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EXPERIMENTAL ARTICLES

The Structure of the Micromycete Complexes of Oligotrophic Peat Deposits in the Southern Taiga Subzone of West Siberia

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Abstract—The analysis of the micromycete complexes of oligotrophic peat deposits in the Vasyugan Marsh by direct count and culture methods showed that micromycete carbon comprises no more than 3% of the total peat carbon and that the microscopic fungal biomass varies from 2 to 13 tons/hectare, depending on the season and the peat deposit thickness. Fungal spores were found in all layers of the peat deposits, whereas the mycelium was found only in the active peat layer. The high abundance of eukaryotic cells in the peats was due to the presence of yeastlike cells rather than fungal spores. Analyses by culture methods showed that micromycetes were present in all peat layers and that their abundance tended to decrease with depth, except for yeasts, which were uniformly distributed in a vertical direction. The micromycete complexes of the peat deposits were similar in their diversity and abundance of dominant species but differed in the composition of minor species. Peat yeasts were dominated by ascomycetes.

Key words: oligotrophic peat deposit, micromycete complex, abundance, morphological structure, taxonomic composition.

Microscopic fungi are the primary degraders of plant debris. In turn, they serve as a source of nutrition for other microorganisms. For this reason, to understand the regularities of organic matter transformation in soils, it is necessary to estimate the mass and to analyze the taxonomic structure of soil fungal communities. Such studies are of special interest in the case of swampy ecosystems, since their peat deposits contain vast amounts of organic matter.

The micromycete complexes of the Siberian peat soils were earlier investigated by culture methods ([1, 2], which do not allow the mycelial component of these complexes to be evaluated, as about 90% of colonies grown on agar media are germinated from fungal spores [3]. On the other hand, the method of direct microscopic count of soil microorganisms [4] makes it possible to determine the abundance of microscopic fungi in soil, to differentiate their mycelium and spores, and to distinguish the dark- and light-pigmented mycelia. The results obtained by this method are more accurate than those obtained by culture methods, which is of particular importance when estimating the ecological diversity indices.

Earlier studies of the taxonomic composition of the micromycete complexes of peat deposits in West Siberia were limited to the determination of their species composition and abundance. Ecologically, however, it is more important to distinguish a typical micromycete complex and to describe it in terms of the common ecological indices, such as the occurrence rate of a species, the species diversity index, and the similarity coefficient. The aim of the present work, which is part of the complex stationary investigations of the Vasyugan Marsh [5], was to obtain representative data on the number, concentration, amount, morphological structure, and taxonomic composition of micromycete complexes in the oligotrophic peat deposits of the southern taiga subzone of West Siberia.

MATERIALS AND METHODS

Investigations were carried out in the natural swampy ecosystem (the Vasyugan Marsh) of the southern taiga subzone of West Siberia. The landscape profile crossed the following three types of peat biogeocenoses (BGC): the tall pine–shrub–sphagnum BGC (station 2), the low pine–shrub–sphagnum BGC (station 3), and the sedge–sphagnum bog BGC (station 5) [5]. The profile with the geochemically related landscape biogeocenoses is a representative ecosystem of the Bakchar marshy region.

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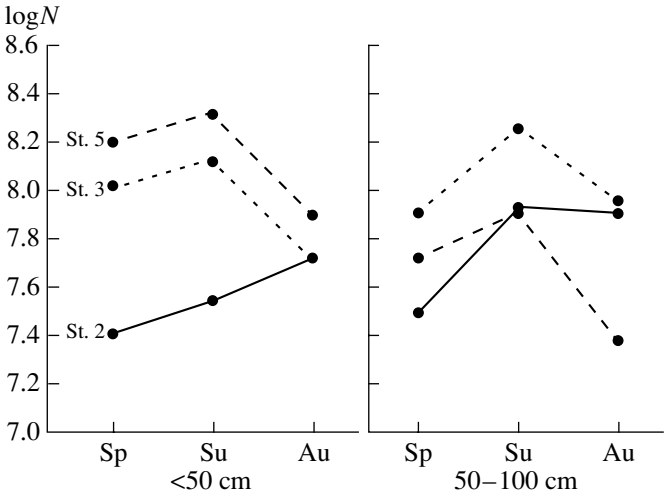

Fig. 1. The number of fungal spores (*N*) in the active layer of the oligotrophic peats at stations 2, 3, and 5 in spring (Sp), summer (Su), and autumn (Au).

