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SOIL BIOLOGY

Dynamics of Biochemical Processes and Redox Conditions in Geochemically Linked Landscapes of Oligotrophic Bogs

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Abstract—The biological activity in oligotrophic peatlands at the margins of the Vasyugan Mire has been studied. It is shown found that differently directed biochemical processes manifest themselves in the entire peat profile down to the underlying mineral substrate. Their activity is highly variable. It is argued that the notion about active and inert layers in peat soils is only applicable for the description of their water regime. The degree of the biochemical activity is specified by the physical soil properties. As a result of the biochemical processes, a micromosaic aerobic–anaerobic medium is developed under the surface waterlogged layer of peat deposits. This layer contains the gas phase, including oxygen. It is concluded that the organic and mineral parts of peat bogs represent a single functional system of a genetic peat profile with a clear record of the history of its development.

Keywords: Vasyugan Mire, peat deposit

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INTRODUCTION

In recent years, many works devoted to the kinetics of biochemical processes in peat deposits of bogs have appeared. These works have expanded our knowledge of peat soils. These soils are considered as the soils with genetic peat profiles down to the underlying substrates, whose history is recorded in the composition and properties of peat layers [26, 28]. The upper active layer of peat bogs represents a part of the peat profile of the modern stage of pedogenesis. The activity of biochemical processes in the peat profile is determined by the botanical composition of peat layers and by their age [7, 9, 10, 15]. In this paper, we analyze the biochemical status and redox conditions in the profiles of oligotrophic peat bog soils along the soil catena.

Peat mires and, especially, oligotrophic peat bogs, are characterized by the high content of plant debris. In the course of peat formation, dead parts of the plants enter the waterlogged medium and are subjected to partial decomposition with the production of solid cellulose polymers and other high molecular weight compounds of the products of decomposition. Being mixed with mineral substances and water solutions of low molecular weight compounds, they compose specific macro- and microstructures in peat deposits. Microstructures of peat yield supramolecular compounds that may form molecular associates and compose structures of different densities. Bulk density of the high-moor peat deposits is less than 0.1 g/cm^3; in the eutrophic peat of low moors, it may reach 0.4 g/cm^3. It is important that peat-forming plants differ in their chemical composition, so that peat deposits are often heterogeneous in their composition and regimes of biochemical processes.

The aim of our study was to reveal specific features of the biochemical regime and aerobic–anaerobic (redox) conditions in peat deposits of an oligotrophic bog.

OBJECTS AND METHODS

We studied a soil catena at the periphery of the Vasyugan Mire. According to [17], this catena is typical of the Bakchar bog area. It consists of several geochemically linked oligotrophic biogeocenoses. The major of them are the dwarf shrub–sphagnum bog with sparse low pine trees in the autonomous part of the catena (site 3) and the dwarf shrub–sphagnum bog with sparse high pine trees in the transitional–accumulative (transaccumulative) part of the catena (site 2). Sphagnum bogs with pine are known under the local name of ryam ecosystems; hereinafter, site 3 is conventionally referred to as low ryam, and site 2 is referred to as high ryam. The studied catena has a total length of 800 m; the leveling survey was performed along it. A more detailed physiographic characterization of the catena was published earlier [24].

The peat deposit of the low ryam has a thickness of up to 3 m; it consists of several peat layers. The lower layer represents eutrophic peat of the low moor; it is covered by the 1.5-m-thick upper layer of oligotrophic (high-moor) peat. At the contact between these two peat layers, a thin layer of transitional woody–sphagnum peat is found. The high ryam is located at the periphery of the high-moor peatland. The peat deposit has a thickness of 1 m. It consists of several peat layers. The lowermost layer is the eutrophic sedge peat of the high degree of decomposition. It overlain by the layers of transitional woody–sphagnum and woody–forb peat. The uppermost peat layer consists of the remains of pine and cotton grass. Thus, the development of the oligotrophic mire ecosystems in this area began from the eutrophic stage under the woody–forb plant associations; gradually, they were replaced by the oligotrophic pine–dwarf shrub–sphagnum associations. In each biogeocenosis along the catena, we studied the groundwater level every ten days. The redox conditions and temperature regimes were studied in 10-cm-thick peat layers down to the depth of 1 m with the help of stationary loggers. The group composition of the organic matter of peat was studied by the method developed by the Central Research Institute for Peat Industry (Instorf) [3]. The iron content in humic acids was determined by the X-ray fluorescent analysis.

