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EXPERIMENTAL ARTICLES

Yeast Population of the Kindo Peninsula Lichens

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Abstract—Yeast abundance and species diversity in the lichens collected at the Kindo Peninsula (Karelia) were studied. A total of 14 lichen species analyzed belonged to the genera *Bryoria, Cladonia, Hypogymnia*, *Icmadophila, Nephroma, Peltigera*, and *Ramalina*. Abundance of cultured yeasts in lichens was intermediate between soil and phyllosphere. The average yeast number on lichens was ~2.5×10^3 CFU/g, while it exceeded 8×10^3 CFU/g on plants and reached only 1×10^3 CFU/g in soil. Yeast population of different parts of *Cladonia* lichens was found to vary significantly in abundance, species diversity, and community structure. The highest yeast abundance and diversity were revealed in the growth zone. Fifteen yeast species were isolated from lichens, including 6 basidiomycetous and 9 ascomycetous ones. Unlike soils and plants, yeast population of lichens consisted mainly of ascomycetous species, with predominance of *Candida sphagnicola* and anamorphous yeasts of the genus *Dothiora*. These results show that yeasts from different taxonomic and ecological groups are a necessary component of lichens; conditions favoring the preservation and development of specific yeast communities differing from the typical soil and phyllosphere yeast complexes are formed in the lichens of northern taiga forests.

Keywords: yeasts, lichens, lichenosphere, Subarctic areas, MSU White Sea Biological Station, *Cladonia*, *Dothiora*

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One of the modern definitions of lichens characterizes them as an ecologically obligatory stable mutualism between a fungal partner (mycobiont) providing an environment and an algal or cyanobacterial population (photobiont) inhabiting this environment (Hawksworth and Honegger, 1994). Over 26000 lichen species are presently known. They occupy practically all known ecological niches on the planet, from arid terrestrial to marine and freshwater ones. They are most common in the areas of temperate climate and in the regions bordering with the Arctic and Antarctic zones (Andreev, 1954; Larson, 1987). Lichen abundance and diversity are minimal at the sites with high anthropogenic load (Zelenskaya et al., 2012).

Based on investigation of the fungal inhabitants of Antarctic lichens (other than lichenized fungi), which revealed high diversity of various taxonomic and ecological fungal groups, the term lichenosphere was proposed for the layer of the lichen thallus with conditions protecting such settlers as the species phylogenetically related to mycobionts, reducers, parasites, Polar species, endemics, and psychrophilic eurybionts (Santiago et al., 2015). Within the lichen, microorganisms are supplied with nutrients and protected from low temperature, oligotrophy, strong winds, and ultraviolet radiation, so that the organisms unadopted to extreme Antarctic conditions may survive and proliferate.

Although lichens have always been considered the typical natural substrates acting as yeast habitats, the data on yeast association with lichens are scarce. Most data on yeast isolation was obtained for the regions where lichens act as edificators, such as Arctic tundra and Antarctic. Prof. van der Walt investigated in detail the lichens of South African savannas (see review by Pankratov et al., 2017). The average yeast abundance in lichen thalli was usually observed near 10^2 CFU/g, although in some samples it was two orders of magnitude higher (Chernov, 1984; Vishniac, 2006). The yeast population of lichens belongs to about fifty species. Lichens are the substrate from which new yeast species are constantly isolated (Pankratov et al., 2017). The recent metagenomic study of a number of lichen species with ascomycetous mycobionts revealed their thalli contained a basidiomycetous component represented by yeast cells and concentrated in the outer cortical layer (Spribille et al., 2016). While these yeast cells belonged to a monophyletic lineage related to the genus *Cyphobasidium* (*Cyphobasidiales, Cystobasidiomycetes, Pucciniomycotina*), their uncultured forms, which probably belong to dozens of species, remain unknown.

The traditional understanding of lichens as a two-component systems is presently being reconsidered. Analysis of the whole microbial complex in the thalli is required for more precise study of the functioning of

this system. Yeasts have long been considered a facultative component of lichens, developing in the zones of degradation. Ability of many yeast species to synthesize biologically active compounds, including plant hormones (Streletskii et al., 2016) may, however, indicate a special regulatory role of yeasts in the lichen thallus.

