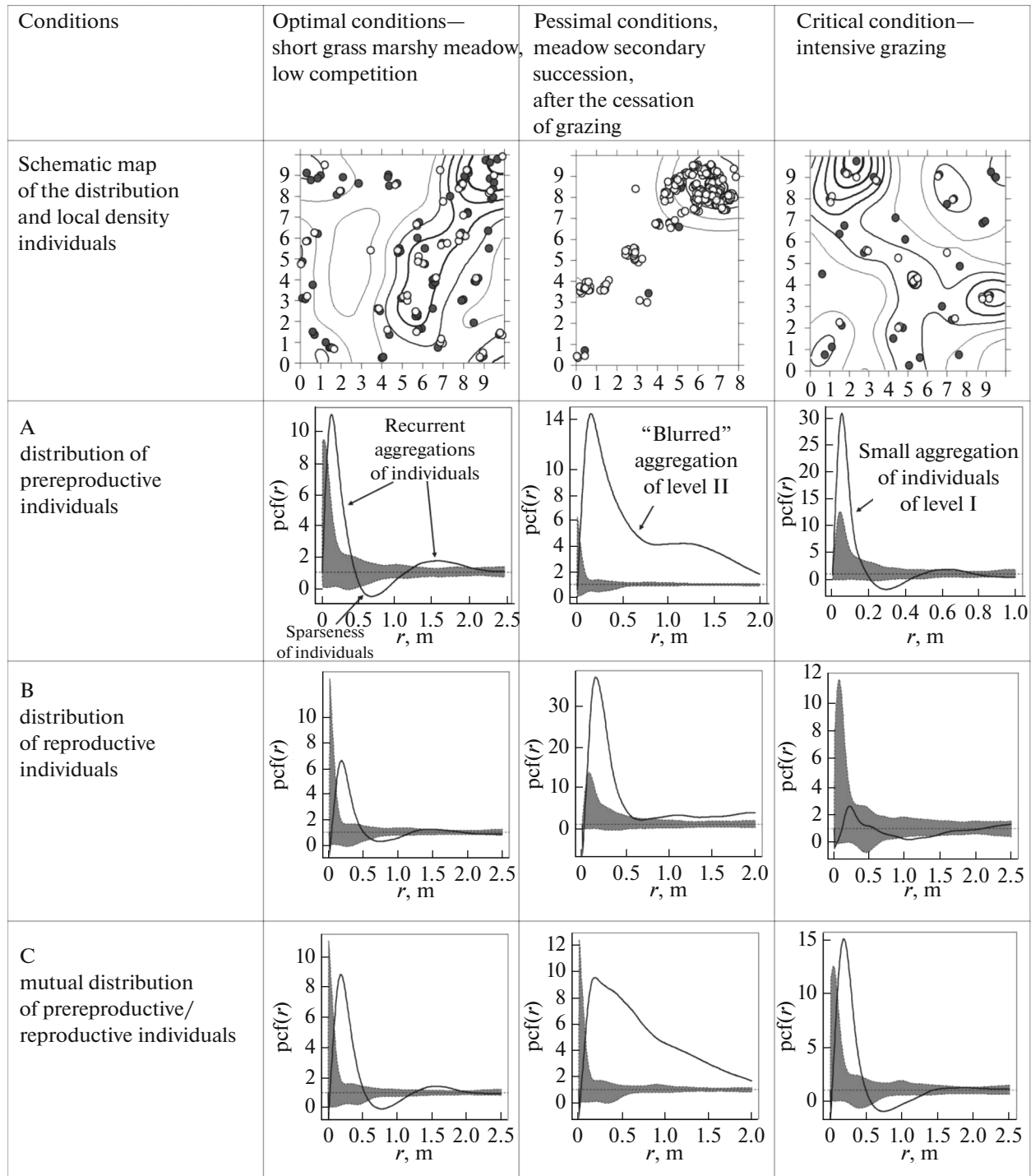
**Fig. 2.** Types of behavior of the correlation function (PCF) in CP of orchids for the mutual distribution of individuals without separation into ontogenetic groups on the  $x$  axis, radii in meters; on the  $y$  axis is the change of the function.



