

EXPERIMENTAL
ARTICLES

Characterization of Yeast Groupings in the Phyllosphere of *Sphagnum* Mosses

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Abstract—Significant differences were revealed in the taxonomic structure of the epiphytic yeast communities formed on *Sphagnum* mosses and on the leaves of vascular plants. On mosses, low abundance of red yeasts was found (the most typical epiphytes on vascular plant leaves), along with a relatively high content and diversity of nonpigmented dimorphic basidiomycetes related to the order *Leucosporidiales*. The species composition of epiphytic yeasts from mosses is different from that of both forest and meadow grasses and of the parts of vascular plants submerged in the turf. The specific composition of the *Sphagnum* mosses yeast community is probably determined by the biochemical characteristics of this environment, rather than by the hydrothermal regime in the turf.

Key words: yeast, phyllosphere, mosses, turf, *Sphagnum*, dimorphic basidiomycetes, *Leucosporidiales*, pigmented yeasts.

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Yeasts are widespread in natural biotopes. The epiphytic yeast communities forming on live and moribund plant parts exhibit the highest diversity. Anamorphic basidiomycete yeasts are known to dominate in plant phyllosphere; filobasidiales and tremellales yeasts of the genus *Cryptococcus*, as well as red-pigmented yeasts *Rhodotorula* and *Sporobolomyces*, are the most numerous [1, 2]. Our long-term investigations of the yeast population of the phyllosphere have demonstrated that these yeast species usually dominate on various species of vascular plants, independent on their taxonomic position and ecological characteristics [2]. However, information concerning the yeast population of cryptogams, including mosses, is scarce [3–5]. The turf is usually considered a part of soil or peat.

Sphagnum mosses are widespread from tropical mountains to arctic and subantarctic regions; *Sphagnum* turf is an important component in the vegetation of various forest and bog biocenoses. Moss cover is a specific habitat for microorganisms; due to its high buffer capacity, it provides a stable hydrothermal regime [6]. The conditions surrounding the epiphytic microorganisms of the moss layer differ significantly from those on leaf surfaces of most vascular plants where microbial development depends on insolation and changes in temperature and humidity. Ultralow mineralization is another factor specific for the environments created by *Sphagnum* mosses. Nitrogen compounds and many metals (important microelements) interact with phenolic compounds of peat and living moss, forming

complexes unavailable to microorganisms [7]. The yeast communities of moss turf may therefore have a specific taxonomic composition.

The goal of the present work was to determine specific characteristics of the yeast communities of *Sphagnum* mosses in comparison with vascular plants.

MATERIALS AND METHODS

Sphagnum samples, mostly belonging to the species *Sphagnum girgensohnii* Russ., *S. magellanicum* Brid., *S. balticum* (Russ.) C.Jens., and *S. angustifolium* (Russ.) C.Jens., were collected in the summers of 2005–2007 in bog and forest biocenoses of the Moscow, Tver, and Tyumen' oblasts. In order to determine the vertical distribution of yeasts, the samples were taken from the upper part of the plant, from its medium, chlorophyll-containing part, and from the lower, chlorophyll-free layer with traces of beginning decomposition. For comparison, the following vascular plants growing with *Sphagnum* were sampled: *Oxycoccus palustris* Pers., *Carex limosa* L., *Chamaedaphne calyculata* L., and *Drosera rotundifolia* L. The above-surface part of the plant and the one located within the turf were analyzed separately.

Yeast numbers and taxonomic composition were analyzed by standard plating on malt agar acidified with lactic acid (4 ml/l; pH 4–4.5) to suppress bacterial growth [8]. For identification of yeast cultures, their morphological and physiological characteristics were determined; the manual [9] was used, as well as additional keys [10–12] based on tests on assimilation of

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aldaric acids and aromatic compounds. To reveal the teleomorphic structures of basidiomycetes, the isolates were grown for two to three weeks on potato–dextrose agar at 10°C [8, 9].

Molecular techniques were used to diagnose difficultly identified strains. For identification of ascomycetous yeasts, restriction analysis of the 5.8S-ITS rDNA region was carried out as described previously [13]. For species identification, the tables from original publications were used [14, 15]. The strains of nonpigmented dimorphic basidiomycetes were initially grouped using PCR with a nonspecific primer M13 (5'-GAGGGT-GGCGGTTCT-3') [16]. Amplification of the target DNA sites was achieved by introducing the yeast biomass directly to the reaction mixture as described previously [13]. A Tertsik amplifier (DNK-technologieya, Russia) was programmed as follows: initial denaturation, 3 min at 94°C; 35 cycles (denaturation, 30 s at 94°C; primer annealing, 30 s at 60°C; DNA synthesis, 1 min at 72°C); and extension, 3 min at 72°C. Amplification products were separated in 1.5% agarose gel with 0.5× TAE buffer for 1 h at 200 V and stained with ethidium bromide. Visualization and treatment of the fragments were carried out using a Bio Rad Gel Doc imaging system (Bio Rad, United States). The similarity of the PCR profiles was determined using the Phoretix1D v2003.02 software package (Nonlinear Dynamics Ltd., United States).

