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EXPERIMENTAL ARTICLES

Seasonal Dynamics of the Structure of Epiphytic Yeast Communities

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Abstract—The seasonal dynamics of the species structure of epiphytic yeasts on the leaves and in the flowers of 25 plant species was studied throughout the period of their vegetation. It was shown that, on average for the vegetation period, the composition of epiphytic yeast communities was nonspecific. The same species of epiphytic yeasts dominated on different plant species, irrespective of their taxonomic identity and ecological peculiarities. However, different species of yeasts exhibited different types of seasonal dynamics of relative abundance. Therefore, a combination of the dynamics of yeast species and the ontogenetic cycles of plants creates a pattern of the dynamics of the epiphytic yeast population, which is unique for each plant species. The species diversity of yeasts on the leaves of a plant is determined by the duration of its ontogenetic cycle: the longer the vegetation of a plant, the higher the diversity of the epiphytic yeasts population. The greatest diversity of epiphytic yeasts was revealed on the leaves of perennial hygrophytes and mesophytes; the minimal diversity, on ephemeroids and annuals with a short ontogenetic cycle.

Keywords: yeasts, phyllosphere, flowers, epiphytic microorganisms, seasonal dynamics.

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The community of epiphytic microorganisms is an inalienable part of any plant. Among the epiphytes inhabiting the plant surface, the yeasts account for a considerable part. The first studies of epiphytic yeasts showed that they are represented by many species [1, 2]. It was established in the series of the subsequent works [3–6] that basidiomycete yeasts predominate on the plant leaves in the temperate zone. The main share among them is accounted for by filobasidial and tremellous cryptococci (*Cryptococcus albidus, Cr. laurentii*), red-pigmented *Rhodotorula* species (*Rh. glutinis, Rh. mucilaginosa*), and ballistospore yeasts (*Sporobolomyces roseus*). Among the ascomycete yeasts, the anamorphous species of the genus *Candida* from the metschnikowian and debaryomycetous clades are the most abundant in the phyllosphere.

The yeasts are especially abundant in phyllosphere-associated substrates characterized by a high sugar content, especially in nectar-yielding flowers and juicy fruits [7]. Unlike the case of leaves, ascomycetous yeasts usually dominate here, especially such species as *Metschnikowia pulcherrima, M. reukaufii, Hanseniaspora* spp., etc. These species are also closely connected with pollinator insects. In the period of mass flowering, their number in the floral nectar may reach 10^6 cells/ml substrate.

At the same time, the peculiarities of the ecology of epiphytic yeasts are not understood in great detail, although such knowledge is required for developing methods of biocontrol of phytopathogens, in which yeasts have been increasingly used in recent years [8], as well as for more effective screening of yeast strains that may be of value for biotechnology. One of the issues that is still unclear is how specific the yeast population of different plant species is. It is logical to suggest such specificity resulting from the physiological and anatomical peculiarities of different plants, the qualitative composition and the amount of the surface exudates secreted, and the presence of specific volatile production. The specificity of the yeast populations of different plant species was postulated long ago [9], and rather different lists of epiphytic yeast species were provided in the previous studies of the yeast population of the phyllosphere. However, these differences are not, as a rule, statistically significant, and repeated analyses does not reproduce them. This results from the episodic character of such investigations: they are usually based on occasional collection of a small number of samples, usually in summer and autumn, which does not allow the high spatiotemporal variability of the yeast communities to be taken into account. In several works, the epiphytic yeast communities have been analyzed with a periodicity of several months [3, 4, 10, 11]. No year-round studies with frequent and regular sampling and analyzing of the samples were conducted.

Data on how the epiphytic yeast complex changes during the vegetation period are virtually nonexistent. That the share of different yeast species should substantially vary in the course of plant ontogenesis may also be predicted due to significant changes in the environmental factors, which influence the phyllosphere development. In addition, plants undergo sig-

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nificant restructuring in the course of ontogenesis, which may affect any change in the composition and amount of the exudates secreted by them.

We therefore conducted the study of yeast communities on the leaves of plants of different ecological groups in dynamics throughout the whole year, beginning with primordial leaf buds and ending with the senile phase of ontogenesis, as well as in related substrates (flowers and tree litter). In a previous communication, we presented the results of a study of the dynamics of the total number of yeasts in the phyllosphere [12]. We found regular variations in the total number of yeasts on plant leaves during the year. In the process, the character of the dynamics of the yeast number depended on the ecological characteristics of the plants and the duration of ontogenesis of their aerial organs.

In this communication, we considered the specific features of the dynamics of the species structure of the epiphytic yeast communities. The main questions we tried to answer were how does the species diversity of yeasts change on plant substrates during the year and what is the specificity of the yeast populations on plants from different ecological and taxonomic groups?

MATERIALS AND METHODS

The studies were conducted in 2001–2006 on the territory of Moscow: in Losinyi Ostrov National Park, in Izmailovskii Park, and in the neighborhood of the town of Burtsevo, Shakhovskoi raion, Moscow oblast. The plant material was collected in two types of biogeocenoses: mixed spruce–birch forest and secondary after-forest meadow on medium-loam sod–podzolic soils. Twenty-five plant species were selected as the study subjects. They are representatives of different living forms, characterized by significantly differing rhythms and types of the ontogenetic cycles of development of the phyllosphere and related substrates, with duration varying for different plant species from 4 to 12 months. The list of plants and their characteristics was given in our previous work [12].

