ISSN 0026-2617, Microbiology, 2007, Vol. 76, No. 5, pp. 630–637. © Pleiades Publishing, Ltd., 2007.
Original Russian Text © A.V. Golovchenko, E.Yu. Tikhonova, D.G. Zvyagintsev, 2007, published in Mikrobiologiya, 2007, Vol. 76, No. 5, pp. 711–719.

EXPERIMENTAL ARTICLES

Abundance, Biomass, Structure, and Activity of the Microbial Complexes of Minerotrophic and Ombrotrophic Peatlands

A. V. Golovchenko[a,1], **E. Yu. Tikhonova**[b], **and D. G. Zvyagintsev**[a]

[a] *Faculty of Soil Science, Moscow State University, Vorob'evy gory, Moscow, 119899 Russia*

[b] *Vavilov Institute of General Genetics, Russian Academy of Sciences, ul. Gubkina 3, Moscow, 117809 Russia*

Received June 19, 2006

Abstract—A very large microbial biomass was revealed in peat bogs by means of fluorescence microscopy. In ombrotrophic peatlands, the pool of the dry-weight microbial biomass in the 1.5-m layer constituted 3–4 t/ha and was twice as high as in the minerotrophic peat bogs. Fungal biomass was predominant (55–99%) in ombrotrophic peatlands, while bacterial biomass predominated (55–86%) in minerotrophic peatlands. In ombrotrophic peatlands, the microbial biomass was concentrated in the upper layers, while in minerotrophic peatlands, it was uniformly distributed in the bulk. After drainage, the microbial pool in the ombrotrophic peatlands increased twofold; that in the minerotrophic peatlands remained at the same level. The potential activity of nitrogen fixation and denitrification was revealed across the whole profile of the peatlands. The average values of these potential activities were five times higher in the minerotrophic peatlands, where bacterial biomass predominated.

Key words: peatlands, microbial biomass, fungi, bacteria, nitrogen fixation, denitrification.

DOI: 10.1134/S0026261707050177

Until recently, inoculation has been the main method to determine the abundance of different microbial groups in peatlands [1–9]. Although this method is indispensable for determination of the relative abundance and taxonomic position of microbial isolates obtained on nutrient media, it can not provide the information concerning the microbial biomass contained within the peat strata. The use of direct microscopic methods (fluorescence microscopy) makes it possible to determine the pool of microbial biomass in the peatlands and the proportion of its main components [2, 10, 11]. The problem of viability of the microorganisms found in peatlands remains unsettled as yet [10, 12]. To obtain a definite answer, information is required concerning the emission of gases not only from the surface but also from different depths of the peat strata. The last decade has witnessed an especially active study of the carbon cycle components in bog ecosystems. The importance of bog ecosystems consists not in the rate of carbon flow, but rather in their carbon reserves that have been accumulated for centuries within the peat deposit and can be quickly converted to CO_2 in the case of inefficient exploitation [13]. Peat deposits all over the world accumulate ca. 0.14×10^9 tons of carbon (C) per year; the amount of C yearly released in the course of natural and anthropogenic destruction of peatlands is from 0.03 to 0.37×10^9 tons [14, 15]. In Russia, the estimated total carbon binding by water-logged soils (corrected for peat mining and bog reclamation) is 16×10^6 tons per year [16]. The global methane production by water-logged soils is estimated at 115 Tg CH_4 per year, i.e., approximately 25% of the global amount of methane released into the atmosphere annually [17].

Existing estimates of the nitrogenase activity and the rate of nitrous oxide emission from peat soils are extremely scarce and often contradictory [18–20].

The aim of this work was therefore to make a comparative assessment of the pool of microbial biomass and to reveal the potential activity of nitrogen fixation and denitrification in the strata of ombrotrophic and minerotrophic peatlands.

MATERIALS AND METHODS

Peatlands of natural and reclaimed swampy regions, namely minerotrophic ones under black alder forests and ombrotrophic ones under pine forests, were the subjects of study. Specifically, we studied the wetlands of the permanent test areas of the Zapadnodvinsk Forest–Bog Base of the Institute of Forestry, Russian Academy of Sciences, in Tver oblast, Russia.

The minerotrophic peatlands (with the depth of 2 m) are composed of valley woody peat and underlaid by sapropel; the ombrotrophic peatlands (with the depth of 1.5 m) are composed of high-moor, transient, and val-