**Fig. 3.** Types of behavior of PCF function in CP of *O. militaris*: schematic maps of the local density of individuals of different ages (white dots are prereproductive-age individuals and black dots are reproductive-age individuals) and the relative distribution of individuals in space: **(A)** prereproductive-age individuals; **(B)** reproductive-age individuals; **(C)** reproductive- and prereproductive-age individuals; on the x axis are radii in meters and on the y axis is the change in PCF function.

of which periodically occurred. Under conditions of low interspecific competition, but under the limiting influence of abiotic factors (pessimal habitats), a high

density of individuals alongside a significant decrease in their size was detected in the CP. Thus, for the CP of *O. militaris*, *D. incarnata*, and *P. bifolia*, parameters

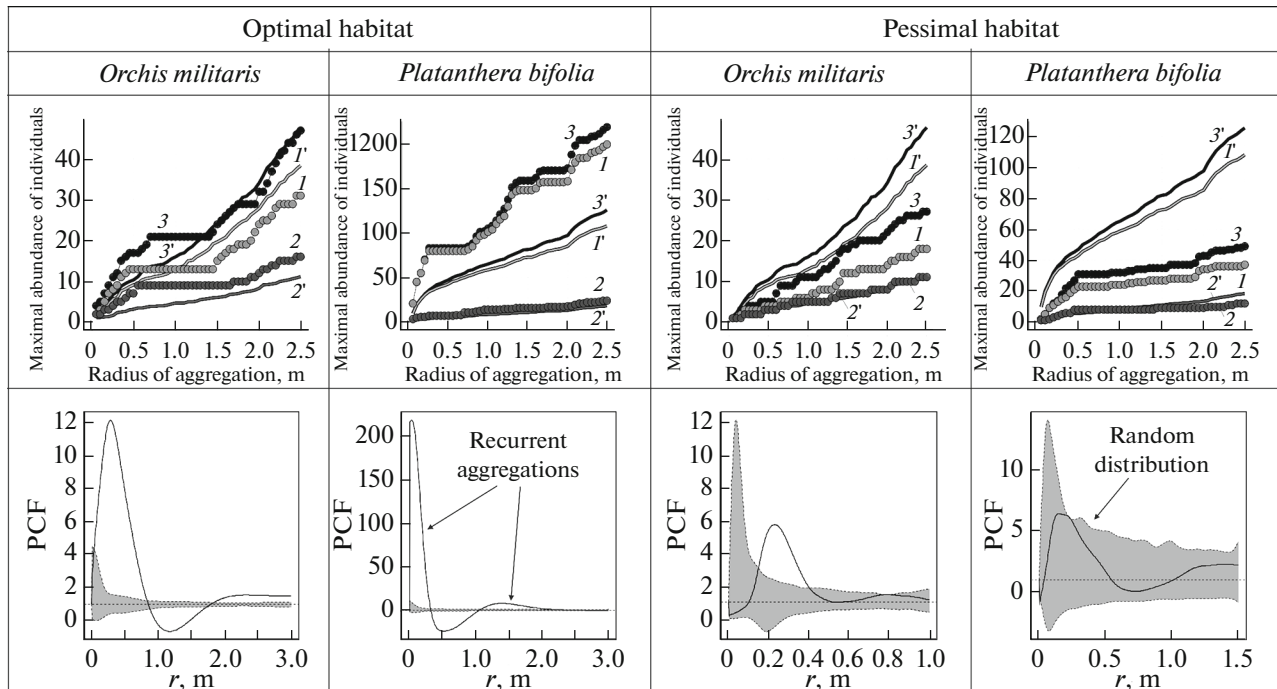


**Fig. 4.** Types of behavior of PCF function in CP of *D. incarnata*: schematic maps of the local density of individuals of different ages (white dots are prereproductive-age individuals and black dots are reproductive-age individuals) and the relative distribution of individuals in space: (A) prereproductive-age individuals, (B) reproductive-age individuals, and (C) reproductive- and prereproductive-age individuals; on the x axis are radii in meters and on the y axis is the change of PCF function.

such as the shoot length, raceme length, leaf area, and number of flowers decreased at high density values.