Samples for analysis were taken during the spring, summer, and autumn periods. The thickness of peat deposits varied from 0.9 m (st. 2) to 3 m (st. 3 and st. 5).

The total number and the biomass of micromycetes were determined by the method of direct count under a luminescence microscope. Peat samples were preliminarily treated in a UZDN-1 ultrasonic disintegrator to desorb fungal cells. The fungal mycelium and spores were stained with calcofluor white [4]. The eukaryotic microbial biomass was calculated with allowance for the diameter of fungal hyphae and spores, using the following formulas: $0.83r^3 \times 10^{-12}$ (spores) and $0.628r^2 \times 10^{-6}$ g (mycelium) [6].

The relative content of microbial carbon in the organic matter of peat was calculated on the basis of its organic carbon content [7] and data on the microbial biomass content. It was assumed in the calculations that carbon comprises 50% of the eukaryotic microbial biomass.

The abundance and the taxonomic composition of soil micromycetes were studied by plating soil suspension dilutions on the acidified Czapek agar [8]. The micromycetes were identified to a species level using standard manuals [9, 10]. The abundance and the taxonomic composition of yeasts were studied by plating soil suspension dilutions on wort agar acidified with lactic acid. The yeasts were obtained in enrichment cultures at room temperature and identified using the manual [11]. Data on the total number of microscopic fungi were expressed in colony-forming units (CFU) per g peat.

The occurrence rate (OR) of various fungal genera was defined as the ratio of the number of the peat samples in which a given genus was detected to the total number of the samples analyzed.

RESULTS AND DISCUSSION

The total length of fungal mycelium in the peat deposits under study varied from 100 m/g to 14 km/g. The content of fungal spores varied from 10 to 210 million spores/g peat. These values characterizing the population of microscopic fungi in the oligotrophic peats are close to those obtained in the study of peat deposits in the Tver region [12].

The active layer of peat deposits extends from the bog surface to the average annual lower level of bog waters during the warm season. The thickness of this layer varies from 30 to 100 cm. The effect of the peat layer depth (analyzed were the 0–25, 25–50, and 50–100 cm peat layers), season (spring, summer, and autumn), and the type of peat deposit (stations 2, 3, and 5) on the ecological parameters of micromycete complexes was studied in terms of variance analysis. The abundance of micromycetes was found to depend (in a statistically significant manner) on the type of peat deposit and on the season. At the same time, the variation in the population density of microscopic fungi with respect to the peat depth within the active layer turned out to be statistically insignificant. With respect to the seasonal dynamics of fungal spores, the peat deposits fell into two groups. The first group included the shallow peat deposit at st. 2, in which the content of fungal spores increased from spring to the summer–autumn period. The second group included the thick peat deposits at st. 3 and st. 5, in which the content of fungal spores was maximal in summer and minimal in autumn. In general, the content of fungal spores in the thick peat deposits at st. 3 and st. 5 was higher than in the shallow peat deposit at st. 2 (Fig. 1). Conversely, the content of the fungal mycelium was higher in the peat at st. 2 than at st. 3 and st. 5. These differences may be determined by different redox conditions in these two types of peat deposits.

It should be emphasized that the population of micromycetes significantly depended on the season and the type of peat deposit and insignificantly depended on the peat layer depth only within the active layer. In deeper layers of the thick peat deposits at st. 3 and st. 5, the dependence of the micromycete population on the first two factors became weaker, whereas its dependence on the peat layer depth became stronger: the Fisher significance test F with respect to the peat layer depth was equal to 23.7 at significance level $p < 0.0001$ for fungal mycelium and 22.2 at significance level $F < 0.0001$ for fungal spores. Unlike the fungal spores, which were detected in all the peat horizons, the fungal mycelium was mainly detected within the active peat layer. The abundance of microscopic fungi was typically greater in the upper layers of the peat deposits.

The concentration of eukaryotic microorganisms (the content of the microbial biomass in mg per g peat) varied from 2 to 44 mg/g peat in the upper 0.5-m-thick peat layer, from 5 to 56 mg/g in the 1-m-thick layer, and from 11 to 36 mg/g peat in the 3-m-thick layer (Table 1).