[1] Corresponding author; e-mail: soilbac@soil.msu.ru

Table 1. Properties of the peat soils studied

Phytocenosis	Depth, cm	Degree of peat decomposition, %	Peat botanical composition	Ash content, %	pH
		Minerotrophic nonreclaimed			
Black alder forest, tall herbage–erns	0–3	–*	leaves (L)	–	–
	3–20	48	minerotrophic woody peat	17.4	6.4
	20–50	50	″	16.2	6.4
	50–100	50	″	16.3	6.3
	100–150	50	″	15.2	6.4
	150–190	48	″	16.0	6.4
	190–200	–	sapropel	–	6.6
		Minerotrophic reclaimed			
Black alder forest, nettle	0–3	–	leaves (L)	–	–
	3–20	50	minerotrophic woody peat	16.3	6.5
	20–50	52	″	16.3	6.5
	50–100	49	″	16.2	6.4
	100–150	51	″	16.0	6.4
	150–190	53	″	15.3	6.4
	190–200	–	sapropel	–	6.6
		Ombrotrophic nonreclaimed			
Pine forest, shrubby–sedge-sphagnum	0–6	–	living moss (magellanicum)	–	–
	6–14	–	moss dust (magellanicum)	–	–
	12–20	14	angustifolium peat	3.7	2.3
	20–50	16	magellanicum peat	2.8	2.6
	50–100	46	woody-herbaceous transitional peat	2.0	2.9
	100–130	40	sedge peat	3.6	3.4
	130–150	–	gley sands	–	–
		Ombrotrophic reclaimed			
Pine forest, shrubby–sedge	0–3	–	L	–	–
	3–6	–	F	–	–
	6–14	–	H	–	–
	14–50	16	ombrotrophic sphagnum–swampy hollow	3.1	2.9
	50–100	46	woody-sedge transitional peat	2.0	2.9
	100–130	40	sedge peat	3.6	3.4
	130–150	–	gley sands	–	–

* Not determined.

ley peat soil layers and underlaid by sands gleyed to different extents. A short characterization of the properties of the peat soils studied is given in Table 1.

The minerotrophic peatlands, both nonreclaimed and reclaimed, are characterized by an increased ash content of peat, a high degree of its decomposition, and the neutral reaction of the medium. The ash content of the ombrotrophic peatlands is not high, five- to eightfold lower than that of minerotrophic peatlands. The ombrotrophic peatlands are characterized by an acidic pH of the medium. The pH of the saline extract varied between 2 and 4. The degree of peat decomposition in the ombrotrophic peatlands depends on the botanical composition and varies across the profile from 14 to 40% (Table 1).

The experimental reclamation of peat soils was carried out in 1973 with a network of open 1.5-m deep ditches spaced 65–130 m apart.

The upper layers of the nonreclaimed minerotrophic peatlands differ form their reclaimed analogues in

Table 2. Distribution of bacteria, actinomycete and fungal mycelium, and fungal spores across the profile of minerotrophic peat soils

Peatland	Minerotrophic nonreclaimed				Minerotrophic reclaimed			
Depth, cm	Bacteria, 10^9 cells/g	Actinomycete mycelium, m/g	Fungal mycelium, m/g	Fungal spores, 10^6 cells/g	Bacteria, 10^9 cells/g	Actinomycete mycelium, m/g	Fungal mycelium, m/g	Fungal spores, 10^6 cells/g
0–20	29 ± 4	262 ± 83	70	29 ± 5	30 ± 4	405 ± 54	130	30 ± 6
20–50	37 ± 8	233 ± 17	20	29 ± 7	27 ± 7	345 ± 71	120	26 ± 4
50–75	32 ± 7	254 ± 77	0	24 ± 5	30 ± 5	414 ± 89	250	28 ± 6
75–100	22 ± 3	180 ± 37	0	21 ± 8	20 ± 4	250 ± 94	0	22 ± 4
100–125	13 ± 2	125 ± 54	0	18 ± 3	13 ± 5	202 ± 12	0	13 ± 2
125–150	13 ± 5	127 ± 42	0	14 ± 3	14 ± 3	212 ± 84	0	20 ± 9
150–190	7 ± 2	76 ± 16	0	10 ± 2	2 ± 0.4	23 ± 3	0	2 ± 1
190–200	4 ± 1	0	0	2 ± 1	–*	–	–	–

* No data, since the depth of peat soils was less than 190 cm.

being waterlogged; there is permanent water on their surface, and the height of the water column varies from 5 to 30 cm, depending on the season. Due to the high rate of litter decomposition in minerotrophic peatlands, thick bedding is not formed there. The bedding consists of a single L (leaves) layer; its height does not exceed 3 cm. In contrast to their nonreclaimed analogues, reclaimed ombrotrophic peatlands are characterized by the absence of stagnant water. This change results in a considerable improvement in the forest quality and in the substitution of the solid moss mat that existed before reclamation with well-defined forest bedding consisting of three layers (L, F, and H) (Table 1).

In the course of determination of the microbiological parameters (the bacterial and fungal spore number; the lengths of the actinomycete and fungal mycelium; the microbial biomass pool; the potential activity of nitrogen fixation and denitrification) both the horizontal (12 wells were analyzed) and vertical variability (the following peat layers were analyzed: 0–20, 20–50, 50–75, 75–100, and 100–150) were taken into account, as well as the operation mode (nonreclaimed peatlands and their reclaimed analogues were studied). Sampling was carried out in July 2001 and 2002.