The phyllosphere of the plants was analyzed throughout the whole short life cycle, beginning with primordial leaf buds and ending with moribund leaves in the litter. The flowers were studied beginning with the buds, including the time of active blooming, withering, and fructification. All the material was sampled two or three times a week. The platings were carried out on the day of sampling or in the following two to three days. A total of 7000 samples of plant substrates were analyzed during the study. For yeast enumeration, the leaves, flowers, and plant residues were ground; five to ten weighed portions were taken from each sample, supplemented with sterile water to obtain a 1 : 50 dilution, and shaken on a Vortex for 10 min. Glucose–peptone medium (glucose, 20 g/l; peptone, 10 g/l; yeast extract, 5 g/l) acidified with lactic acid to pH 4–4.5 to prevent bacterial growth was used. Each weighed portion was used for inoculation in two repeats. The inocula were incubated at room temperature for 5–7 days. Using a binocular loupe, the grown yeast colonies were grouped into morphological types, which were counted separately. Two or three strains of each type of colony were isolated into pure culture. The collection obtained was differentiated into species by the standard set of morphological and physiological characteristics [13] using an extended physiological spectrum [14]. All the necessary physiological tests were carried out according to the standard methods using special Difco media. The characteristics of all yeast species described to date have been considered for the identification.

The final identification was carried out using analysis of the rDNA ITS1-5.8S-ITS2 and D1/D2 nucleotide sequences. The amplification of the 26S rDNA ITS1-5.8S-ITS2 region or D1/D2 domain was carried out using the primers ITS1f (5'-CTTGGTCATTTAGAGGAAGTA) and NL4 (5'-GGTCCGTGTTTCAAGACGG). The PCR product was purified with the BigDye XTerminator Purification Kit (Applied Biosystems, United States). The primer NL4 was used for sequencing. DNA sequencing was carried out with the BigDye Terminator V3.1 Cycle Sequencing Kit of reagents (Applied Biosystems, United States) with subsequent analysis of the reaction products on an Applied Biosystems 3130 × 1 Genetic Analyzer sequencer at NPO Sintol (Moscow). The yeast sequences obtained in the course of this work were deposited in the EMBL-EBI and NCBI databases.

The total number of yeasts expressed in colony-forming units per gram of dry matter (CFU/g) and the share of each species in relation to the total number of yeasts, as well as the rate of occurrence of each species, were determined for each sample analyzed using the data obtained.

RESULTS AND DISCUSSION

A total of 64 species of yeasts were isolated from the phyllosphere and related substrates in the course of the work (Table 1). However, most of the species were the minor ones, whose occurrence did not exceed 0.5%. Many of the yeast species dominating on the leaves of the plants analyzed have been repeatedly revealed in the phyllosphere earlier. Among them, there were such species as *Cryptococcus albidus, Cr. laurentii, Rhodotorula glutinis, Rh. mucilaginosa*, and *Sporobolomyces roseus*. In recent years, these species have repeatedly been subjected to taxonomic revision, resulting in description of a number of new independent species, mainly on the basis of molecular genetic criteria. As a result, they are presently considered as the names of the supraspecies complexes (sensu lato) combining several phenotypically similar independent species, including the initial species with the same name (sensu stricto). Nevertheless, no statistically significant and

Table 1. List of the isolated yeast species and their relative abundance values

Species	Rate of occurrence*, %	Average ratio**, %	Probability of dominance***, %
Bulleromyces albus Boekhout et Fonseca	0.09	0.034	0.04
Candida bombi Montrocher (FN667838)	0.14	0.107	0.11
Candida friedrichii van Uden et Windisch (FN667839)	0.36	0.526	0.43
***Candida oleophila* Montrocher** (FN667840)	6.39	5.527	5.10
***Candida oregonensis* Phaff et do CarmoSousa** (FN667841)	0.03	0.009	0.00
Candida parapsilosis (Ashford) Langeron et Talice (FN667842)	0.06	0.085	0.07
Candida saitoana Nakase et Suzuki (FN667843)	0.01	0.001	0.00
Candida spp. (11 unidentified species)	0.05	0.173	0.00
Candida zeylanoides (Castellani) Langeron et Guerra (FN667844)	0.03	0.043	0.04
***Cryptococcus albidus* (Saito) Skinner** (FN667845)	6.47	5.795	5.98
Cryptococcus diffluens (Ruinen) von Arx et Weijman (FN667846)	0.11	0.130	0.11
Cryptococcus flavus (Saito) Phaff et Fell	0.01	0.001	0.00
***Cryptococcus laurentii* (Kufferath) Skinner**	0.93	0.575	0.61
***Cryptococcus macerans* (Frederiksen) Phaff et Fell** (FN667847)	0.47	0.100	0.05
***Cryptococcus magnus* (Lodder et Kregervan Rij) Baptist et Kurtzman** (FN667848)	38.69	33.473	34.52
***Cryptococcus podzolicus* (Bab'eva et Reshetova) Golubev** (FN667849)	0.99	0.934	0.98
Cryptococcus sp. 1	0.1	0.110	0.12
Cryptococcus sp. 2	0.06	0.021	0.04
***Cryptococcus terricola* Pedersen** (FN667850)	0.99	0.697	0.77
***Cryptococcus victoriae* Montes et al.** (FN667851)	4.82	4.036	4.20
Cryptococcus wieringae Fonseca et al. (FN667852)	0.56	0.241	0.29
***Cystofilobasidium capitatum* (Fell et al.) Oberwinkler et Bandoni** (FN667853)	3.12	1.080	1.03
Cystofilobasidium infirmominiatum (Fell et al.) Hamamoto et al. (FN667854)	0.01	0.001	0.00
Cystofilobasidium sp.	0.03	0.043	0.04
***Debaryomyces hansenii* (Zopf) Lodder et Kreger-van Rij** (FN667855)	7.87	6.958	6.51
Galactomyces geotrichum (Butler et Petersen) Redhead et Malloch	0.1	0.049	0.04
Guehomyces pullulans (Lindner) Diddens et Lodder (FN668004)	0.5	0.377	0.35
***Hanseniaspora uvarum* (Niehaus) Shehata et al.** (FN667856)	1.19	0.873	0.79
***Kazachstania barnettii* (Vaughan-Martini) Kurtzman** (FN667857)	1.06	0.953	0.86
***Leucosporidium scottii* Fell et al.** (FN667858)	1.26	0.757	0.76
Metschnikowia gruessii Giménez-Jurado (FN667859)	0.06	0.083	0.07
***Metschnikowia pulcherrima* Pitt et Miller**	3.63	2.599	2.43
***Metschnikowia reukaufii* Pitt et Miller** (FN667860)	3.88	2.816	2.47
Mrakia frigida (Fell et al.) Yamada et Komagata (FN667861)	0.03	0.003	0.00
Nadsonia elongata (Nadson et Konokotina) Sydow	0.01	0.021	0.01
Pichia galeiformis (Endo et Goto) Goto et al. (FN667992)	0.17	0.171	0.16
Pichia guilliermondii Pijper (FN667993)	0.21	0.127	0.16
Pichia kluyveri Bedford (FN667994)	0.1	0.074	0.07
Pichia membranifaciens (Lodder et Kregervan Rij) Wickerham et Burton (FN667995)	0.11	0.074	0.07
***Rhodotorula fujisanensis* (Soneda) Johnson et Phaff** (FN667996)	1.06	0.612	0.56
Rhodotorula glutinis **(Fresenius) Harrison**	6.35	2.895	2.83
Rhodotorula graminis di Menna	0.21	0.048	0.07
Rhodotorula hinnulea (Shivas et Rodrigues de Miranda) Rodrigues de Miranda et Weijman	0.1	0.013	0.00