Table 1. Seasonal variations in (A) the concentration of microscopic fungi, (B) the fungal biomass, and (C) the percent of fungal carbon in the total carbon pool of the oligotrophic peat deposits

Peat at	A, mg/g peat			B, kg/m^2			C, %		
	0.5-m layer	1-m layer	3-m layer	0.5-m layer	1-m layer	3-m layer	0.5-m layer	1-m layer	3-m layer
St. 2	13–44	16–56	–*	0.2–0.9	0.4–1.3	–*	1–2	0.5–1	–*
St. 3	2–8	10–21	13–24	0.05–0.1	0.2–0.4	0.3–0.5	0.2–1	0.4–0.8	0.1–0.2
St. 5	2–26	5–30	11–36	0.05–0.7	0.2–0.9	0.5–1.2	0.2–3	0.3–2	0.3–1

* Sign "–" indicates that no data available, as the thickness of the peat deposit did not exceed 1 m.

The concentration of micromycetes was at a maximum in the shallow peat deposit at st. 2, where most microscopic fungi (80% of the total eukaryotic microorganisms) concentrated in the upper 0.5-m-thick peat layer. In the peat deposits at st. 3 and st. 5, whose thickness reached 3 m, microscopic fungi were distributed more uniformly: their fraction in the upper 50-cm peat layer comprised 35%, while 38% in the 50–100 cm layer, and the remaining 27% in the 100–300 cm layer.

In the thick peat deposits (st. 3 and st. 5), the micromycete population was primarily determined by the peat layer depth ($F = 93.5$ at $p < 0.0001$), whereas its dependence on the season ($F = 33.4$ at $p < 0.0001$) and especially on the type of peat deposit ($F = 17.8$ at $p < 0.0004$) was weaker. The relatively uniform vertical distribution of micromycetes in the thick peat deposits was obviously due to their organogenic nature. In general, the vertical distribution of microorganisms in most soils differs from that observed in the thick peat deposits: their concentration decreases in the direction from the litter to mineral soil and then decreases further with the mineral soil depth.

Seasonal dynamics in the micromycete population was most profound in the upper layer of the 3-m-thick peat deposits. In the peat deposit at st. 3, the concentration of the eukaryotic microbial biomass was maximal in summer. At the same time, at st. 5 situated on the periphery of the open sedge–sphagnum bog, the concentration of micromycetes was maximal in spring. At depths of 1–3 m, the dependence of the micromycete population on the season and the type of peat deposit was insignificant (Fig. 2).

Thus, the peat deposits under study differed in the concentration and the vertical distribution of fungal biomass. In the shallow peat deposit, the total content of eukaryotic microorganisms was greater than in the thick peat deposits, and they concentrated in the upper 0.5-m-thick peat layer. In the thick peat deposits, the vertical distribution of the microbial biomass was relatively uniform. The statistically significant dependence of the micromycete population on the peat layer depth, the type of peat deposit, and the season was only revealed for the 3-m-thick peat deposits.

Depending on the season, the eukaryotic microbial biomass varied from 200 g/m^2 to 1.3 kg/m^2 in the 1-m peat layer and from 300 g/m^2 to 1.2 kg/m^2 in the 3-m peat layer (Table 1). The total content of microscopic fungi in the peat deposits (2–13 tons/ha) was no less than in eluvial soils. The relative content of the micromycete carbon in the total organic carbon of the peat did not exceed 3% in the 0.5-m-thick layer, 2% in the 1-m-thick layer, and 1% in the 3-m-thick layer (Table 1).

The peat deposits under study differed in the morphological structure of the eukaryotic microbial biomass, namely, in the proportion between the active component of microscopic fungi (mycelium) and their inactive component (spores). In the shallow peat deposit at st. 2, the fungal mycelium dominated at depths of 0–75 cm, whereas fungal spores absolutely dominated at depths of 75–100 cm, where their fraction reached 84–100%. In the thick peat deposit at st. 3, fungal spores dominated at all depths: in the upper layer of this peat, the content of fungal spores was 10–30% greater than that of the fungal mycelium, whereas the lower peat layer contained 100% fungal spores. In this characteristic, the peat at st. 5 was intermediate between the peats at st. 2 and st. 3: the fungal mycelium dominated at depths shallower than 1.5–2 m, whereas fungal spores dominated at deeper depths.

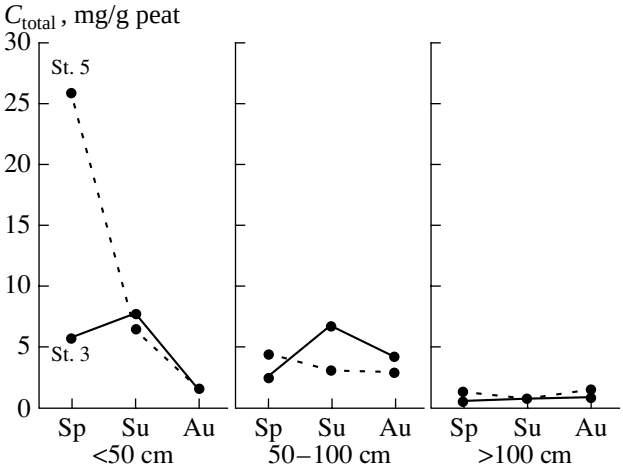

Fig. 2. The total concentration of the micromycete mycelium and spores (C_{total}) in the thick oligotrophic peat deposits at stations 3 and 5.