The total number and biomass of microorganisms were determined by the direct method using fluorescence microscopy [21]. The cells were preliminarily desorbed using the ultrasound UZDN-1 disperser. For enumeration of the cells of soil bacteria and actinomycete mycelium, the samples were stained with an aqueous solution of acridine orange; calcofluor white was used for staining the fungal mycelium and spores. The calculations of the prokaryote biomass were carried out assuming that the dry-weight biomass for one bacterial 0.1 μm^3 cell constitutes 2×10^{-14} g and 1 m of 0.5-μm actinomycete mycelium weighs 3.9×10^{-8} g [22]. The eukaryotic microbial biomass was calculated from the measured fungal spore and the mycelium diameter according to the following expressions: $0.628\,(r_1)^2 \times 10^{-6}$ g for mycelium and $0.836(r_2)^3 \times 10^{-12}$ g for spores, where r_1 is the mycelium radius; r_2 is the fungal spore radius. The average diameter of the fungal hyphae (hyphal *d*) and spores (spore *d*) was higher in the minerotrophic peatlands (hyphal *d*, 4.8–5.8 μm; spore *d*, 4.8–5.0 μm) than in ombrotrophic ones (hyphal *d*, 4.2–4.4 μm; spore *d*, 4.4–4.6 μm).

The potential rates of the processes of nitrogen fixation and denitrification were determined using the gas chromatography method. To measure nitrogen fixation, the acetylene method was used; to assess the denitrifying activity of soil microorganisms, the method based on the use of acetylene as a nitrous oxide reductase inhibitor was used [21].

RESULTS AND DISCUSSION

The number of bacterial cells in the peatlands studied varied from 2 to 75 × 10^9 cells/g. The length of the actinomycete mycelium was dozens and hundreds of m/g. The density of bacterial populations in nonreclaimed peatlands, both ombrotrophic and minerotrophic, did not differ significantly from that of their reclaimed analogues (Tables 2, 3).

The length of fungal mycelium in ombrotrophic peat soils was measured in kilometers and was 10 to 100 times higher than in minerotrophic peat soils. The range of fluctuations of the spore number in ombrotrophic peatlands was 4–67 × 10^6 spores/g and was twice as high as in the minerotrophic peat soils (2–30 × 10^6 spores/g). The differences in the fungal mycelium and spore content in reclaimed and nonreclaimed variants were more pronounced in ombrotrophic peatlands (the number of fungal spores was higher in nonreclaimed peatlands, and the fungal mycelium length was greater in their reclaimed analogues) (Tables 2, 3).

Table 3. Distribution of bacteria, actinomycete and fungal mycelium, and fungal spores across the profile of ombrotrophic peat soils

Peatland	Ombrotrophic nonreclaimed				Ombrotrophic reclaimed			
Depth, cm	Bacteria, 10^9 cells/g	Actino-mycete myce-lium, m/g	Fungal mycelium, m/g	Fungal spores, 10^6 cells/g	Bacteria, 10^9 cells/g	Actinomycete mycelium, m/g	Fungal myce-lium, m/g	Fungal spores, 10^6 cells/g
0–3	4 ± 1	57 ± 12	1100	16 ± 2	9 ± 1	87 ± 14	1200	20 ± 3
3–6	9 ± 1	83 ± 7	3700	36 ± 5	9 ± 1	100 ± 25	1800	16 ± 4
6–14	32 ± 1	159 ± 14	6500	38 ± 13	31 ± 2	214 ± 31	7500	28 ± 3
14–20	71 ± 13	354 ± 89	4500	67 ± 3	75 ± 8	416 ± 45	8400	51 ± 1
20–50	30 ± 7	176 ± 58	800	51 ± 6	47 ± 7	208 ± 37	2400	40 ± 6
50–100	23 ± 3	63 ± 16	200	32 ± 2	39 ± 7	122 ± 2	900	34 ± 10
100–130	23 ± 2	133 ± 36	0	23 ± 2	8 ± 2	101 ± 2	200	4 ± 1
130–150	4 ± 1	0	0	5 ± 1	6 ± 2	0	0	4 ± 1

The results of the three-factor analysis of variance revealed that the number of microorganisms in the peatlands studied changed to a larger degree across the profile (vertical variability) than in space (horizontal variability). The exploitation mode was the second most significant factor. Its influence was more pronounced for ombrotrophic peatlands (Table 4).

Bacteria, actinomycete mycelium, and fungal spores were revealed across the whole peatlands profile. In minerotrophic peatlands, their abundance remained at a high level within the upper 1-m layer, then it decreased gradually (1.5–2-fold) in the 100–190-cm layer; in the underlying rock, it was five to ten times lower (Table 2). The stable values of the number of microorganisms in the upper part of the profile of the minerotrophic high-ash peatlands are the result of the uniformity of the substrate, which is represented by woody valley peat with a high degree of decomposition (Table 1).

In the ombrotrophic peatlands, the upper horizons (0–20 cm) have specific characteristics. Thus, in the nonreclaimed ombrotrophic peatland, they consist of living moss and its dust. In the reclaimed ombrotrophic peatland, all the bedding layers are well-defined; its depth varies between 14 and 18 cm (Table 1). The length of actinomycete mycelium and the number of bacteria and fungal spores in these peatlands gradually increase in a successional series of conveyer-like treatment of deciduous matter and reach the maximal values in the peat layer (14–20 cm) underlying the moss dust (in nonreclaimed upper-moor peatland) and the humus bedding layer (in reclaimed ombrotrophic peatland). The number of these microorganisms gradually decreases at greater depths. The sands underlying ombrotrophic peatlands were characterized by the minimal values of the abundance of microorganisms both in reclaimed and nonreclaimed analogues (Table 3).