The isolates of nonpigmented dimorphic basidiomycetes fitting the description of the order *Microbotryales* and similar to the genus *Leucosporidium* [17, 18] were identified using a polyphasic approach. The strains were initially grouped using restriction analysis of the 5.8S-ITS rDNA region and D1D2 26S rDNA region with endonucleases *HaeIII* and *HinfI*. The results of fragment separation were compared to those theoretically calculated using aligned sequences of the following type strains (GenBank accession numbers for D1D2, 26S and 5.8S-ITS, respectively are given in parentheses): *Leucosporidium scottii* (AF070419; AF444495), *L. fellii* (AF189907; AF444508), *L. antarcticum* (AF189906; AF444529), *L. golubevii* (AY212997; AY212987), *Leucosporidiella fragaria* (AF070428; AF444530), *L. muscorum* (AF070433), *L. creatinivora* (AF189925; AF444629), *L. yakutica* (AY213001; AY212989), *Rhodotorula ingeniosa* (AF189934; AF444534), *Rh. vanillica* (AF189970; AF444575), *Rh. fujisanensis* (AF189928; AF444490), *Mastigobasidium intermedium* (AF189889; AF444564) treated using the MegAlign software package (DNASar, United States). The species and groups of closely related species were thus revealed, which were determined using restriction profiles of the 5.8-ITS region with the endonucleases used. The resolution of gel electrophoresis does not permit effective discrimination between restriction profiles of the D1D2 region of 26S rDNA. Further identification to the species level was carried out considering the known discriminating assimilation characteristics [18].

DNA was extracted from the biomass of basidiomycetous strains according to the modified procedure [19]. Amplification of the target rDNA fragments was carried out in 30 µl of reaction mixture containing the following: PCR buffer; 0.25 mM dNTP (Fermentas, Lithuania); 0.30 µM of each primer (ITS1, ITS4, NL1, NL4); and 1.25 U *Taq*-polymerase (Sintol, Russia). A Tertsik amplifier was programmed as follows: initial denaturation, 3 min at 94°C; 30 cycles (denaturation, 2 min at 94°C; primer annealing, 1 min at 60°C; DNA synthesis, 2.5 min at 72°C); and extension, 10 min at 72°C. Analysis of restriction fragment length was carried out as described previously [13, 20]. Endonucleases *HaeIII* and *HinfI* (Fermentas, Lithuania) were used. The products were separated in 1.5% agarose gel with 0.5× TAE buffer for 1–1.5 h at 140–150 V. Visualization and treatment of the fragments were carried out using a Bio Rad Gel Doc imaging system (Bio Rad, United States).

RESULTS

Total number of yeasts in *Sphagnum* turf. The average yeast number in the *Sphagnum* samples investigated was 1.5×10^3 CFU/g. The highest number of yeasts (up to 10^5 CFU/g) were detected in the samples from Losinyi Ostrov National Park and Shakhovskoi raion (Table 1). Thus, the number of yeasts inhabiting moss turf is intermediate between these values for higher vascular plants (up to 10^7 CFU/g) and soil upper mineral horizons (usually less than 10^3 CFU/g).

Yeast distribution in the layers of moss turf (*Sphagnum* upper part, medium chlorophyll-containing part, and lower part) was similar for the forest and bog biocenoses. Yeast numbers in the medium layer of moss cover were higher than in the upper one; in the lower layers, the numbers decreased. In a spruce forest, yeast numbers in all the layers of moss turf were approximately by half an order of magnitude higher than in an ombrotrophic bog (Fig. 1).

The average number of yeasts was reliably lower on *Sphagnum* mosses than on bog vascular plants from the same environment (Fig. 2). Average yeast numbers on the lower plant parts immersed into the moss turf were also lower than on *Sphagnum*. Thus, the specific hydrothermal regime of the moss turf is not the leading factor determining development of epiphytic yeast.

Species structure of yeast communities. The yeasts isolated from *Sphagnum* mosses and bog plants belonged to the following taxa: *Blastobotrys* sp., *Bulleromyces albus* Boekhout et Fonseca, *Candida membranaefaciens* (Hansen) Hansen, *C. oleophila* Montrocher, *C. sake* (Saito et Ota) van Uden et Buckley, *C. zeylanoides* (Castellani) Langeron et Guerra, filobasidiales cryptococci related to *Cryptococcus albidus* (Saito) Skinner and *Cr. magnus* (Lodder et Kreger-van Rij) Baptist et Kurtzman, tremellales cryptococci related to *Cr. laurentii* (Kufferath) Skinner and *Cr. vic-*