Table 1. (Contd.)

Species	Rate of occurrence*, %	Average ratio**, %	Probability of dominance***, %
Rhodotorula ingeniosa (di Menna) von Arx et Weijman	0.04	0.030	0.04
***Rhodotorula minuta* (Saito) Harrison**	2.22	1.034	0.92
***Rhodotorula mucilaginosa* (Jorgensen) Harrison** (FN667997)	34.02	19.945	20.82
Rhodotorula pinicola Bai et al. (FN667998)	0.06	0.028	0.04
Rhodotorula sp. 1	0.07	0.009	0.00
***Saccharomyces paradoxus* Bachinskaya** (FN667999)	0.63	0.575	0.55
***Sporobolomyces roseus* Kluyver et van Niel** (FN668000)	9.37	4.531	4.24
Starmerella bombicola Rosa et Lachance (FN668001)	0.06	0.071	0.07
***Torulaspora delbrueckii* (Lindner) Lindner** (FN668002)	0.6	0.365	0.35
***Trichosporon laibachii* (Windisch) Guého et Smith** (FN668003)	0.27	0.118	0.19
Wickerhamomyces anomalus (Hansen) Kurtzman et al. (FN668005)	0.07	0.046	0.05

Notes: The species whose relative abundance significantly depends on the season or the type of substrate are indicated by boldface. The numbers of the sequences deposited in the EMBL-EBI and NCBI databases are indicated in brackets.

* The share of the samples in which the species was revealed in relation to the total number of the samples analyzed.

** The average ratio of the total number of yeast in a sample.

*** The share of the samples in which the species was revealed as the predominant one in relation to the total number of the samples analyzed.

reproducible data showing the confinement of most such new, more homogeneous species to specific habitats have been obtained so far. Moreover, most of them have been described based on a small sample of strains or even individual strains. Further investigations will probably make it possible to reveal the patterns of their distribution; however, considering the low rate of occurrence of most of these elementary species, this will require significantly larger data arrays. Our many years of studies showed that each of the superspecies complexes was mainly represented in the phyllosphere by one or two species. Thus, within the *Cryptococcus albidus* complex *Cr. albidus* sensu stricto and *Cr. wieringae* were found most often; within the *Cr. laurentii* complex, *Cr. laurentii* sensu stricto and *Cr. victoriae* were common (see Table 1).

The factor analysis of variance was used for quantitative assessment of the dependence of the relative abundance of different yeast species on the substrate type (living leaves, litter, flowers, fruits), the plant species, and the annual cycle period (the months of collection). Its results showed that only 25 yeast species (bold-typed in Table 1) revealed significant dependence (at $p < 0.5$) on at least one of the factors considered. These species constitute, on average, over 90% of the total number of the epiphytic yeast population. Given a sufficient number of samples, they may be isolated from practically any plant. No yeast species significantly confined only to certain plant species were revealed.

The species the relative abundance of which significantly depends on the season and related changes in the hydrothermal regimen constituted the most numerous group. Among them, the "autumn to winter" and "summer to autumn" species whose peaks of relative abundance are noted in the autumn–winter and summer periods, respectively, may be singled out (Fig. 1). As a rule, these species are also confined to certain types of substrates. These seasonal–substrate species constitute the majority of epiphytic yeast species. Importantly, the peaks of relative abundance for different species do not coincide. This can be interpreted in the sense that these yeast species are not purely nominal and are not arbitrary, but actually correspond to the species level of organization at which specific regularities, in particular, the rule of the ecological individuality of a species, operate.