Apart from the Arctic and Antarctic regions, lichens are a necessary component of the plant cover in the Russian subarctic zone, which is located between 60° and 70° N. The Pertsov White Sea Biological Station (WSBS MSU) is located on the Kindo Peninsula, 1 km from the Arctic Circle (66°34′ N) and is an important scientific center of this region. A total of 168 lichen species grows at the peninsula (*Katalog...*, 2008). While yeast population of soil and plant substrates and of the littoral in the vicinity of the station has been studied thoroughly (Babjeva and Reshetova, 1998; Kachalkin, 2014), lichens were not analyzed in these works.

Apart from more complete assessment of yeast diversity in Subarctic Russia, investigation of the yeast component in the lichens will provide quantitative data on the yeast population and its role. The goal of the present work was to analyze yeast abundance, taxonomic structure, and localization of yeast communities in the lichens of the Kindo Peninsula.

MATERIALS AND METHODS

Subjects of the research were the thalli of the lichens *Bryoria lanestris, Cladonia arbuscula, C. cornuta, C. deformis, C. rangiferina, C. squamosa, C. stellaris, Hypogymnia physodes*, *Icmadophila ericetorum, Nephroma arcticum, Peltigera canina, P. leucophlebia, P. membranacea*, and *Ramalina pollinaria*. The samples were collected in August 2016 at the Kindo Peninsula in the vicinity of WSBS MSU at the area occupied by a young pine forest, a *Sphagnum* bog, mixed forest, and pine forest on the coastal rocks. To compare the lichen yeast population with that of other background substrates, soil (the upper humus horizon) and some vascular plants (*Calluna vulgaris, Vaccinium myrtillus*, and *V. vitis-idaea*) were sampled. Sterile gloves and instruments were used to prevent contamination of the lichen thalli with alien microflora (tweezers and scissors were treated with 70% ethanol and flamed). The distance of 45 to 50 cm from the samples prevented transfer of contaminating microorganisms to the sampled lichens. The thalli were transferred into sterile plastic bags and sealed. Prior to analysis, the samples were stored at 15–20°C (for short-term storage and transportation) or at 8°C (storage under laboratory conditions).

The number of analyzed samples was 99.

Yeast abundance and species composition were studied by plating. Microbiological analysis was carried out five to seven days after sampling. The samples of *Cladonia* epigeal lichens were separated into three layers (the lower one, adjacent to soil, the intermediate one, and the upper growth zone most remote from soil), from each separate platings were made. Homogenized thalli (~0.4 g) were diluted 1 : 50 with sterile water in test tubes. The suspensions were vortexed for 15 min at 2000 rpm (MultiReax, Heidolph, Germany) and plated in triplicates onto glucose-peptone-yeast medium (GPY agar) containing the following (g/L): glucose, 20; peptone, 10; yeast extract, 5; agar, 20; and levomycetin (500 mg/L) for suppression of bacterial growth. The plates were incubated for five to seven days at 20–22°C. Grown yeast colonies were examined under a dissection microscope to determine and enumerate their morphological types. Representatives of each colony type were isolated in pure cultures. Yeasts from plants and soil were isolated according to the same procedure from 1 : 50 and 1 : 10 dilutions, respectively.

Species identification was carried out by analysis of the sequences of the D1/D2 domains of the 26S rDNA region (LSU). DNA isolation and PCR were carried out as was described previously (Glushakova et al., 2016). DNA was sequenced using the Big Dye Terminator V3.1 Cycle Sequencing Kit (Applied Biosystems, United States), and reaction products were analyzed on an Applied Biosystems 3130xl Genetic Analyzer at Syntol (Moscow, Russia). The NL4 primer was used for sequencing (5'-GGT CCG TGT TTC AAG ACG G). The results were identified using the data from NCBI GenBank (ncbi.nlm.nih.gov) and the MycoID database (www.mycobank.org).

RESULTS

Yeast abundance on the studied lichens varied from 1.7 to 3.5 × 10^3 CFU/g (Table 1). Abundance of cultured yeasts on the studied plants exceeded 8 × 10^3 CFU/g, while in the upper humus horizon (topsoil) of the studied soil samples it was barely 10^3 CFU/g. Thus, yeast abundance on lichens was slightly lower than on the studied xerophilic bog plants (*Calluna vulgaris, Vaccinium myrtillus*, and *V. vitisidaea*). However, in the case of mesophilic and hydrophilic plants, which may harbor up to 10^6 CFU/g (Fonseca and Inácio, 2006; Glushakova and Chernov, 2007), the difference in abundance of epiphytic yeasts is much higher. Yeast numbers on lichens were also somewhat lower than those for the moss sod, where it reached 3–10 × 10^3 CFU/g (Kachalkin and Yurkov, 2012).