Table 1. Vegetation and soil of the sampling sites

Site, region	Phytocenose	Soil	Average yeast number, log (CFU/g)
Donino village, Lyubertsy raion, Moscow oblast	Birch forest, sedge–motley grass	Peat–podzolic–gley	3.0
	Spruce forest, sedge–moss	Peat–podzolic–gley	3.2
Kurovskoe bog, Tishkovo village, Pushkin raion, Moscow oblast	Pine forest, sedge–moss	Peat–bog	2.6
Burtsevo village, Shakhovskoi raion, Moscow oblast	Birch forest, motley grass–moss	Peat–bog	3.6
Losinyi Ostrov National Park, Moscow	Birch forest, motley grass–moss	Peat–bog	3.8
Zapadnodvinskii raion, Tver oblast	Pine forest, andromeda–cotton grass–moss	Peat–bog	2.8
Nadym raion, Tyumen' oblast	Cotton grass–sedge–moss bog	Peat–bog	2.8

toriae Montes et al., *Cr. podzolicus* (Bab'eva et Reshetova) Golubev, *Cr. terricola* Pedersen, *Cystofilobasidium capitatum* (Fell et al.) Oberwinkler et Bandoni, *Debaryomyces hansenii* (Zopf) Lodder et Kreger-van Rij, *D. vanrijiae* (van der Walt et Tscheuschner) Abadie

et al., *Hanseniaspora guillermontii* Pijper, *Metschnikowia pulcherrima* Pitt et Miller, *M. reukaufii* Pitt et Miller, *Mrakia frigida* (Fell, Statzell Hunter et Phaff) Yamada et Komagata, *Pichia membranaefaciens* (Lodder et Kreger-van Rij) Wickerham et Burton, *Rhodotorula fujisanensis* (Soneda) Johnson et Phaff, *Rh. glutinis* sensu lato Gadanho et Sampaio, *Rh. mucilaginosa* (Jorgensen) Harrison, *Sporobolomyces roseus* Kluyver et van Niel, *Guehomyces pullulans* (Lindner) Fell et Scorzetti, and a group of closely related species of the class *Microbotryomycetes* [18]; the results of identification of the latter are presented further.

The species most common on the surface of *Sphagnum* mosses are also the ones regularly isolated from the phyllosphere of vascular plants: filobasidiales cryptococci [1], *C. oleophila* [13], and *D. hansenii* [20]. However, the ratio of the most typical epiphytes, pigmented dimorphic basidiomycetes of the species *Sp. roseus*, *Rh. glutinis* sensu lato, *Rh. mucilaginosa*, and *Cyst. capitatum* on mosses did not exceed 7% and was lower than on vascular plants (Table 2). The numbers of tremellales cryptococci close to *Cr. laurentii* and *Cr. victorae* were also relatively low; the ratio of these organisms on grasses was considerably higher.

A relatively high abundance of nonpigmented dimorphic basidiomycetes, mostly members of the class *Microbotryomycetes* (approx. 12% average) is another characteristic feature of the yeast communities of *Sphagnum* mosses. The ratio of these yeasts on vascular plants usually does not exceed 1%. Unlike the *Sphagnum* mosses of bog biocenoses, those from forest biocenoses exhibited high abundance of typical pedobiont yeasts *Cr. terricola* and *Cr. podzolicus*; these species are common in the mineral horizons of moderate soils. Their ratio increased significantly in the lower layer of moss turf.

Analysis of the vertical distribution of the yeast community in the layers of moss turf in bog and forest

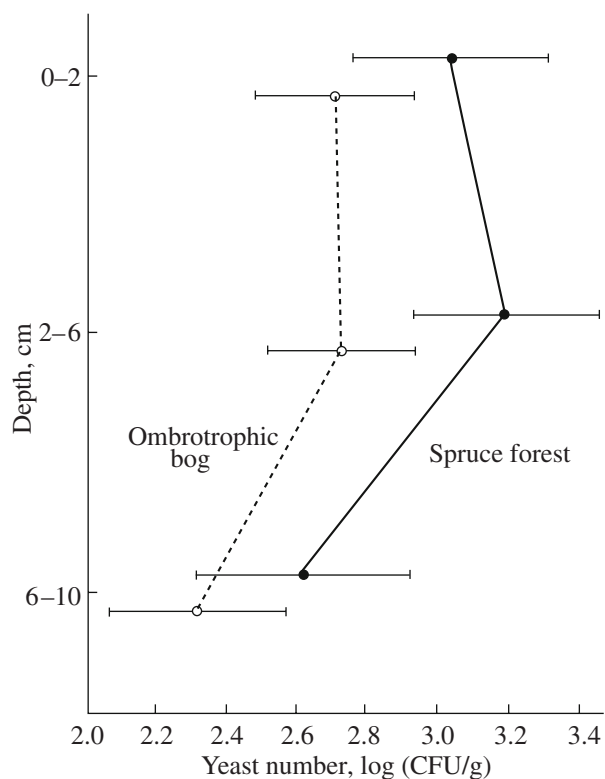


Fig. 1. Distribution of yeast numbers between moss bog layers (spruce forest, sedge–moss; vicinity of the Donino village and the Kurovskoe bog).