At the same time, for certain species, the relative abundance value mainly depended on a certain substrate type and practically did not change throughout the year. Such species include *Rhodotorula mucilaginosa* and *Cryptococcus albidus*, which appeared to be confined to living leaves. *R. mucilaginosa* was also regularly isolated from the decomposing plant substrates.

The overall species diversity of the epiphytic yeast communities also changed regularly during the year (Fig. 2). The Shannon's diversity index was calculated for each sample analyzed. The Shannon's index average values on the leaves and flowers increased gradu-

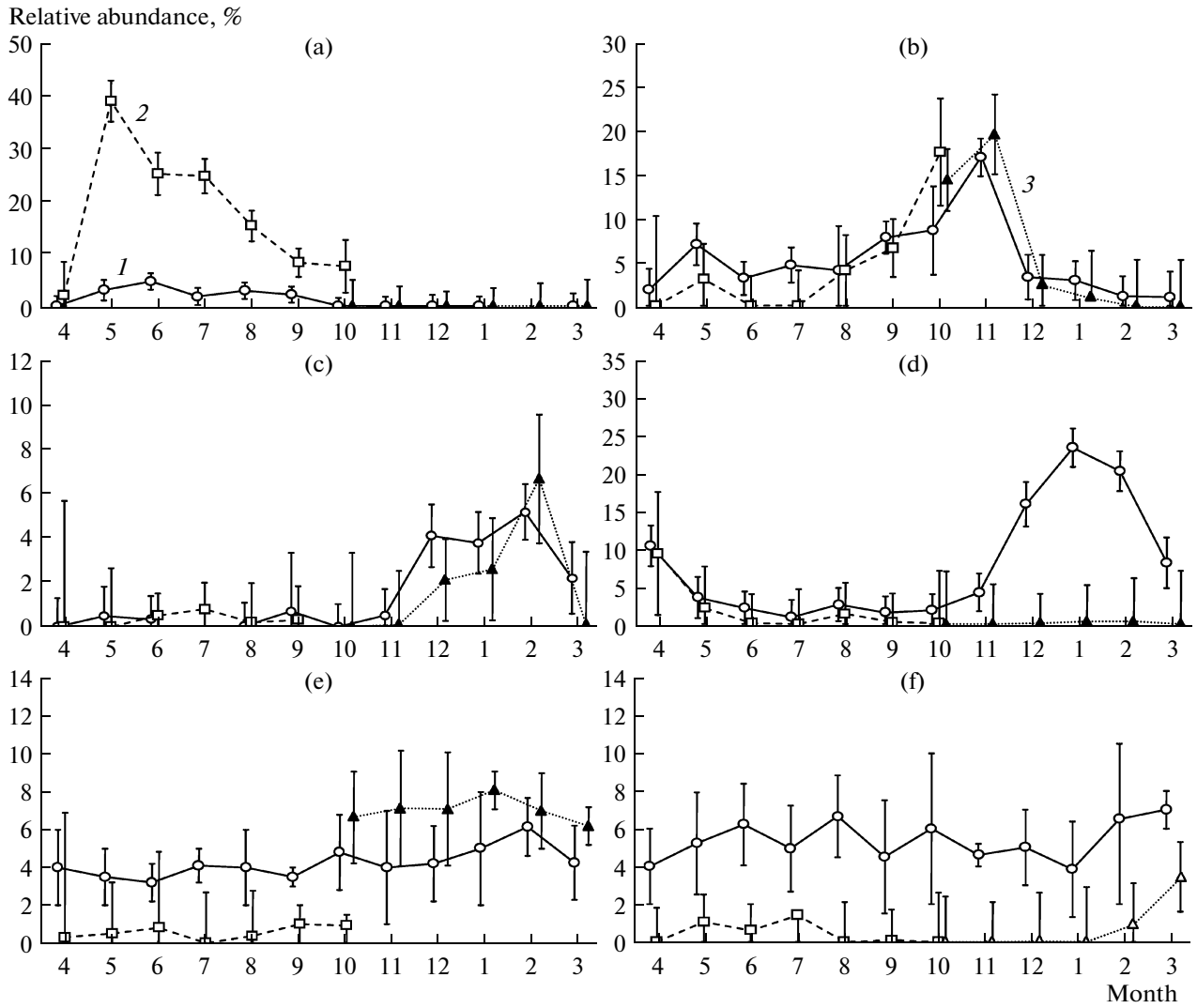

Fig. 1. Dynamics of the average monthly values of relative abundance of different species of epiphytic yeasts; substrates: living leaves (*1*), flowers (*2*), litter (*3*); *Metschnikowia reukaufii* (a), *Candida oleophila* (b), *Kazachstania barnettii* (c), the *Cryptococcus laurentii/Cr. victoriae complex* (d), *Rhodotorula mucilaginosa* (e) *Cryptococcus albidus* (f).

ally from the beginning of the vegetation period and reached the maximum at the end of autumn. During the winter, the diversity of the yeast groupings on the leaves and in the litter decreased again. The greater number and diversity of epiphytic yeasts in autumn were reported earlier [10, 15, 16].