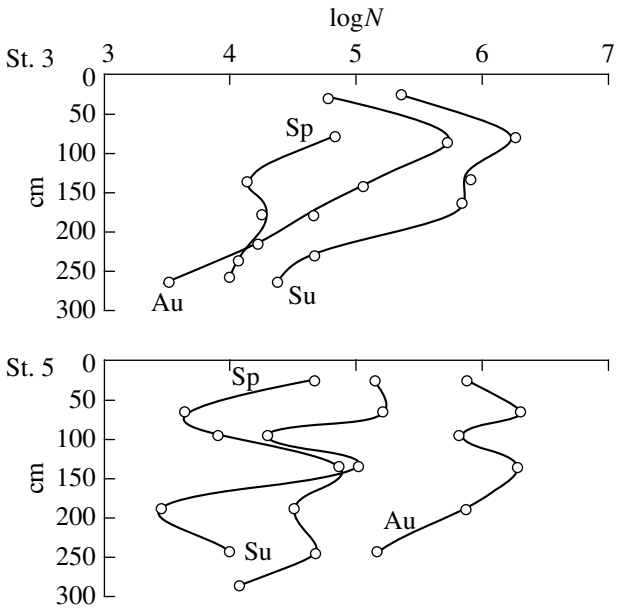

Fig. 3. The number of yeasts (*N*) in the thick oligotrophic peat deposits at stations 3 and 5 in spring (Sp), summer (Su), and autumn (Au).

Thus, the morphological structure (the proportion between the mycelium and spores) of the micromycete complexes of the peat deposits is very variable with respect to both the peat depth and the season. This implies that the peat micromycetes, or at least a fraction of them, undergo multiplication. Some fungal spores are indistinguishable from yeast cells. Accordingly, the high population of eukaryotic cells in the peats can be explained by the high content of yeastlike cells rather than of fungal spores. This suggestion is confirmed by our earlier observation that the major portion of seemingly fungal spores found in the upland peat of the Tver region multiplied by budding, whereas the number of genuine fungal spores, which germinate with the formation of the germ tube, was low [13].

Table 2. The occurrence rates of yeasts in the oligotrophic peat deposits

Genus	Number of species of a given genus	Occurrence rate, %
Basidiomycetous yeasts		
Cryptococcus	5	67
Rhodotorula	6	71
Sporobolomyces	1	55
Trichosporon	1	19
Ascomycetous yeasts		
Candida	4	19
Debaryomyces	1	7
Pichia	1	7

Oligotrophic peats are favorable for the growth of yeasts, since such peats have a high content of plant debris and are characterized by low pH values and anoxic conditions. For the thick peats at st. 3 and st. 5, we determined the total and relative abundances of yeasts, as well as their distribution, diversity, and dominant and indicator species.

The total yeast population of these peats varied from hundreds to millions of CFU per g peat, averaging 10^3 CFU/g peat, which is considerably greater than the content of yeasts in the mineral soil horizons and close to the content of yeasts in the forest litter. Unlike the distribution of yeasts in the automorphic forest soils, where yeasts concentrate in the superficial layer, the distribution of yeasts in the peats at hand was uniform, except for the deep peat layers, where the yeast population was low (Fig. 3). The vertical variation in the yeast population was greater than its longitudinal variation (i.e., along the landscape profile), indicating the statistical significance of the vertical variation. Seasonal variations in the population and diversity of yeasts were low: the Shannon diversity index of yeasts varied from 1.4 to 1.7 for the peat at st. 3 and from 1.2 to 1.5 for the peat at st. 5.

Yeasts are considered to be ecologically related to the initial succession stages of plant debris. A statistical analysis showed that there is a negative correlation between the yeast population and the degree of peat degradation ($r = -0.44$ at $p < 0.05$). This implies that the lower the degree of peat degradation, the higher the yeast population of the peat.