The peatlands of various trophicity had different distributions of the fungal mycelium. In the ombrotrophic peatlands, fungal mycelium was present in most of the layers of the peat column, while in minerotrophic peatlands, it was found only in the upper layers (Tables 2, 3). Additional mycological studies of minerotrophic peatlands conducted in the other seasons confirmed the previously revealed pattern of its profile distribution.

Minerotrophic peat soils forming under vigorously growing grasses and deciduous trees have a high organic matter content and neutral pH; they seem the optimal medium for the development of various forms of microorganisms. However, the conditions in these soils are unfavorable for the development of fungal mycelium. The physical properties of minerotrophic peat soils are close to those of soddy–gley soils, which have a relatively large pore space with the prevalence of ultramicropores less than 5 μm in diameter [23]. In such micropores, the development of microscopic fungi is problematic, since the fungal activity is higher in

Table 4. Assessment of the degree of influence of the factors* on the numbers of microorganisms of different groups in the peat soils studied (by the results of the three-factor analysis of variance)

Peatland	Minerotrophic			Ombrotrophic		
Factor	1	2	3	1	2	3
Fungal mycelium	11.03	–**	32.10	29.76	6.84	410.71
Fungal spores	7.96	6.91	28.63	13.67	–	85.54
Bacteria	37.82	88.79	616.52	28.74	3.11	95.29
Actinomycete mycelium	6.34	–	14.83	13.45	–	17.69

Notes: * The factors considered and their gradations: 1, exploitation mode (nonreclaimed and reclaimed peat soils); 2, the space factor (horizontal variability); 3 the depth of peat bed (vertical variability). The numerical values represent Fisher's test at a level of significance of <0.001.

** The influence of the factor is not statistically significant.

Table 5. Distribution of the microbial mass (mg/g) across the profile of the peat soils studied

Layer, cm	Ombrotrophic peat soils		Minerotrophic peat soils	
	Nonre-claimed	Reclaimed	Nonre-claimed	Reclaimed
0–20	35.9 ± 10.2	39.7 ± 12.2	1.2 ± 0.2	1.7 ± 0.3
20–50	17.3 ± 2.3	52.9 ± 15.5	1.2 ± 0.3	1.3 ± 0.3
50–100	1.2 ± 0.2	2.3 ± 0.3	1.5 ± 0.4	3.6 ± 0.6
100–150	1 ± 0.2	1.3 ± 0.4	1.1 ± 0.3	1.1 ± 0.4

large pores, while the bacterial activity is higher in small pores [24]. The detection of minimal amounts of mycelium, which is an active component of the complex of soil micromycetes, in the soil of minerotrophic reclaimed peatlands may be the result of grazing by the mesofauna (its biomass is high in these soils) [25].

The pore space is distributed more uniformly in ombrotrophic peat soils; favorable conditions are therefore created for the development of microscopic fungi, especially in the reclaimed analogues in which stagnant water is absent after forest reclamation.

Our previous experiments on determining the viability of fungal mycelium and spores in ombrotrophic peat soils revealed that the fungi, which are the main decomposers of organic matter, were in the viable state across the whole profile. The percentage of viable fungal hyphae was 60–100; of viable spores, 83–100. The capacity for germination in spores and yeast-like cells was detected throughout the peat soil profile. The percentage of their germination in the 1-m column varied from 46 to 87; in the remaining part of the profile, from 6 to 40. Unlike the spores, only the fungal hyphae of the upper 1-m layer were capable of germinating and forming microcolonies. The percentage of germination of fungal mycelium was highest in the layer consisting of the dust of living bog moss (sphagnum); in the 10–50-cm layer, the number of the colonies grown decreased twofold; and in the underlying 0.5-m column, it decreased fourfold compared to the upper horizon. The hyphae that failed to germinate had a well-defined contour and clear-cut partitions and septa and were brightly luminescent, i.e., they looked as if they were alive. The germination of such hyphae could probably have occurred under different experimental conditions. The fungi revealed in deep peat soil layers are preserved in the state of anabiosis and maintain a high pool of "live" carbon in bog ecosystems [12].

The dry-weight microbial biomass content in the upper 20-cm layer of the peatlands studied varied from 1 to 40 mg/g; in the 20–50-cm layer, from 1 to 53 mg/g; at a depth of 50–100 cm, from 1 to 4 mg/g; and in the 1–2-m column, from 0.5 to 1 mg/g. The upper layers contributed significantly to the microbial biomass of ombrotrophic peatlands. In minerotrophic peatlands, the microbial biomass was relatively uniformly distributed across the peat column (Table 5).

The analysis of the biomasses of the fungal mycelium and spores, bacteria, and actinomycete mycelium calculated for the 1.5-m deep column (taking into account the depth and the volume weight of peat horizons) showed that, in nonreclaimed ombrotrophic peatlands, the fungal mycelium biomass (262 g/m^2) predominated. It was seven times higher than the fungal spore biomass and four times higher than the bacterial biomass. In minerotrophic peatlands, the opposite pattern was observed, i.e., the predominance of bacterial biomass (98 g/m^2), which exceeded the fungal mycelium biomass sevenfold and the spore biomass twofold (Table 6).