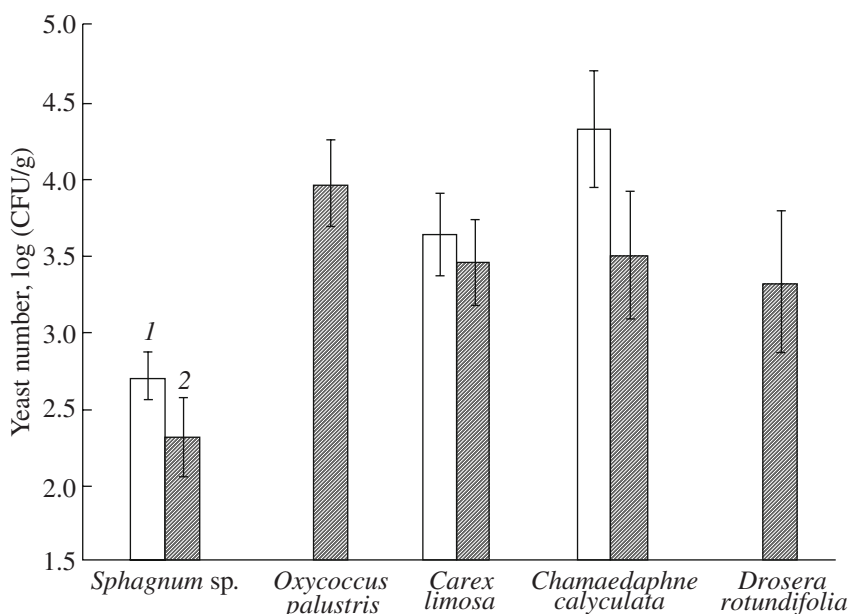


Fig. 2. Average yeast numbers on upper plant parts (1) and on the parts submerged into moss turf (2) (Kurovskoe ombrotrophic bog).

biocenoses revealed that high numbers of filobasidiales cryptococci and nonpigmented dimorphic basidiomycetes were present in all *Sphagnum* layers. In both biotopes (forest and bog), the ratio of tremellales cryptococci close to *Cr. laurentii* and *Cr. victoriae* and of nonpigmented basidiomycetes increased in the middle section of the moss turf profile. Pigmented epiphytic species *Rh. mucilaginosa* and *Rh. glutinis* sensu lato, ascosporous yeasts *D. hansenii*, and *Candida* species were found mostly in the upper layers.

Comparison of the yeast communities from *Sphagnum* mosses and bog vascular plants from the same habitats revealed differences both in numbers and in species structure (Table 3). Comparison of the lower layers of moss turf and the lower parts of vascular plants embedded in this turf demonstrated the highest difference in abundance of the typical phytobiotic taxa [1, 21]. For example, high numbers of *Rh. glutinis* sensu lato, *D. hansenii*, and tremellales and filobasidiales cryptococci were regularly isolated from higher plants, including bog ones, while they constituted only a minor portion of the yeast community in the lower layers of *Sphagnum* mosses.

The most general presentation of the differences in the yeast community structure on *Sphagnum* mosses and higher plants (bog and not bog) is achieved by their ordination by the principal components method (Fig. 3). It can be seen that the species structure of yeast communities on mosses varies significantly depending on the sampling location. Forest and meadow grasses exhibit high similarity of yeast species composition, while *Sphagnum* mosses and bog plants differ both from them and from each other.

Identification of nonpigmented dimorphic basidiomycetes. Thus, high relative abundance of nonpigmented dimorphic basidiomycetes is a characteristic feature of the yeast communities of *Sphagnum* turf; they replace the red-pigmented species and tremellales cryptococci common in the phylloplane of vascular plants. Identification of these species by the standard set of morphological and physiological criteria was difficult; 12 strains representing morphologically and physiologically uniform groups were therefore subject to additional investigation for more detailed identification.

According to the tests on assimilation of carbon and nitrogen sources, all the isolates were classified as members of the class *Microbotryomycetes* sensu Bauer et al., close to the order *Leucosporidiales* [22]. Cultivation on the media used for formation of mycelium or ballistospores [9] did not reveal any teleomorphic structures in the isolates.

In order to determine the taxonomic homogeneity of the strains, preliminary research was carried out using PCR with a nonspecific primer (M13). After digital processing (clusterization) of electrophoresis results, strains with completely identical profiles were determined. Restriction analysis of conservative rDNA regions is known to result in rapid and reliable identification of yeast species [14, 15]. It has been previously demonstrated that phylogenetic trees constructed using the 5.8S-ITS region and the D1D2 region of 26S rDNA had identical topology [17]. We analyzed both conservative fragments; however, as was mentioned above, the 5.8S-ITS region yielded better results for identification of the *Microbotryomycetes* isolates.