During the year, the ascomycetous to basidiomycetous yeast ratio on the plant leaves and flowers changed significantly (Fig. 3). The share of ascomycetous yeasts on the leaves gradually increased from the beginning of the vegetation period and reached a maximum in autumn. In winter, the relative abundance of ascomycetes decreased. In fresh litter, the share of ascomycetous species was approximately the same as on the leaves. The highest ratio of ascomycetous yeasts was noted in nectar-yielding flowers, where they were predominantly represented by the species of the genus *Metschnikowia*. In summer, in the period of mass blooming, the share of these species in the flowers dramatically increased and sometimes exceeded 50%.

Earlier, it was repeatedly suggested that different plant species, due to their specific physiological peculiarities, differences in the composition of secreted volatile production, alkaloids, surface exudates, etc., should be characterized by a different composition of epiphytic yeasts [9]. However, no serious statistical confirmation has been obtained as yet. As a rule, works on the study of the taxonomic composition of epiphytic microorganisms on different plant species have been sporadic and had a limited number of replicates. Therefore, due to the substantial spatial and temporal variability of the yeast communities, the attempts to obtain valid results were not successful. Having analyzed about 7000 samples of 25 plant species for five

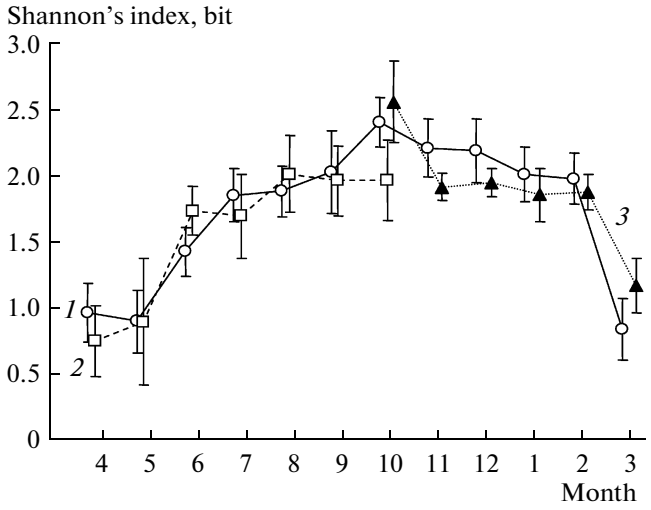

Fig. 2. Dynamics of the average monthly values of the index of diversity of the epiphytic yeast communities; *1–3* as in Fig. 1.

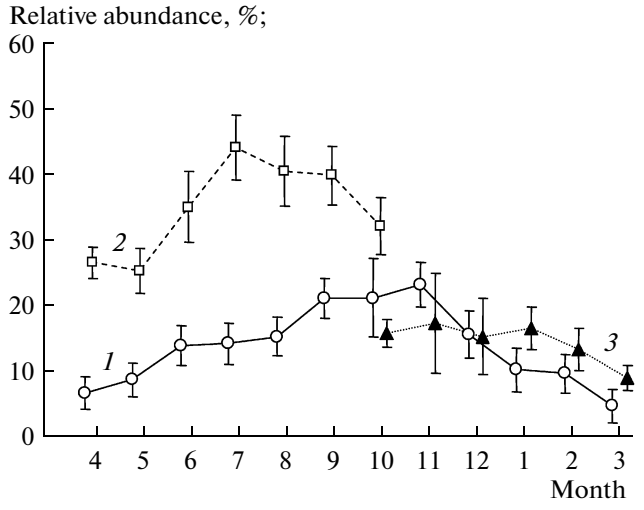

Fig. 3. Dynamics of the average monthly values of relative abundance of the ascomycetous yeasts; *1–3* as in Fig. 1.

years, we obtained significant data, which show that the epiphytic yeast communities of different plant species are, on average, very similar in both the species composition and the ratio of the average abundance of the predominant species if they are to be assessed during the whole period of ontogenesis (Table 2).

The absence of significant differences in the species structure of the yeast population of different plant species, if considered, on average, during the whole period, is well illustrated by the results of the discriminant analysis. It showed that the relative abundance of the predominant species of epiphytic yeasts was very similar for different plant species. Despite the fact that certain leaf samples in certain terms of analysis may differ significantly, most samples are very similar, which is evidenced by considerable overlapping of the correlation ellipses (Fig. 4).

However, the pattern of changes in the ratio of different yeast species on the plant surface throughout the ontogenesis period appears to be specific for each plant species (Figs. 5, 6). This possibly results from the fact that each yeast species is characterized by a unique annual dynamics and each plant species, in its turn, by the specific features of ontogenesis.

With a similarity between the composition of the dominants, the number of minor species, which are isolated from one plant species, may differ significantly. The total number of epiphytic yeast species, which can be revealed on one or another plant, is primarily determined by the duration of its ontogenesis, as well as by the ecological group it belongs to (Fig. 7). We succeeded in revealing the greatest diversity of epiphytic yeasts on the leaves of summer and winter green hygrophytes and mesophytes, for example, *Oxalis acetosella* and *Dactylis glomerata* and the the minimal diversity on ephemeroids and annuals with a short ontogenetic cycle, such as *Ficaria verna* and *Impatiens noli-tangere*.

The data obtained suggest some conclusions about the peculiarities of the epiphytic yeast population and the character of its seasonal dynamics. In the temperate zone, the species of epiphytic yeasts closely associated with certain plant species seem to be absent. The number of different yeast species mainly depends on the hydrothermal conditions and the ontogenetic stage of development of a specific plant but correlates weakly with its taxonomic position. On average per year, the composition of the dominant species of epiphytic yeasts on different plant species appears to be approximately the same and their general diversity depends on the time of the phyllosphere existence. The number of most yeast species undergoes substantial seasonal variations. We suggest that such a situation is primarily determined by the climate of the temperate zone with markedly pronounced seasonality and considerable differences in the temperature–humidity regimen between different seasons. Under such conditions, the yeast species that possess wide adaptive possibilities and are weakly specialized gain an advantage.