The reclamation of ombrotrophic peatlands contributed to a 2.5-fold increase of the fungal and actinomycete mycelium biomass and a twofold increase of bacterial biomass. The fungal spore biomass did not change significantly. In minerotrophic peatlands, the fungal mycelium biomass increased significantly (fivefold) after reclamation, whereas the biomass of fungal spores, bacteria, and actinomycete mycelium remained at virtually the same level as in nonreclaimed analogues (Table 6).

When calculating the total microbial biomass per 1.5-m deep column, we found that reclaimed ombrotrophic peat soils had the highest content of microorganisms. The pool of microbial biomass in it varied from 7.4 to 8.8 t/ha. The other soils, in order of decreasing microbial biomass, formed the following sequence: nonreclaimed ombrotrophic peat soils (2.8–3.8 t/ha), reclaimed minerotrophic peat soil (2.0–2.4 t/ha), and nonreclaimed minerotrophic peat soil (1.5–2.3 t/ha).

Table 6. Biomass of fungal mycelium, fungal spores, bacterial cells, and actinomycete mycelium averaged over the 1.5-m layer of the peat soils studied

Peatland	Biomass, g/m^2			
	fungal mycelium	fungal spore	bacteria	actinomycete mycelium
Minerotrophic nonreclaimed	14.5 ± 3.2	50.0 ± 9.3	97.9 ± 8.6	1.4 ± 0.3
Ombrotrophic nonreclaimed	262.1 ± 10.8	36.9 ± 4.9	60.3 ± 5.9	0.5 ± 0.1
Minerotrophic reclaimed	70.3 ± 7.9	59.5 ± 7.1	85.2 ± 10.3	2.1 ± 0.3
Ombrotrophic reclaimed	645.4 ± 28.7	47.0 ± 4.3	124.2 ± 12.8	1.3 ± 0.4

On the whole, the pool of microbial biomass in the 1.5-m layer of the ombrotrophic peat soils was two to four times higher than in the minerotrophic ones; the reclaimed analogues exhibited higher values.

The ombrotrophic and minerotrophic peatlands differed not only in the pool of microbial biomass but also in its structure.

The general pattern of the prokaryotic biomass exceeding the eukaryotic one, which was revealed by analysis of the microbial biomass structure in most of the soil types [26], was confirmed for reclaimed ombrotrophic peat soils, where the microscopic fungi accounted for 59–99% of the biomass and the bacteria and actinomycete mycelium for 1–41%. In the morphological structure of micromycetes of this peatland, the mycelium (70–99%) predominated over spores (1–30%).

In nonreclaimed minerotrophic peat soils, we observed the opposite tendency, namely, the prokaryotic component predominated in the microbial biomass structure. Its share varied across the profile from 55 to 86%. The fungal component accounted for 14–45% of the microbial biomass. Fungal spores predominated in the morphological structure of micromycetes. The share of bacteria in the prokaryotic complex significantly exceeded that of the actinomycete mycelium. The predominance of the prokaryotic component in the microbial biomass was noted earlier in soddy-gley soil [23].

Two other peatlands studied (nonreclaimed ombrotrophic and reclaimed minerotrophic) occupied an intermediate position. In the upper 1.5-m layer of these peat soils, the fungal component predominated in the structure of microbial biomass; in the lower layer, the prokaryotic one was predominant. A similar microbial biomass structure was revealed by us when we explored the ombrotrophic peatlands in Tomsk oblast [11].

Thus, the microbial biomass structure in the ombrotrophic peat soils studied by us did not differ from the other soil types, since the eukaryotic component predominated there across most of the profile. The minerotrophic high-ash peat soils can be added the scarce spectrum of soils in which the microbial biomass of prokaryotic microorganisms predominated across the bulk of the profile.

No direct correlation is known to exist between the number and activity of microorganisms in soils, and the high degree of soil saturation with microbial groupings does not necessarily signify the activity of the microbial complex in it. The values of the activity of these processes occurring at different depths would be more relevant in solving the question of the state of microorganisms in peat soils. However, this information is difficult to obtain experimentally, and only the potential activity of the microbial processes can be determined at the present stage. Nitrogen fixation and denitrification are the microbiological processes determining, in many respects, the assets and liabilities of nitrogen balance in different soils.