Table 2. Average relative abundance (%) of yeast species in *Sphagnum* turf

Species	Forest		Bog			Average
	1	2	3	4	5	
<i>Cryptococcus</i> spp. (<i>Filobasid.</i>)	34.8	38.5	32.4	24.2	29.4	26.3
<i>Candida</i> spp.	0.1	30.0	0.1	13.8	50.4	15.6
<i>D. hansenii</i>	0.9	0.6	0.1	7.3	0.4	12.6
<i>Leucosporidiales</i>	19.2	6.6	37.1	9.0	3.8	12.5
<i>Rh. fujisanensis</i>	14.9	2.3	0.1	19.3	0.1	6.1
<i>Cr. terricola</i>	2.4	0.1	25.7	0.1	0.1	4.6
<i>Cr. podzolicus</i>	11.6	1.4	0.1	0.1	1.3	2.4
<i>Sp. roseus</i>	1.8	0.1	0.1	7.6	0.1	4.3
<i>Rh. glutinis</i> sensu lato	2.4	6.0	0.1	1.2	3.6	2.2
<i>Rh. mucilaginosa</i>	0.1	0.1	0.1	7.9	0.1	1.4
<i>Blastobotrys</i> sp.	1.2	3.5	3.1	2.5	0.4	5.8
<i>M. pulcherrima</i>	0.1	6.1	0.1	0.4	6.7	2.2
<i>D. vanriijae</i>	6.1	0.1	0.1	0.1	0.1	1.1
<i>Cryptococcus</i> spp. (<i>Tremel.</i>)	3.2	0.4	0.2	5.8	0.3	1.6
<i>M. reukaufii</i>	0.1	3.3	0.1	0.1	1.6	0.8
<i>P. membranaefaciens</i>	0.1	0.1	0.1	0.1	1.1	0.2
<i>Cyst. capitatum</i>	0.9	0.1	0.1	0.1	0.1	0.1
<i>Rh. minuta</i>	0.1	0.5	0.1	0.1	0.1	0.1
<i>H. guilliermondii</i>	0.1	0.3	0.1	0.1	0.1	0.1

Note: Sampling regions: 1, Lyubertsy; 2, Losinyi ostrov; 3, Nadym; 4, Pushkin; 5, Shakhovskoi.

Table 3. Relative abundance (%) of yeasts in different moss turf layers and on different parts of bog plants (Kurovskoe ombrotrophic bog)

Species	<i>Sphagnum</i> sp.		<i>Carex limosa</i>		<i>Chamaedaphne calyculata</i>	
	0–6 cm	6–10 cm	Upper parts	Parts in moss turf	Upper parts	Parts in moss turf
<i>Candida</i> spp.	26.4	11.1	3.9	0.1	32.7	2.4
<i>Rh. fujisanensis</i>	22.2	11.1	37.9	23.9	0.2	4.0
<i>Cryptococcus</i> spp. (<i>Filobasidiales</i>)	20.8	21.7	22.4	25.1	64.3	16.3
<i>D. hansenii</i>	11.0	14.0	10.1	0.1	0.1	18.6
<i>Rh. mucilaginosa</i>	5.6	13.7	4.8	0.1	0.1	0.1
<i>Leucosporidiales</i>	3.8	11.8	1.0	15.6	0.1	37.0
<i>Rh. glutinis</i> sensu lato	3.2	0.1	0.9	0.3	1.6	5.5
<i>Cryptococcus</i> spp. (<i>Tremellales</i>)	3.0	9.3	11.4	10.9	0.1	0.1
<i>Blastobotrys</i> sp.	2.0	4.4	1.5	3.7	0.1	0.1
<i>M. pulcherrima</i>	1.3	0.1	0.1	0.1	0.1	0.1
<i>Cr. flavus</i>	0.2	0.1	0.1	0.1	0.1	0.1
<i>Cr. terricola</i>	0.1	0.3	0.1	7.6	0.1	1.1
<i>Cyst. capitatum</i>	0.1	0.1	3.6	5.0	0.1	1.1
<i>Rh. ingeniosa</i>	0.1	1.9	0.1	0.1	0.1	0.1
<i>Sp. roseus</i>	0.1	0.1	2.0	7.0	0.1	0.1
<i>G. pullulans</i>	0.1	0.1	0.1	0.1	0.1	13.5