We succeeded in isolating 114 yeast strains belonging to 17 species (either cosmopolitan or specific to peats [14, 15]) of 7 genera. Some yeast isolates of the asporogenous genera *Candida*, *Cryptococcus*, and *Rhodotorula* were not identified to a species level (Table 2). The isolates were mainly represented by eurybiont basidiomycetous yeasts, which were dominated by three species (*Cryptococcus albidus* Skinner, red epiphytic *Rhodotorula glutinis* Harrison, and *Sporobolomyces roseus* Kluyver et van Niel). The stenobiont basidiomycetous yeasts of the genera *Pichia*, *Debariomyces*, and *Candida* were frequently encountered as well. Of interest is the isolated rare species *Candida paludigena* Golubev et Blagodatskaya, which is believed to be associated with the upland swampy ecosystems [16]. The yeast population of the peats exhibited a higher occurrence rate and diversity of ascomycetous yeasts as compared with other soil and plant habitats.

The population of other micromycete groups in the peats was low (from 0.2 to 28.6 thousand CFU/g peat), which is one to two orders lower than in the lowland peat deposits of the Tver region [16]. Multifactorial variance analysis showed that the micromycete population depended on the peat layer depth, season, and the type of peat deposit, the peat layer depth being the most statistically significant factor ($F = 24.3$ at $p < 0.005$).

Analysis by culture methods revealed micromycetes at all depths, up to 3 m. As a rule, the density of micromycetes decreased with the peat layer depth, was maximal in spring and autumn, and minimal in summer. Similar trends in the seasonal dynamics of micromycetes were observed for other types of soils, including hydromorphic ones [17].

Among the isolated 55 species of micromycetes belonging to 24 genera, most species (94.6%) were typical soil saprotrophs from the class *Deuteromycetes*. The most frequently encountered micromycetes were *Penicillium* and the sterile mycelium *Mycelia sterilia* (Table 3). It should be noted that the latter is also the dominant component of the micromycete complexes of the swampy tundra soils [18]. The third most frequently encountered micromycete was *Trichoderma*. Micromycetes of the genera *Phialophora* and *Oidiodendron*, as well as an unidentified mycelium and yeasts, were encountered rarely. The range of accidental genera in the peats under study was very wide (Table 3).

In general, the peat deposits were dominated by light-pigmented micromycetes of the family *Moniliaceae* (the genera *Penicillium*, *Trichoderma*, *Acremonium*, *Aspergillus*, *Geotrichum*, etc.), which are the typical components of the micromycete complexes of northern nonimpacted areas. The relative abundance of dark-pigmented micromycetes of the family *Dematiaceae* (the genera *Aurebasidium*, *Oidiodendron*, *Phialophora*, etc.) varied from 0 to 44%, depending on the season and the peat layer depth. The seasonal dynamics of this group of micromycetes was observed only for the upper peat layer, where their relative abundances were 0, 21, and 34% in spring, summer, and autumn, respectively. The presence of fungi of the family *Dematiaceae* in the upper peat layer can be explained by an increased insolation of this layer in summer and by the intake of dark-pigmented epiphytic fungi from the forest litter in autumn, since it is known that dark pigments (melanins) protect micromycetes from various unfavorable factors, such as excess insolation and anthropogenic impact [19]. In the lower peat horizons, the relative abundance of dark-pigmented micromycetes was seasonally stable and did not exceed 20%.

The widest species diversity of peat micromycetes was observed for the genus *Penicillium* (20 species), the most abundant and frequently encountered species being *P. funiculosum* Thom, *P. lividum* Westling, *P. thomii* Maire, and *P. spinulosum* Thom detected in all peat horizons in all seasons. Seasonal dependence was observed only for representatives of the genus *Phialophora*, which were detected in the peats at the end of the vegetative period.

The peat at st. 3 gave rise to the greatest number of isolates (32 species). For comparison, the number of species isolated from the peats at st. 2 and st. 5 was equal to 26 and 23, respectively. Typically, micromycete species were uniformly distributed in the peat horizons. However, some species (e.g., *Trichoderma koningii* Oud. and *T. viridi* Pers.) were mainly detected in the upper peat horizon and did not exhibit seasonal dependence. Therefore, the primary ecological factor of these species is the peat depth.