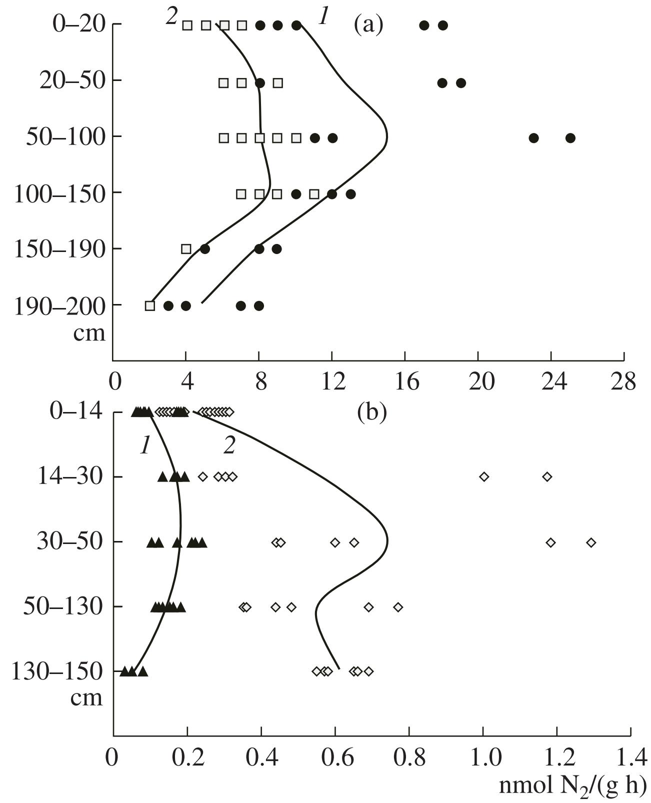

Fig. 1. Potential nitrogen fixation activity in the (a) minerotrophic and (b) ombrotrophic peat soils studied: (*1*) nonreclaimed and (*2*) reclaimed.

The level of potential activity of nitrogen fixation in the peat soils studied varied from 0.2 to 25 nmol N_2/(g h); that of denitrification, from 3 to 500 nmol N_2O/(g h). The amplitude of fluctuations and the average values of the potential activity of nitrogen fixation and denitrification were 2–10 times higher in the minerotrophic peat soils than in the ombrotrophic ones (Figs. 1, 2).

The potential activity of nitrogen fixation and denitrification was revealed in all the peat layers, including the underlying rock.

A higher level of nitrogenase activity in the middle part of the profile and its decrease close to the underlying rock are features shared by all the peat soils studied (Fig. 1).

The denitrifying activity in the peat soils studied decreased depth. However, in nonreclaimed peat soils characterized by an excessive moisture content and neutral pH values, a high level of activity was maintained in the greater part of the profile (0–175 cm) (Fig. 2).

The exploitation mode influenced the activity of the two processes studied in a different way. The comparison of nonreclaimed and reclaimed peatlands showed that natural minerotrophic peat soils were characterized

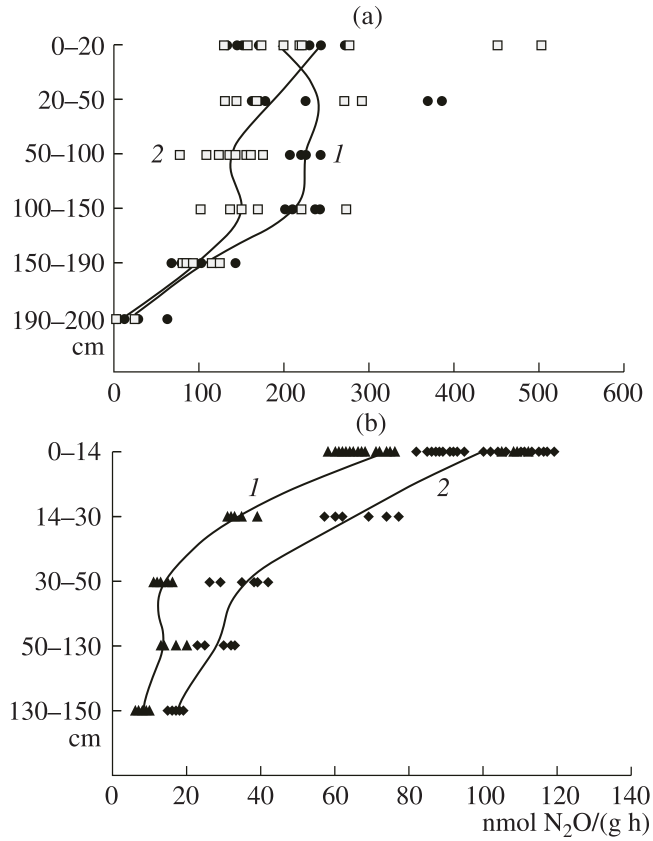

Fig. 2. Potential denitrification activity in the (a) minerotrophic and (b) ombrotrophic peat soils studied: (*1*) nonreclaimed and (*2*) reclaimed.

by far higher levels of nitrogen fixation and denitrifying activity than their reclaimed analogues. For ombrotrophic peatlands, the opposite tendency was revealed, i.e., the reclamation favorably influenced the potential activity of the main nitrogen cycle processes.

The data pertinent to the activity of nitrogen fixation and denitrification in soils available in the literature are related, in most cases, only to the upper horizons used for agricultural purposes. That is why the values obtained were compared only for the upper soil horizons [27, 28]. The level of the potential nitrogen fixation and denitrification activity in high-ash minerotrophic peat soils should be considered as high, because it is comparable to, or exceeds, the level established for the chernozem and meadow chernozem soils. The ombrotrophic peatlands are closer to soddy podzolic soils in terms of the potential nitrogen fixation and denitrification activity.