The numbers of yeasts isolated from lichens may depend significantly on the part of the thallus studied. In the uppermost layer of the epigeal *Cladonia* lichens, which is most remote from soil and acts as the growth zone, yeasts number exceeded 6 × 10^3 CFU/g, being slightly, but significantly higher for all species, and decreased gradually from the intermediate part of the

Table 1. Relative abundance (%) and numbers of yeasts on the studied lichens, plants, and soils

Species	*Bryoria lanestris*	*Cladonia* spp.	*Hypogymnia physodes*	*Icmadophila ericetorum*	*Nephroma arcticum*	*Peltigera canina*	*Peltigera leucophlebia*	*Peltigera membranacea*	*Ramalina pollinaria*	Plants	Soils
Aureobasidium pullulans	4.97	2.17	4.13	1.20	6.70	–	–	1.87	5.07	21.98	10.76
Bannozyma arctica	–	2.81	–	–	–	–	–	–	–	–	–
Candida friedrichii	–	0.15	–	–	–	–	–	–	–	0.95	–
Candida parapsilosis	–	0.03	–	–	0.87	–	–	–	–	0.55	–
Candida sphagnicola	92.87	80.73	72.03	87.17	67.13	96.53	96.73	62.87	68.13	1.25	2.06
Debaryomyces hansenii	–	0.70	–	–	–	–	–	–	–	3.42	3.68
Dothiora cannabinae	0.57	6.35	11.27	–	11.07	–	–	19.87	16.20	1.82	1.64
Dothiora europea	–	1.87	3.00	4.53	2.87	3.47	3.27	7.70	1.67	5.30	0.38
Dothiora schizospora	–	0.79	–	3.97	–	–	–	5.40	–	–	1.11
Filobasidium unigutulatum	–	0.26	–	–	–	–	–	–	–	17.28	8.56
Meyerozyma guilliermondii	–	1.06	4.57	3.13	1.90	–	–	–	1.87	3.13	8.09
Phaffia sp. KBP Y-5978	0.37	0.15	–	–	–	–	–	–	–	–	–
Rhodotorula mucilaginosa	1.23	2.74	5.00	–	9.47	–	–	2.30	3.33	34.05	55.00
Sporobolomyces roseus	–	0.12	–	–	–	–	–	–	3.73	0.23	–
Vishniacozyma carnescens	–	0.11	–	–	–	–	–	–	–	10.03	8.73
Ascomycetes, %	98	94	95	100	91	100	100	98	93	38	28
Numbers, log(CFU/g)	3.54	3.43	3.49	3.24	3.27	3.24	3.36	3.41	3.47	3.93	2.98

thallus to the lower layer contacting with soil (Table 2). Similar increase in yeasts number on the parts of a thallus growth zone most remote from the soil was observed for all studied *Cladonia* species.

Yeast species diversity. Among 15 yeast species isolated from all the samples, 9 belonged to ascomycetous and 6 to basidiomycetous yeasts (Table 1). Apart from *Bannozyma arctica* and *Phaffia* sp. KBP Y-5978, most species were found both on lichens and in the underlying soil and on surrounding plants. The structure of the lichen yeast communities was, however, fundamentally different from those of other substrates. While 91 to 100% of the isolates obtained from lichens belonged to ascomycetous species, ascomycete share in soil and on plants did not exceed 30–40%. Our finding on predominance of basidiomycetes in soils and on the plants of the Kindo Peninsula are supported by the earlier data of Babjeva and Reshetova (1998).

Candida sphagnicola was the absolutely predominant species on lichen thalli. It was originally found and described in 2012 as one of the few ascomycetous yeast species occurring on *Sphagnum* moss in the Tver region (Russia) (Kachalkin and Yurkov, 2012). Investigation of association of this species with specific parts of *Cladonia* talli revealed its highest abundance in the lower part adjacent to soil (Table 2). Anamorphous *Dothiora* yeast species (*D. cannabinae, D. europea, D. schizospora*) constituted a significant share of ascomycetous yeasts isolated from lichens and associated with the upper, actively growing part. Members of the genus *Dothiora* are widespread plant pathogens capable of epiphytic existence; some species of the same subclass *Dothideomycetidae* are known as lichen mycobionts (Schoch et al., 2009). *Bannozyma arctica* (formerly *Rhodotorula arctica*) belongs to the rare yeast species. It was originally described based on Far Eastern soil strains. This species was also previously found on Antarctic *Usnea* lichens (Santiago et al., 2015). *Phaffia* sp. KBP Y-5978 is another rare species, which is phylogenetically related to *Phaffia* sp. CBS 11768, the strain isolated from soil in Germany, and differs by ~8% from *Phaffia rhodozyma* according to the sequences of the D1/D2 rDNA domains. These genetic differences indicate that the isolate designated as *Phaffia* sp. may belong to a new species and probably to a new genus (Vu et al., 2016).