Table 3. The taxonomic composition of the micromycete complexes of the oligotrophic peat deposits

Abundance group	Genera
Dominant (OR > 60%)	*Penicilium, Mycelia sterilia*
Frequent (OR = 30–60%)	*Trichoderma*
Rare (OR = 10–30%)	*Phialophora, Oidiodendron, Aureobasidium, Candida,* nonidentified mycelium
Occasional (OR < 10%)	*Ghrysosporium, Septonema, Acremonium, Hainessia, Aspergillus, Mortierella, Chloridium, Doratomyces, Geotrichum, Gliocladium, Gliomastix, Mucor, Paecilomices, Torula, Zygodesmus,* nonidentified yeastlike mycelium

Note: Parenthesized is the range of the occurrence rates (OR).

The Sörensen similarity coefficient of the micromycete complexes of the peats was relatively small (0.44–0.48), indicating their noticeable difference in the taxonomic composition (largely due to the variable content of micromycetes with low temporal and spatial occurrence rates).

The majority of the isolated micromycetes were slow-growing cellulolytics, which are typical inhabitants of all types of soil in this region. At the same time, fast-growing saccharolytic micromycetes, first of all mucorales, which mainly utilize easily degradable organic substances, were detected very rarely.

Thus, analysis by culture methods showed the presence of micromycetes in all the peat layers. The number of micromycetes was relatively small and decreased with the peat depth. The species diversity of isolated micromycetes was low. Dominant were fungi of the genus *Penicillium*, as well as *Mycelia sterilia* and light-pigmented fungi. The micromycete complexes of the peat deposits were similar in the content of dominant species but differed in the content of minor species. Dominant were slow-growing micromycetes.

To conclude, the analysis of peat samples by direct microscopic count revealed the presence of both the active component of the micromycete complex (mycelium) and its inactive component (spores). The dynamics of micromycetes in the active peat layer was largely determined by two factors, the season and the type of peat deposit. The effect of the peat layer depth was pronounced only in the thick peat deposits. In this case, fungal spores were uniformly distributed in a vertical direction, whereas the fungal mycelium was mainly detected in the upper 1-m-thick peat layer. Rarely, micromycete hyphae could be detected at depths down to 2 m.

The predominant location of the micromycete mycelium in the upper soil horizons may be related to two factors: (1) fungi are strictly aerobic organisms, so that only some fungal species can grow at relatively great depths; and (2) being saprotrophs, fungi follow the organic matter of soil, whose content decreases with depth in almost all types of soil [20]. Swampy ecosystems are characterized by a specific hydrologic regime, when their peat deposits may be flooded for a long time. Surface run-off and seasonal moisture displacement in upland marshes are observed to depths of 0.7–0.8 m, whereas filtration processes occur down to 1.5 m [21]. Marshes contain large quantities of organic matter in the form of peat deposits (plant debris of different degradation degree), whose thickness may comprise many meters. Therefore, peat might seem to favor the development of micromycetes.

Actually, however, the micromycete mycelium was found to grow only in the upper 1-m-thick peat layer, whereas yeast cells and fungal spores were more uniformly distributed over the peat horizons. The distribution and the state of various microbial groups in thick peat deposits are determined by many factors, such as the low content of oxygen in bog waters, the toxicity of phenolic compounds (which drastically increases under anoxic conditions), the presence of anticeptics and antioxidants, and the low temperature of the buried peat layers.

Some eukaryotic cells occurring at great depths were found to be viable, as is evident from their seasonal dynamics investigated by direct microscopic observation and by culture methods. It is the culture methods that allowed micromycetes to be detected in the peats at 3-m depths, whereas direct microscopic examination failed to detect the micromycete mycelium at great depths. This implies that micromycete colonies grown on nutrient media from peat samples taken from great depths originated from fungal spores.

Some fungal spores found in the upper peat layer were almost indistinguishable from yeast cells. Accordingly, the high population of eukaryotic cells in the peats under study may be explained by the high content of yeastlike cells rather than of fungal spores. This suggestion is confirmed by the observation that the major portion of seemingly fungal spores found in the peats multiply by budding, whereas the number of genuine fungal spores, which germinate with the formation of the germ tube, is low. Analysis by culture methods showed that yeasts were uniformly distributed over the oligotrophic peat deposits. The total content of yeasts in the peat deposits was considerably greater than in eluvial soils.

The content of the eukaryotic microbial biomass in the peat deposits was the same or even higher than in eluvial soils. However, as compared with the total pool of organic matter in the peats, which is mainly represented by phytomass and plant debris (mortmass), the content of the eukaryotic microbial biomass was insignificant: the carbon of micromycete origin comprised only 3% of the total peat carbon.

The micromycete complexes of the peat deposits were dominated by fungi of the genus *Penicillium*, *Mycelia sterilia*, light-pigmented micromycetes, and diverse ascomycetous yeasts.

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