To study the biological activity of the peat, peat samples were taken with a peat auger. The botanical composition of the samples was taken into account. The total number and biomass of microorganisms were directly determined by the method of luminescent spectroscopy. For the quantitative estimates of bacterial cells and mycelium of actinomycetes, sample preparations were stained with acridine orange; calcofluor white was used to stain the mycelium and spores of fungi [8, 18].

The numbers of ammonifiers and amylolytic organisms were studied by the classical method of inoculation of soil suspensions on diagnostic media (meat–peptone agar and starch-and-ammonia agar) [18].

The determination of basal respiration, microbial biomass, and the microbial metabolic quotient was conducted by the method of substrate-induced respiration with the use of a Kristall-5000.1 gas chromatograph [1, 21].

We also determined the catalase activity by the gasometric method in modification by Kruglov and Paromenskaya [14] and the polyphenoloxidase activity by the method of Karyagina and Mikhailovskaya [16]. The catalase activity was expressed in mL O_2/g per 2 min; and the polyphenoloxidase activity, in mg 1,4-benzoquinone/g per 30 min.

The statistical treatment of the results was performed with the use of Microsoft Office Excel software; the confidence interval was set at 0.95. The analyses were made in the Test Laboratory of Tomsk State Pedagogical University (No. ROSS RU.0001.516054).

Table 1. Carbon budget in the geochemically linked landscapes of the oligotrophic bog, g C/m^2 per year

Biogeocenosis	Input	Output	Sequestration
Dwarf shrub–sphagnum pine bog with high pine (site 2, high ryam)	267.3	97.6	169.7
Dwarf shrub–sphagnum pine bog with low pine (site 3, low ryam)	235.2	66.9	168.3
Average	251.2	82.2	169.0

RESULTS

The sites studied in the upper (site 3) and lower (site 2) parts of the catena are geochemically linked, and it possible to trace the major migration flows of substances between them. The peat deposit of site 2 is actually a continuation of the peat deposit of site 3 that formed upon the ingression of the bog over the adjacent territory. Active swamping of the studied territory is proved by a predominance of carbon accumulation in the peat deposits along the catena; its average rate is estimated at 169.0 g C/m^2 per year (Table 1). This process is more active at site 2 (high ryam).

Natural processes affecting peat deposits at the two sites differ considerably. The high ryam (site 2) is located in the marginal part of the vast mire; it represents a transaccumulative part of the oligotrophic bog affected by migration flows from the autonomous part of the catena (site 3). The biochemical processes at site 2 attest to the activity of bog formation. Thus, despite the young age of the peat deposit at this site, it is characterized by the highest degree of decomposition of plant residues (35–55%); under the modern climatic conditions, active formation of this peat deposit takes place. Initially, the swamping of this area began from the transitional stage; after the formation of the lower 75-cm-thick peat layer (which took about 700 years), the accumulation of oligotrophic peat began. It can be supposed that this change in the character of peat accumulation was favored by the landscape position of this site, in which the accumulation of surface and bog water flows from the upper peat layer at site 3 took place. As a result, the peat materials in the transaccumulative part of the catena was enriched in easily hydrolyzable compounds and, hence, in the ash matter (at site 2, the ash content of peat deposits reaches 5.2–9.8%, whereas in the upper 1-m-thick layer of peat deposit at site 3 it is only about 2.0–2.7%). This proves the lateral migration of mobile substances from site 3 to site 2. Macro- and microelements migrate towards the transaccumulative part of