The plants of the temperate zone, in spite of all their individual distinctions, are classified into a limited number of morphophysiological and ontogenetic types. Among them, there are virtually no species creating sharply specific conditions for the epiphytic microorganisms developing on them. This explains the high degree of unification of the structure of yeast communities on different species of plants.

At the same time, it was shown in a number of studies conducted in different tropical and subtropical regions that certain species of plants and ascomycetous yeasts are capable of forming highly specific mutu-

Table 2. Rate of occurrence (%) of the predominant yeast species on the leaves of different plant species (an average per year)

Plant species	*Cr. magnus*	*Rh. mucilaginosa*	*Cr. albidus*	*D. hansenii*	*C. oleophila*	*Sp. roseus*	*Cr. laurentii*	*Rh. glutinis*	*M. pulcherrima*	*M. reukaufii*	*Cyst. capitatum*	*Rh. minuta*
Acer negundo	25.7	15.0	9.5	9.5	7.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Aesculus hippocastanum	31.0	14.1	13.5	13.5	0.0	0.0	0.0	0.3	0.0	0.0	0.9	0.0
Ajuga reptans	36.7	20.3	12.5	8.9	9.8	4.6	3.3	1.8	0.8	0.1	0.3	0.3
Alchemilla vulgaris	29.4	18.1	12.6	12.6	5.3	3.7	4.2	2.4	0.1	4.1	0.0	0.1
Asarum europaeum	20.4	10.8	9.6	9.6	0.0	0.0	11.3	11.7	1.8	0.0	3.8	0.2
Betula verrucosa	30.4	25.0	0.0	0.0	12.6	0.0	5.2	7.0	0.5	0.0	0.0	0.0
Carex pilosa	29.4	17.5	16.3	16.3	0.7	2.5	5.6	5.6	0.0	0.0	0.6	1.6
Dactylis glomerata	25.2	22.0	16.7	19.8	5.7	7.6	0.6	0.0	1.9	0.1	0.0	0.0
Equisetum sylvaticum	25.6	14.5	18.1	18.1	5.7	1.8	0.0	0.6	0.5	7.3	1.6	0.6
Ficaria verna	34.7	25.0	2.6	2.6	0.0	12.6	8.6	1.9	0.0	0.0	0.0	6.3
Fraxinus excelsior	35.7	19.0	2.7	2.7	0.0	0.0	3.6	0.0	2.5	0.0	0.0	0.0
Impatiens glandulifera	34.5	12.1	0.2	0.2	0.0	3.6	7.2	5.0	6.0	0.6	0.0	1.7
Impatiens noli-tangere	41.3	22.0	2.5	2.5	0.0	11.3	5.2	8.2	3.0	0.2	0.0	0.9
Impatiens parviflora	39.6	27.7	0.0	0.0	6.2	6.1	4.6	4.3	0.7	0.8	0.0	0.0
Larix decidua	34.3	25.6	8.1	8.1	0.0	13.4	3.4	0.0	0.5	0.0	1.3	0.0
Oxalis acetosella	30.5	15.3	7.0	7.0	2.0	13.4	17.8	1.1	0.7	0.0	3.2	1.8
Picea abies	39.8	16.7	11.9	11.9	5.0	0.8	4.4	1.0	0.0	0.0	0.1	5.6
Plantago major	27.2	10.0	4.6	4.6	16.6	0.0	0.3	3.5	5.5	4.0	0.0	0.0
Populus alba	31.2	12.5	7.4	7.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Quercus robur	46.7	34.0	0.0	0.0	5.6	0.0	1.5	1.2	0.5	0.0	9.6	0.0
Sambucus racemosa	34.2	32.0	0.0	0.0	0.0	0.0	0.0	0.0	6.6	0.3	0.0	0.0
Symphoricarpos albus	34.2	13.3	0.0	0.0	0.0	0.0	0.0	7.0	0.0	0.0	0.0	3.2
Syringa vulgaris	45.5	32.0	0.2	0.2	13.4	0.0	5.0	0.0	0.0	1.7	0.0	0.0
Taraxacum officinale	25.6	10.5	11.0	11.0	12.7	3.6	0.2	1.6	5.2	7.5	3.8	0.1
Tilia cordata	46.3	28.7	0.0	0.0	12.6	0.0	5.0	0.0	3.2	0.0	0.0	0.0
Vaccinium vitis-idaea	29.1	15.6	6.8	6.8	7.1	2.5	0.0	0.0	6.7	4.6	0.8	3.6