The peatlands studied differed in the microbial biomass structure. In ombrotrophic peatlands, the fungal mycelium biomass was predominant and in minerotrophic peatlands, the bacterial biomass. The high values of fungal abundance in ombrotrophic peatlands explain the maximal microbial biomass values, which were twice as high as in minerotrophic peatlands. In the soils of minerotrophic peatlands, conditions were unfavorable for the microscopic fungi, which was confirmed by their low number, not deep penetration into the peat bulk, and the predomination of spores, rather than mycelium in the morphological structure. The special hydrophysical characteristics, as well as the high biomass of soil invertebrates in the upper horizons, are the factors which may be responsible for the regulation of the density of the fungal populations in lowland peat soils. Ombrotrophic peatlands, having large pools of viable fungal biomass, are nevertheless characterized by low rates of peat mineralization. The hydrothermal and redox conditions in the deep layers of ombrotrophic peat soils, which are unfavorable for the microorganisms, promote further accumulation and conservation of both plant residues and microbial biomass in peat.

The vertical variability (distribution across the profile) influenced the microbial abundance values in the peat soils studied to a larger degree than the horizontal variability. In minerotrophic peat soils, the microbial biomass was distributed relatively uniformly within the bulk, whereas in ombrotrophic peat soils, most of the microbial biomass was concentrated in the upper layers.

The study of nitrogen fixation and denitrification conducted by us showed that all the layers of the peat soils analyzed are potentially active.

Minerotrophic high-ash peat soils exhibited a high potential level of activity of these processes compared to the ombrotrophic peatlands and other soil types.

Reclamation contributed significantly to the improvement in the physical and chemical characteristics of ombrotrophic peat soils, resulting in a twofold increase in the biomass of fungi, actinomycete mycelium, and bacteria, as well as in increased activity of the main processes of the nitrogen cycle compared to the nonreclaimed analogues.

In reclaimed minerotrophic peatlands, the fungal mycelium biomass increased significantly, whereas the bacterial biomass did not undergo significant changes; therefore, no increase in the potential activity of nitrogen fixation and denitrification was observed.

The total pool of the microbial biomass in reclaimed peat soils was characterized by higher values than in nonreclaimed ones. The pool of microbial biomass in reclaimed ombrotrophic peatlands was four times higher than in reclaimed minerotrophic peatlands.

We thank M.G. Smagina and T.V. Glukhova (Institute of Forestry, Russian Academy of Sciences) for their help in collecting samples and valuable discussions.

This work supported by the Russian Foundation for Basic Research, project no. 07-04-00252.