Apart from these species, the lichen yeast population included euribiotic ascomycetes (*Aureobasidium pullulans, Candida friedrichii, Debaryomyces hansenii*, and *Meyerozyma guilliermondii*) and an opportunistic pathogen *Candida parapsilosis*. Basidiomycetous yeasts were represented by *Tremellomycetes* known as soil and plant inhabitants (*Filobasidium unigutulatum* and *Vishniacozyma carnescens*), as well as red-pigmented epiphytic and eurybiont species from *Sporidiobolaceae* (*Sporobolomyces roseus* and *Rhodotorula mucilaginosa*). Among these species, *A. pullulans, C. parapsilosis, D. hansenii, Rh. mucilaginosa*, and *Sp. roseus* strains have been repeatedly isolated from Arctic and Antarctic lichens (Santiago et al., 2015; Pankratov et al., 2017).

Structure of the lichen yeast communities differed significantly from the yeast population of the studied plants and soils, although many species isolated from lichens were isolated from surrounding substrates as well. The absolute dominant in the yeast community of plants was an eurybiotic dark-pigmented species *A. pullulans*. Predominance of this species among the epiphytes of vascular plants of the Kindo Peninsula was reported previously, as well as isolation from plant substrates of the species *D. hansenii, Rh. mucilaginosa,* and *Sp. roseus,* which were isolated in the course of the present work (Babjeva and Reshetova, 1998). These species, as well as *C. parapsilosis* and *M. guilliermondii,* were also isolated from the White Sea littoral (Kachalkin, 2014). These species were also isolated from lichens, although their relative abundance on plants and in soil was much higher, except for the species *C. parapsilosis* and *Sp. roseus*. Predominant species on plants and in soil below the plants were *F. unigutulatum* and *V. carnescens*, which were infrequently isolated from lichens.

As was stated above, *C. sphagnicola*, which has not been reported as a lichen-inhabiting species, was found to predominate in the yeast community of the Kindo Peninsula lichens. The differences in the yeast population of different lichen species and genera amounted to the varying share of certain yeast species with low relative abundance or of the minor components within the community.

DISCUSSION

Analysis of the literature data revealed that while the yeast population of Arctic and Antarctic lichens was represented mainly by basidiomycetous species, ascomycetous yeasts were often isolated from African lichens (see review by Pankratov et al., 2017). Predominance of ascomycetes on the northern taiga lichens may be explained by development of conditions favoring yeast preservation and growth, which is known for this biocenosis. The yeast population of Arctic and Antarctic soils and plants is represented mainly by basidiomycetes. For the Arctic and Antarctic soil and plant substrates, the share of basidiomycetous yeasts was estimated early as 82 and 89%, respectively (Connell et al., 2014; Zalar and Gunde-Cimerman, 2014). In the zone of the northern taiga forests, the share of basidiomycetous yeasts isolated from plants and soil is significantly lower, 65% (Babjeva and Reshetova, 1998). Moreover, the moss sod may act as a reservoir for the preservation of basidiomycetous yeasts in the northern taiga forests, where abundance and species diversity of these yeasts in significantly higher than the values for ascomycetous yeasts (Kachalkin et al., 2008; Kachalkin and Yurkov, 2012). The number of bryo-

Table 2. Structure (relative abundance, %) and numbers of the yeasts from different layers (upper, intermediate, and lower) of *Cladonia* epigeal lichens