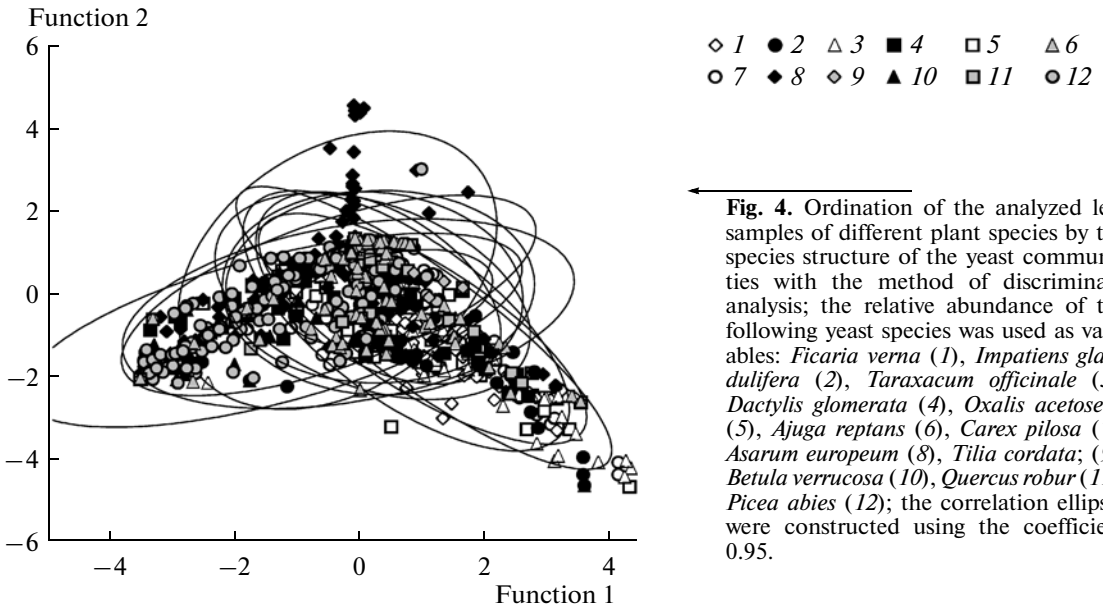

Fig. 4. Ordination of the analyzed leaf samples of different plant species by the species structure of the yeast communities with the method of discriminant analysis; the relative abundance of the following yeast species was used as variables: *Ficaria verna* (*1*), *Impatiens glandulifera* (*2*), *Taraxacum officinale* (*3*), *Dactylis glomerata* (*4*), *Oxalis acetosella* (*5*), *Ajuga reptans* (*6*), *Carex pilosa* (*7*), *Asarum europeum* (*8*), *Tilia cordata*; (*9*), *Betula verrucosa* (*10*), *Quercus robur* (*11*), *Picea abies* (*12*); the correlation ellipses were constructed using the coefficient 0.95.

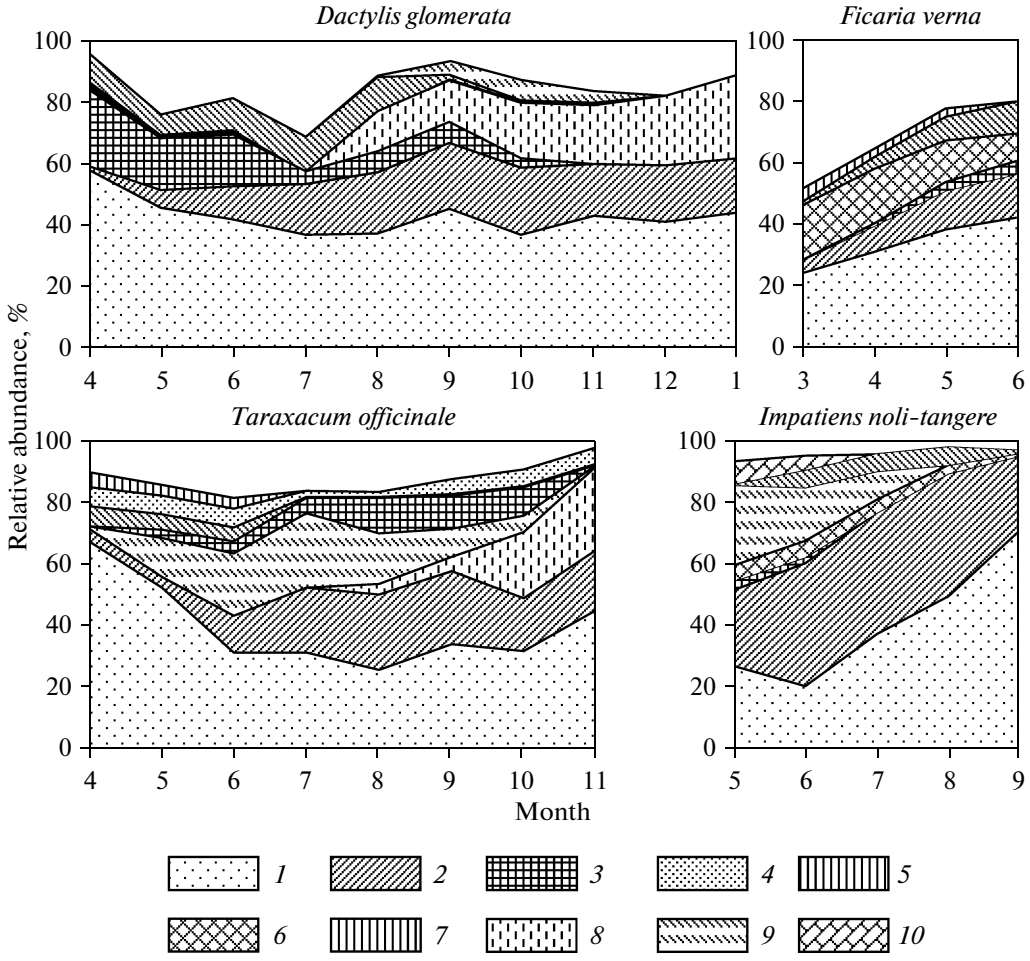

Fig. 5. Examples of the dynamics of relative abundance of the dominant species of epiphytic yeasts on the leaves of annuals: *Cryptococcus magnus* (*1*), *Rhodotorula mucilaginosa* (*2*), *Debaryomyces hansenii* (*3*), *Cryptococcus albidus* (*4*), *Rhodotorula glutinis* (*5*), the *Cryptococcus laurentii/Cr. victoriae* complex (*6*), *Cystofilobasidium capitatum* (*7*), *Candida oleophila* (*8*), *Metschnikowia pulcherrima* (*9*), *Torulaspora delbrueckii* (*10*).