REFERENCES

1. Martin, N.J., Siwasin, J.U., and Holding, A.J., The Bacterial Population of a Blanket Peat, *J. Appl. Bacteriol.*, 1982, no. 53, pp. 35–48.
2. Zimenko, T.G., *Mikrobnye tsenozy torfyanykh pochv i ikh funktsionirovanie* (Microbial Cenoses of Peaty Soils and Their Functioning), Minsk: Nauka i Tekhnika, 1983.
3. Kiister, E., Microorganismen im Moor, *Telma*, 1986, vol. 16, pp. 235–244.
4. Smagina, M.V., Microorganisms and Ecological Peculiarities of Organic Matter Transformation in Meliorated Swamp Forests, *Cand. Sci. (Biol.) Dissertation*, Krasnoyarsk, 1988.
5. Zvyagintsev, D.G., Zenova, G.M., and Shirokikh, I.G., Structure o Actinomycete Complexes in Peat Soils, *Mikrobiologiya*, 1992, vol. 61, no. 2, pp. 323–329.
6. Zagural'skaya, L.M., *Mikrobnaya transformatsiya organicheskogo veshchestva v lesnykh pochvakh Karelii* (Microbial Transformation of Organic Matter in Boreal Soils of Karelia), St. Petersburg: Nauka, 1993.
7. Grodnitskaya, I.D. and Sorokin, N.D., Soil-Microbiological Monitoring of Forest-Mire Ecosystems in Western Siberia, *Pochvovedenie*, 2004, vol. 37, no. 8, pp. 945–951 [*Eurasian Soil Sci.* (Engl. Transl.), vol. 37, no. 8, pp. 824–829].
8. Thormann, M.N., Currah, R.S., and Bayley, S.E., Microfungi Isolated from *Sphagnum fuscum* from a Southern Boreal Bog in Alberta, Canada, *The Bryologist*, 2001, vol. 104, no. 4, pp. 548–559.
9. Thormann, M.N., Bayley, S.E., and Currah, R.S., Microcosm Tests of the Effects of Temperature and Microbial Species Number on the Decomposition of *Carex aquatilis* and *Sphagnum fuscum* Litter from Southern Boreal Peatlands, *Can. J. Microbiol.*, 2004, vol. 50, pp. 793–802.
10. Golovchenko, A.V., Polyanskaya, L.M., Dobrovol'skaya, T.G., Vasil'eva, L.V., Chernov, I.Yu., and Zvyagintsev, D.G., Spatial Distribution and Structure of the Microbial Complexes of Boreal Peatlands, *Pochvovedenie*, 1993, no. 10, pp. 78–89.
11. Golovchenko, A.V., Dobrovol'skaya, N.G., and Inisheva, L.I., Structure and Stocks of Microbial Biomass in Oligotrophic Peat Bogs of the Southern Taiga in Western Siberia, *Pochvovedenie*, 2002, vol. 35, no. 12, pp. 1468–1473 [*Eurasian Soil Sci.* (Engl. Transl.), vol. 35, no. 12, pp. 1296–1302].
12. Golovchenko, A.V. and Polyanskaya, L.M., Viability of Fungal Mycelium and Spores in Peat Soils, *Materialy soveshchaniya "Bolota i zabolochennye lesa v svete zadach ustoichivogo prirodopol'zovaniya"* (Proc. Conf. "Swamps and Swampy Forests in Connection with the Problems of Stable Exploitation of Natural Resources"), Moscow: GEOS, 1999, pp. 106–109.
13. Smagin, A.V., *Gazovaya faza pochv* (The Gas Phase of Soils), Moscow: Mosk. Gos. Univ., 2005.
14. Bridges, E.M. and Batjes, N.H., Soil Gaseous Emissions and Global Climate Change, *Geography*, 1996, vol. 81, no. 2, pp. 249–279.
15. Efremova, T.T., Efremov, S.P., and Melent'eva, N.V., The Reserves and Forms of Carbon Compounds in Bog Ecosystems of Russia, *Pochvovedenie*, 1997, vol. 30, no. 12, pp. 1470–1477 [*Eurasian Soil Sci.* (Engl. Transl.), vol. 30, no. 12, pp. 1318–1325].
16. Vomperskii, S.E., The Role of Bogs in the Carbon Cycle, *Biogeotsenoticheskie osobennosti bolot i ikh ratsional'noe ispol'zovanie. Chteniya pamyati V.N. Sukacheva* (Biogeocenotic Peculiarities of Bogs and Their Rational Use. Lectures in Memory of V.N. Sukacheva), vol. 11, Moscow: Nauka, 1994, pp. 5–37.
17. Houghton, R.A., Callander, B.A., and Varney, S.K., *Climate Change*, Cambridge: Cambridge Univ. Press, 1992.
18. Bambalov, N.N., Rakovich, V.A., Maryganova, V.V., et al., Biogeochemical Cycles of Nitrogen and Carbon in Natural Bog Ecosystems and Those Anthropogenically Impacted, in *Materialy soveshchaniya "Bolota i zabolochennye lesa v svete zadach ustoichivogo prirodopol'zovaniya"* ((Proc. Conf. "Swamps and Swampy Forests in Connection with the Problems of Stable Exploitation of Natural Resources"), Moscow: GEOS, 1999, pp. 164–166.
19. Kravchenko, I.K. and Doroshenko, E.V., Nitrogen-Fixing Activity in Peat Soils from a Raised Bog, *Mikrobiologiya*, 2003, vol. 72, no. 1, pp. 111–116 [*Microbiology* (Engl. Transl.), vol. 72, no. 1, pp. 98–102].
20. Lang, K.L., Silova, J., Ruuskanen, J., and Martikainen, P.J., Emissions of Nitric Oxide from Boreal Peat Soils, *J. Biogeog.*, 1995, vol. 22, pp. 359–364.
21. *Metody pochvennoi mikrobiologii i biokhimii* (Methods in Soil Microbiology and Biochemistry), Zvyagintsev, D.G., Ed., Moscow: Mosk. Gos. Univ., 1991, p. 303.
22. Kozhevin, P.A., Polyanskaya, L.M., and Zvyagintsev, D.G., Development Dynamics of Different Microorganisms in Soil, *Mikrobiologiya*, 1979, vol. 48, no. 4, pp. 490–494.
23. Alekhina, L., Golovchenko, A.V., Pochatkova, T.N., Dobrovol'skaya, T.G., and Zvyagintsev, D.G., The Effect of Hydrophysical Soil Properties on the Structure of Microbial Complexes, *Pochvovedenie*, 2002, vol. 35, no. 8, pp. 1002–1009 [*Eurasian Soil Sci.* (Engl. Transl.), vol. 35, no. 8, pp. 890–897].
24. Zvyagintsev, D.G., *Pochva i Mikroorganizmy* (Soil and Microorganisms), Moscow: Mosk. Gos. Univ., 1987.
25. Terekhova, V.A., Golovchenko, A.V., Semenova, T.A., Rakhleeva, A.A., and Trofimov, S.Ya., Peculiarities of Structural-Functional Organization of the Microbiota of the Mezha River Bed Area Soils, *Tez. Dokl. Konf. "Malye Reki: Sovremennoe Ekologicheskoe Sostoyanie, Aktual'Nye Problemy"* (Proc. Conf. "Small Rivers: Modern Ecological State and Pertinent Problems"),Tol'yati, 2001, p. 203.
26. Polyanskaya, L.M., Microbial Succession in Soil, *Doctoral (Biol.) Dissertation*, Moscow, 1996.
27. Umarov, M.M., *Assotsiativnaya azotfiksatsiya* (Associative Nitrogen Fixation), Moscow: Mosk. Gos. Univ., 1986.
28. Stepanov, A.L., Microbial Transformation of Nitrous Oxide in Soils, *Doctoral (Biol.) Dissertation*, Moscow, 2000.