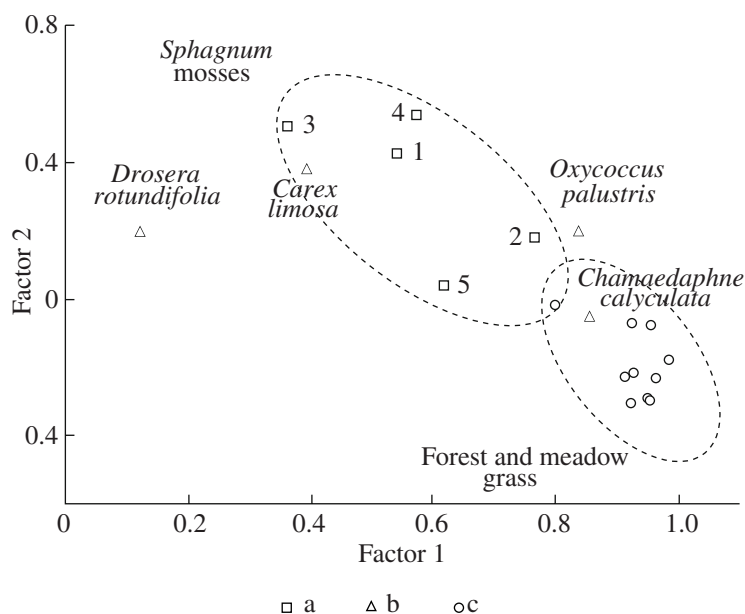


Fig. 3. Ordination of various plant species according to the species structure of the yeast community by the principal components method: (a) *Sphagnum* mosses, (b) bog vascular plants, and (c) forest and meadow grasses (from [2]); sampling regions: 1, Lyubertsy; 2, Losinyi ostrov; 3, Nadym; 4, Pushkin; 5, Shakhovskoi. The ellipses mark the 95% probability regions; the first two factors describe over 70% of the total data dispersion.

This research determined the taxonomic groups which may be differentiated using *HaeIII* and *HinfI* endonucleases (Table 4). The results of analysis confirmed that the strains belonged to the class *Microbotryomycetes*; they were subdivided into the following taxonomic groups: *Rh. fujisanensis*, *Rh. ingeniosa/Rh. vanillica*, and members of the anamorphic genus *Leucosporidiella*. The test on assimilation of aromatic compounds enabled identification of the isolates according to the diagnostic characteristics [11, 18] (the data on restriction analysis of 5.8S-ITS with *HaeIII* and *HinfI* restriction endonucleases, respectively are given in parentheses): *L. fragaria* (J.A. Barnett & Buhagiar) Sampaio 2003 (520 + 100, 280 + 180 + 150), *L. muscorum* (di Menna) Sampaio 2003 (500 + 100, 180 + 150 + 150 + 100), *Rh. fujisanensis* (Soneda) Johnson et Phaff 1978 (400 + 100 + 100, 250 + 180 + 150), and *Rh. ingeniosa* (di Menna) von Arx et Weijman 1979 (500 + 100, 250 + 180 + 150).

DISCUSSION

Sphagnum mosses are a specific habitat for epiphytic microorganisms. Modification of such physical factors as moisture accumulation and stabilization of the temperature regime are not the only components of the *Sphagnum* medium-forming role. The biochemical characteristics of *Sphagnum* mosses probably play an important part in formation of the specific environment. The presence of catechols and tannins provides for greater resistance to decomposition compared to higher plants [23]. Moss secondary metabolites (terpenoids

and polyphenol compounds), as well as excreted organic acids, limit the growth of many microorganisms. A somewhat specific composition of microbial communities (including yeast ones) formed on *Sphagnum* mosses was to be expected.

Our results demonstrate that the yeast communities of *Sphagnum* turf are indeed different from the phylloplane population of other plant groups. Low abundance of red-pigmented epiphytic yeasts is the main difference; high numbers of these organisms are isolated from vascular plants. They are replaced by non-

Table 4. Restriction fragment lengths of the 5.8S-ITS rDNA region for the yeasts of the order *Microbotryales* close to the genus *Leucosporidium*. The data are rounded according to the resolution of agarose gel electrophoresis

Species	<i>HaeIII</i>	<i>HinfI</i>
<i>Rh. fujisanensis</i>	400 + 100 + 100	250 + 180 + 150
<i>M. intermedium</i>	380 + 150 + 100	280 + 180 + 150
<i>L. antarcticum</i>	550 + 100	300 + 180 + 150
<i>L. scottii</i>	470 + 50	250 + 180 + 100
<i>L. golubevii</i>	490 + 90	250 + 150 + 120 + 50
<i>L. yakutica</i>	490 + 90	250 + 180 + 150
<i>L. fellii/L. muscorum</i>	500 + 100	180 + 150 + 150 + 100
<i>L. fragaria</i>	520 + 100	280 + 180 + 150
<i>L. creatinivora/Rh. ingeniosa/Rh. vanillica</i>	500 + 100	250 + 180 + 150

pigmented dimorphic basidiomycetes, which are significantly less abundant and diverse on other plant substrates. Comparison of the average ratio of pigmented and nonpigmented basidiomycetes on higher plants and *Sphagnum* mosses of the tundra–boreal zone was performed on the basis of the results of the present paper and our previous long-term works on the composition of yeast communities in plant phyllosphere [24]. The average relative abundance of pigmented yeasts in *Sphagnum* samples was almost three times lower than on the surface of vascular plants (approx. 10 and 30%, respectively).