In general, the spatial structure of the CP of tuberoid orchids under optimal conditions had discrete or discrete–continuous types of spatial structure

with the formation of aggregations of level I (radius up to 1 m) and aggregations of level II—more rarely aggregations of level III (radius up to 2–5 m). Their complete ontogenetic (age) spectrum was detected mainly in the aggregations of level II, often limited



**Fig. 5.** Dynamics of the abundance and behavior of PCF function in CP of tuberoid orchids under optimal and pessimal conditions. Curves: (1, 1') prereproductive-age individuals; (2, 2') reproductive; (3, 3') all individuals. Thick lines show maximal density in specific habitats; thin lines show maximal average density for all the studied populations of the species.

within the radius of 1.5–3 m, with several expressed centers of high density of individuals. Aggregations of level I usually do not have complete ontogenetic structures; they are asynchronous in their development and reflect the different stages of the development of CP. The spatial “pattern” is defined mainly by generative individuals at a density of at least 2–4 ind./m<sup>2</sup>. The long-term localization of symbiotic fungi, playing an important role in the successful germination of seeds of tuberoid orchids, is associated with older plants (Tatarenko, 2007). The formation of aggregations where the “group effect” was exhibited and their random distribution in space increases the competitiveness of plants and ensures the successful existence of the species in the community within repetitive micro-loci.

Under pessimal and critical conditions, tuberoid orchids also form a discrete spatial structure, but the size of aggregations of level I decrease significantly and aggregations of level II are formed rarely and do not form under critical conditions; the age spectrum of the aggregations is not complete and often even aged. One characteristic feature is the reduction of the abundance of generative individuals in the first place. The deterioration of conditions and the decrease of plant density (up to 0.3–0.5 ind./m<sup>2</sup>) is accompanied by the random location of both generative individuals

and the totality of individuals, indicating the oppressed state of the CP.

Minimal areas of aggregations where all ages are represented were calculated based on the analysis of ontogenetic groups of plants in radii of different sizes. According to Zaugol'nova (1994), these “aggregations that have all age groups, steadily existing and providing a continuous cycle of generations on the occupied territory” could be called “the elemental demographic unit of the population,” or the elemental population. Data for areas occupied by the elemental population and its abundance for the studied species of orchids are presented in the table. The area of aggregations of tuberoid orchids that have all the age groups increases under pessimal conditions and under critical conditions; this area cannot be calculated due to the absence of certain age groups.

## CONCLUSIONS

Inside the microsite, the spatial structure of the CP of tuberoid orchids at the level of the microlocus of order I is determined by endogenous factors; at the level of the microlocus of order II it is defined by intra-specific competition or heterogeneity of the environments. In both cases the nature of the borders is discrete or continuous-discrete. Randomly distributed similar microloci form larger aggregations of levels III and IV with mainly continual borders, determined by



Average size of the area occupied by the elemental population and its abundance of some species of tuberoid orchids

Species	<i>Orchis militaris</i>	<i>Neottianthe cucullata</i>	<i>Platanthera bifolia</i>	<i>Dactylorhiza fuchsii</i>	<i>Dactylorhiza incarnata</i>	<i>Gymnadenia conopsea</i>
Area of CP, m <sup>2</sup>	5.9–7.06	2.9–4.3	5.5–7.3	3.5–7.4	3.3–6.8	4.3–7.06
Average/maximal abundance	9.9/36	17.8/87	8.9/63	11.3/22	15.1/47	9.1/30

abiotic environmental factors and interspecific relations. The formation of aggregations of levels I and II that are quite clearly limited in space is the main regularity of the spatial structure of tuberoid orchids detected in microloci of 3–7.5 m<sup>2</sup>. If the spatial distribution of individuals on such area becomes random, it indicates the critical status of the population. Such a discrete-continuous type of spatial microstructure of populations of tuberoid orchids is due to their biological features: a symbiosis with mycorrhizal fungi, which, probably, is characterized by spotty distribution; a small radius of dissemination and germination of seeds only in the presence of fungi (mainly near the generative individuals); a small size of individuals; pendulum type of growth of underground shoots; and practically nonexistent vegetative propagation. The “group effect” which occurs in such a microstructure increases the competitiveness of plants by the creation of special microconditions; the protection of prereproductive individuals may contribute to the maximal concentration of symbiotrophic fungi around the maternal plant and ensures the presence of all age groups. In general, the spatial–ontogenetic structure of populations is species-specific and, by analogy with developmental (age) spectrum, corresponds to the biological and ecological characteristics of the species. The structure has wide diagnostic capabilities and can be used for the analysis of populations of plant species with a similar type of ontogeny, life forms, strategies, propagation, and mechanism of the spatial growth of shoots.

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*Translated by V. Mittova*