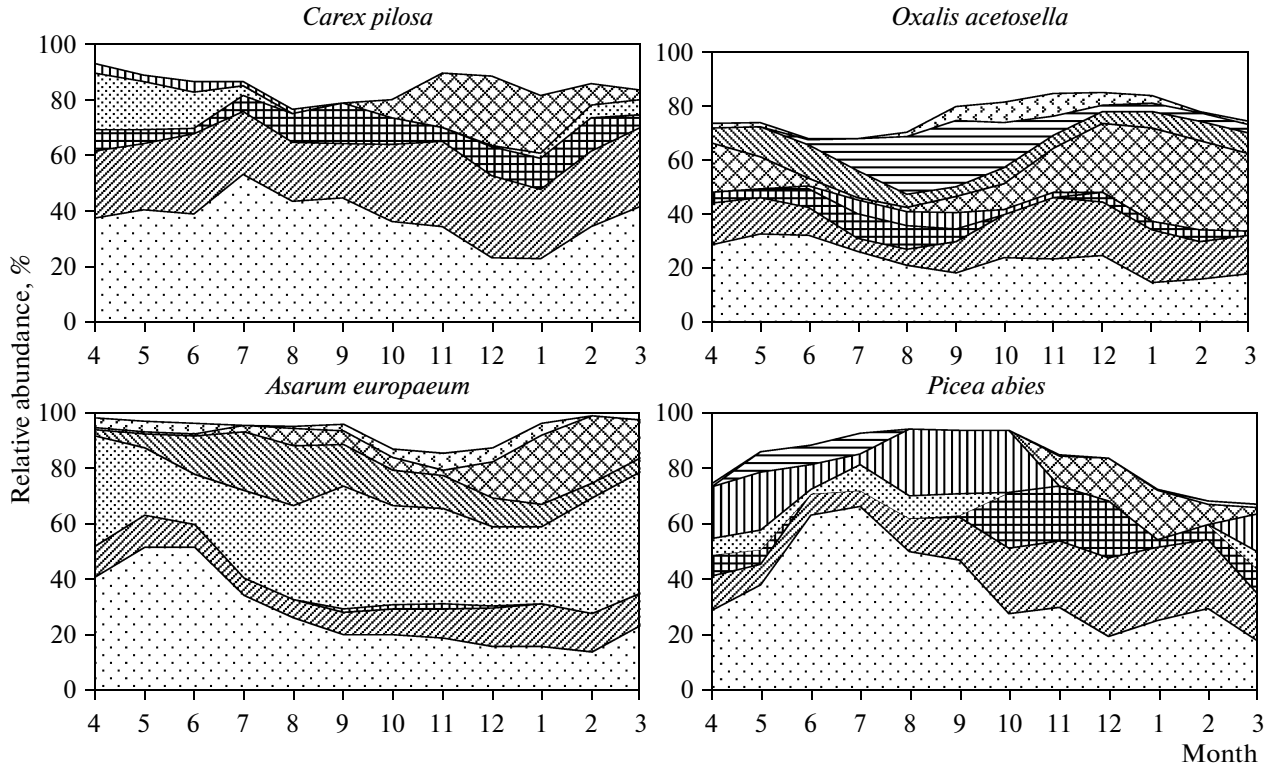

Fig. 6. Examples of the dynamics of relative abundance of the dominant species of epiphytic yeasts on the leaves of summer to winter green species of plants; *1–10* as in Fig. 4.

alistic complexes, which are sustained by the activity of the species of insects associated with them. The latter serve as vectors of yeast transfer affording primary contamination by strictly definite species [17, 18].

Our results show that it is necessary to study the microbial communities in the annual (seasonal) dynamics for the specific features of their taxonomic structure to be assessed correctly. A natural continuation of our work is unraveling of the autecological features of the yeast species that distinguish them as independent ecological units and explain the character of their seasonal dynamics.

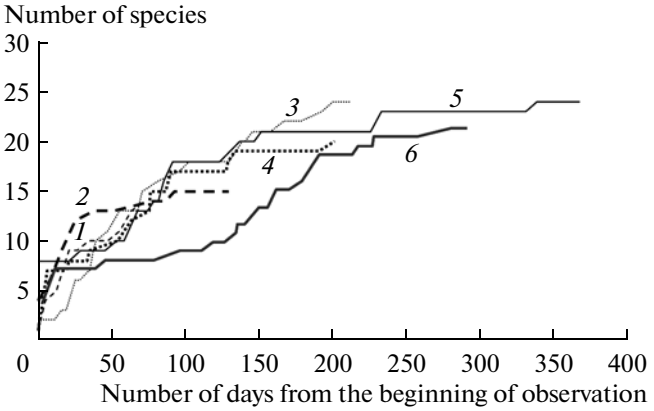

Fig. 7. Number of the isolated yeast species depending on the duration of plant ontogenesis: *Ficaria verna* (*1*), *Impatiens noli-tangere* (*2*), *Taraxacum officinale* (*3*), *Equisetum silvaticum* (*4*), *Oxalis acetosella* (*5*), *Dactylis glomerata* (*6*).

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