These data disagree with an earlier study of the yeastlike population of *Sphagnum* peat and moss tow (mainly from West Siberian bogs) [5], where pigmented species comprised about 50% of the total yeast number. This may be caused by the regional or local peculiarities of the bogs. However, these differences are more likely to originate from duration of sample storage. In the present work, the samples were analyzed within several days, whereas in the cited work analysis usually took place after several months of storage. The ratio of pigmented yeasts is known to increase in plant and soil samples stored for a long time in a dried or frozen state. This is possibly due to protective functions of carotenoids, including their antioxidant properties. This is probably the reason why the ratio of carotenoid-containing yeasts is highest on the leaves of vascular plants, i.e., in environments where yeasts encounter both insolation and periodic desiccation.

Increased abundance of psychrophilic yeasts of the class *Microbotryomycetes*, including *L. scottii*, in moss turf has been reported previously and was associated with the constantly low temperature of this environment [25, 26]. However, comparison of abundance and structure of the yeast groupings from moss layers and the lower part of bog vascular plants revealed that the hydrothermal regime is not the only factor determining the peculiarities of *Sphagnum* mosses as a yeast habitat.

The role of *Sphagnum* mosses in formation of yeast communities is mainly in the alteration of nutrient supply, viz., nitrogen and microelements deficiency, as well as a significant content of organic, uronic, and aromatic acids in the exudates. Yeasts with a broad assimilation spectrum, capable of utilization of organic acids and aromatic compounds, prevail among the dominating taxa revealed in the moss turf. This applies to the detected members of nonpigmented basidiomycete genera *Leucosporidiella*, *Rhodotorula*, and *Mrakia*. We believe that mosses, especially *Sphagnum*, are a characteristic natural habitat of these yeasts and probably contain a species diversity of the members of these taxa even higher than we detected in the present work. Basidiomycetous yeasts of the class *Microbotryomycetes* are a poorly studied group of fungi; further research on the moss yeast population may be promising in the taxonomic aspect.

Apart from pigmented yeasts, the members of the anamorphic genus *Cryptococcus* are often present among the dominant species of plant phylloplane (filobasidiales *Cr. magnus*, *Cr. albidus*, *Cr. oierensis*, and *Cr. wieringae* and tremellales *Cr. victoriae*, *Cr. carne-scens*, and *Cr. flavus*) [1]. The results of our investigation demonstrated that filobasidiales cryptococci able to utilize some aromatic compounds were abundant in the sphagnum, while tremellales cryptococci, which are mostly unable to utilize these substrates, were relatively rare.

Thus, yeast compounds of the *Sphagnum* turf differed from the epiphytic ones occurring on the leaves of forest, meadow, and bog vascular plants. *Sphagnum* mosses are an interesting, albeit poorly investigated, natural habitat and a potential source of new and poorly known species, especially of nonpigmented dimorphic basidiomycetes.

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REFERENCES

1. Fonseca, A. and Inacio, J., Phylloplane Yeasts, in *Biodiversity and Ecophysiology of Yeasts. The Yeast Handbook*, Rosa, C.A. and Peter, G., Eds., Springer, pp. 263–301.
2. Glushakova, A.M., Ecology of Epiphytic Yeasts, *Cand. Sci. (Biol.) Dissertation*, Moscow: Mosk. Gos. Univ., 2006.
3. di Menna, M.E., Yeasts in Antarctic Soils, *Antonie van Leeuwenhoek J. Microbiol. Serol.*, 1966, vol. 32, pp. 29–38.
4. Tosi, S., Casado, B., Gerdol, R., and Caretta, G., Fungi Isolated from Antarctic Mosses, *Polar Biol.*, 2002, vol. 25, pp. 262–268.
5. Polyakova, A.V., Chernov, I.Yu., and Panikov, N.S., Yeast Diversity in Hydromorphic Soils with Reference to a Grass-Sphagnum Wetland in Western Siberia and a Hummocky Tundra Region at Cape Barrow (Alaska), *Mikrobiologiya*, 2001, vol. 70, no. 5, pp. 714–720 [*Microbiology* (Engl. Transl.), vol. 70, no. 5, pp. 617–623].
6. Savich-Lyubitskaya, L.I. and Smirnova, Z.N., *Opredelitel' Listostebel'nykh Mkhov SSSR. Verkhoplodnyye mkhi* (Identification Guide of Leafy Mosses of the USSR. Acrocarpous Mosses), Leningrad: Nauka, 1970.
7. Painter, T.J., Carbohydrate Polymers in Food Preservation: An Integrated View of the Maillard Reaction with Special Reference To Discoveries of Preserved Foods in *Sphagnum*-Dominated Peat Bogs, *Carbohydr. Polymers*, 1998, vol. 36, pp. 335–347.
8. Maksimova, I.A. and Chernov, I.Yu., *Rukovodstvo K Prakticheskim Zanyatiyam Po Biologii Drozhzhei* (Practical Manual on Yeast Biology), Tula, 2006, vol. 96.