Species	*Cladonia arbuscula*	*Cladonia cornuta*	*Cladonia deformis*	*Cladonia rangiferina*	*Cladonia squamosa*	*Cladonia stellaris*
Aureobasidium pullulans	3.2 3.6 0.5	5.4 – –	– 3.2 –	3.1 – 2.9	7.4 – –	0.7 6.1 2.9
Bannozyma arctica	25.1 15.0 10.5	–	–	–	–	–
Candida friedrichii	0.5 – –	–	–	– 0.7 –	–	– 0.9 0.6
Candida parapsilosis	0.3 – –	–	–	0.2 – –	–	–
Candida sphagnicola	50.3 60.1 76.3	87.4 100 100	78.1 80.6 98.2	64.7 77.9 87.5	55.8 95.4 99.0	69.7 81.1 91.0
Debaryomyces hansenii	2.3 1.7 0.8	–	–	– 0.5 1.2	5.4 – –	0.7 – –
Dothiora cannabinae	8.8 7.2 6.0	4.0 – –	13.7 12.5 1.8	9.5 7.1 1.9	12.8 4.6 –	21.0 3.4 –
Dothiora europea	2.1 5.0 1.2	3.2 – –	–	3.3 0.5 0.9	7.0 – 1.0	3.7 2.9 2.9
Dothiora schizospora	2.3 0.6 1.0	–	–	0.4 0.3 0.7	6.6 – –	2.4 – –
Filobasidium unigutulatum	– 1.9 –	–	–	1.0 0.4 1.3	–	–
Meyerozyma guilliermondii	1.4 1.3 3.4	–	4.2 – –	1.5 2.5 2.6	–	– 1.9 0.2
Phaffia sp. KBP Y-5978	– – 0.3	–	–	0.7 0.4 –	–	0.4 – 0.9
Rhodotorula mucilaginosa	3.6 3.6 –	–	4.0 3.7 –	13.6 9.2 1.1	3.8 – –	1.5 3.7 1.5
Sporobolomyces roseus	0.1 – –	–	–	2.0 – –	–	–
Vishniacozyma carnescens	–	–	–	– 0.8 –	1.2 – –	–
Numbers, log(CFU/g)	3.80 3.52 3.06	3.68 2.51 2.98	3.51 3.39 3.10	3.81 3.62 3.13	3.75 3.10 2.60	3.72 3.57 3.01

phytic species in the Kindo Peninsula area around the station exceeds 230 (*Katalog...*, 2008). The presence of both moss and lichen mats in the forest may result in the separation of ecological niches for different types of microbial inhabitants, including yeasts. The moss and lichen cover may be responsible for establishment of selective conditions depending on yeast adaptation to specific environments.

Apart from development of the favorable and protective conditions for yeast preservation and growth in lichen mats (nutrient source, water reserve, and protection from temperature fluctuations), lichens are known to produce specific organic compounds with antibiotic properties. Some lichen species exhibit antibiotic activity against synanthropic yeast species of the genera *Candida* and *Malassezia* (Açikgöz et al., 2013; Pandey et al., 2013). Other members of the lichen thallus microbial consortia, including bacteria, are also capable of antibiotic synthesis (Pankratov et al., 2017). Thus, apart from the possible negative effect of the lichen, the yeast population should be adapted also to impacts from other colonizing microorganisms. Such negative impacts may be leveled out in extreme Arctic and Antarctic habitats due to the stronger effect of unfavorable environmental factors.

Detection of high yeast abundance in the upper, growing part of the lichen thallus, where the photosynthetic activity of the photobiont is the highest, is an important result of this work. Photobiont cells (*Trebouxia* and *Coccomyxa* in the studied lichens) are known to produce considerable amounts of polysaccharides and polyols as ribitol, mannitol, and arabitol (Woranovicz-Barreira et al., 1999; Elix and Stocker-Wörgötter, 2009; Alam et al., 2015). Many yeast species, including *C. sphagnicola,* the dominant on the studied lichens, are known to assimilate polyols (Kachalkin and Yurkov, 2012). Since lichens are consortia combining the functions of an autonomous symbiosis and an ecosystem, activity of endobiotic bacteria may result in polysaccharides becoming more available to the yeast population as well.

Our results show that the yeast population of the Kindo Peninsula lichens is represented by the species of diverse taxonomic and ecological groups. Association with specific parts of the lichen thallus was shown for some yeast species. A number of species has been previously repeatedly isolated form other substrates in this region or from various lichen species of diverse regions. Predominance and high diversity of ascomycetous yeasts was not previously reported for Karelia lichens. Analysis of the results makes it possible to assume that in the lichens of the subarctic zone conditions are formed for the preservation and development of specific yeast communities which considerably differ from those of typical higher plants, mosses, phyllosphere, and soil yeast complexes.

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