9. *The Yeasts, a Taxonomic Study. Fourth Revised and Enlarged Edition*, Kurzman, C.P. and Fell, J.W., (Eds.), Amsterdam: Elsevier Science, 1998.
10. Fonseca, A., Utilization of Tartaric Acid and Related Compounds by Yeasts: Taxonomic Implications, *Can. J. Microbiol.*, 1992, vol. 38, pp. 1242–1251.
11. Sampaio, J.P., Utilization of Low Molecular Weight Aromatic Compounds by Heterobasidiomycetous Yeasts: Taxonomic Implications, *Can. J. Microbiol.*, 1999, vol. 45, pp. 491–512.
12. Fonseca, A., Scorzetti, G., and Fell, J.W., Diversity in the Yeast *Cryptococcus albidus* and Related Species as Revealed by Ribosomal DNA Sequence Analysis, *Can. J. Microbiol.*, 2000, vol. 46, pp. 7–27.
13. Glushakova, A.M., Yurkov, A.M., and Chernov, I.Yu., Massive Isolation of Anamorphous Ascomycete Yeasts *Candida oleophila* from Plant Phyllosphere, *Mikrobiologiya*, 2007, vol. 76, no. 6, pp. 896–901 [*Microbiology* (Engl. Transl.), vol. 76, no. 6, pp. 799–803].
14. Esteve-Zarzoso, B., Belloch, C., Uruburu, F., and Querol, A., Identification of Yeasts by RFLP Analysis of the 5.8S rRNA Gene and the Two Ribosomal Internal Transcribed Spacers, *Int. J. Syst. Bacteriol.*, 1999, vol. 49, pp. 329–337.
15. Frutos, R.L., Fernandez-Espinar, M.T., and Querol, A., Identification of Species of the Genus *Candida* by Analysis of the 5.8S rRNA Gene and the Two Ribosomal Internal Transcribed Spacers, *Antonie van Leeuwenhoek*, 2004, vol. 85, pp. 175–185.
16. Lieckfeldt, E., Meyer, W., and Borner, T., Rapid Identification and Differentiation of Yeasts by DNA and PCR Fingerprinting, *J. Basic Microbiol.*, 1993, vol. 33, pp. 413–425.
17. Scorzetti, G., Fell, J.W., Fonseca, A., and Statzell-Tallman, A., Systematics of Basidiomycetous Yeasts: a Comparison of Large Subunit D1/D2 and Internal Transcribed Spacer rDNA Regions, *FEMS Yeast Res.*, 2002, vol. 2, pp. 495–517.
18. Sampaio, J.P., Gadanho, M., Bauer, R., and Weis, M., Taxonomic Studies in the *Microbotryomycetidae*: *Leucosporidium golubevii* sp. nov., *Leucosporidiella* gen. nov. and the New Orders *Leucosporidiales* and *Sporidiobolales*, *Mycol. Progr.*, 2003, vol. 2, pp. 53–68.
19. Sampaio, J.P., Gadanho, M., Santos, S., Duarte, F.L., Pais, C., Fonseca, A., and Fell, J.W., Polyphasic Taxonomy of the Basidiomycetous Yeast Genus *Rhodospodium*: *R. kratochvilovae* and Related Anamorphic Species, *Int. J. Syst. Evol. Microbiol.*, 2001, vol. 51, pp. 687–697.
20. Yurkov, A.M. and Chernov, I.Yu., Geographical Races of Certain Species of Ascomycetous Yeasts in the Moscow and Novosibirsk Regions, *Mikrobiologiya*, 2005, vol. 74, no. 5, pp. 687–692 [*Microbiology* (Engl. Transl.), vol. 74, no. 5, pp. 597–601].
21. Glushakova, A.M. and Chernov, I.Yu., Seasonal Dynamics in a Yeast Population on Leaves of the Common Wood Sorrel *Oxalis acetosella* L., *Mikrobiologiya*, 2004, vol. 73, no. 2, pp. 226–232 [*Microbiology* (Engl. Transl.), vol. 73, no. 2, pp. 184–188].
22. Bauer, R., Begerow, D., and Sampaio, J.P., Weiß, M., and Oberwinkler, F., The Simple-Septate Basidiomycetes: a Synopsis, *Mycol. Progr.*, 2006, vol. 5, pp. 41–66.
23. Mironycheva-Tokareva, N.P. and Parshina, E.K., Dynamics of Organic Matter Decomposition in Bogs of Different Genesis, *Bolota i biosfera, Materialy tret'ei nauchnoi shkoly* (Bogs and Biosphere. Proc. 3rd Sci. School), Tomsk, 2004, pp. 23–31.
24. Chernov, I.Yu., Latitudal–Zonal and Spacial–Succession Trends in the Distribution of Yeasts, *Zh. Obshch. Biol.*, 2005, vol. 66, no. 2, pp. 123–135.
25. Chernov, I.Yu., Sinecological Analysis of Yeast Groups in Taimyr Tundra, *Ekologiya*, 1985, no. 1, pp. 54–60.
26. Maksimova, I.A. and Chernov, I.Yu., Community Structure of Yeast Fungi in Forest Biogeocenoses, *Mikrobiologiya*, 2004, vol. 73, no. 4, pp. 558–566 [*Microbiology* (Engl. Transl.), vol. 73, no. 4, pp. 474–481].