Table 2. Extreme (numerator) and average (denominator) characteristics of the activity of microbial biomass during several growing seasons; (±) confidence interval

Depth, cm	Bacteria, billion cells/g	Mycelium, m/g		Fungal spores, million spores/g
		actinomycetal	fungal	
Site 2				
0–25	36.1–61.3 / 51.3 ± 6.6	308.7–445.7 / 386.9 ± 20.1	16.7–30.1 / 25.0 ± 3.5	29.3–60.3 / 48.8 ± 5.7
25–50	8.1–48.6 / 18.4 ± 4.5	96.4–205.4 / 122.4 ± 11.1	5.4–11.3 / 9.3 ± 1.3	14.7–29.4 / 21.9 ± 3.3
75–100	6.2–35.9 / 12.9 ± 2.6	46.3–96.3 / 62.6 ± 5.8	0–3.1 / 2.1 ± 0.8	5.3–13.0 / 9.1 ± 2.7
Site 3				
0–50	35.2–59.3 / 12.9 ± 2.6	188.9–556.3 / 460.5 ± 14.6	30.2–41.6 / 35.3 ± 2.5	33.6–64.3 / 54.3 ± 8.7
100–150	18.6–54.3 / 33.0 ± 5.0	186.3–369.4 / 274.4 ± 10.6	2.3–28.1 / 12.3 ± 1.5	24.8–51.3 / 40.3 ± 7.4
200–250	3.8–44.1 / 13.3 ± 2.3	44.1–109.5 / 55.0 ± 3.1	0–5.7 / 1.2 ± 0.5	3.9–12.9 / 7.7 ± 1.3

the catena in the free form and in the form of complexes with humic acids. The iron content in humic acids of the peat deposit in the autonomous part of the catena is about 0.10–0.25%; in the transaccumulative part, it reaches 1.25%. The same tendency is seen from data on the contents of humic acids. In the upper meter of peat at site 3 (low ryam, autonomous part of the catena), it varies from 19.8 to 25.2%; in the same peat layer of the high ryam, it reaches 22.7–39.8%. The inflow of substances at the high ryam site accelerates the development of the oligotrophic peat deposit; it is interesting that the eutrophic stage of the peat formation was virtually absent at this site [24].

The chemical properties of the geochemically linked landscapes of the oligotrophic bog greatly affected their biological components. Long-term studies of the dynamics of soil microflora by the inoculation method proved that ammonifiers and amylolytic microorganisms participating in the decomposition of the peat organic matter have a definite tendency for the increase in their numbers in the lower peat layers with the higher humification level. The high population density of these microorganisms is only observed in the old-forming peat deposits. Thus, the average activity of ammonifiers was the greatest in the lower peat layer at site 3, where the radiocarbon age of peat reaches 5200 ± 180 years (SOAN-8041); at site 2, it is considerably lower (650 ± 80 years (SOAN-8042). At the same time, the density of ammonifiers in the upper peat layer (0–50 cm) at site 3 is virtually the same as that in the entire peat profile at site 2. The same regularity is also observed for the amylolytic microorganisms in different parts of the growing season. This attests to the fact that the biochemical processes affecting the upper meter of peat deposits at both sites within the past millennium have been similar in their intensity.

Direct measurements of the activity of microbiological processes in the studied peat deposits present valuable information on the state of microbial communities in them. We studied the microbial communities of these peat deposits by the method of luminescent microscopy, which made it possible to distinguish between the active (mycelium) and the inactive (spores) components of the micromycetal complex (Table 2). At site 2, bacteria predominated in the upper 25 cm, and their content significantly decreased in the lower part of the profile (75–100 cm). At site 3, a significant decrease in the number of bacteria was observed in the layer of 200–250 cm. At this depth, the density of bacterial population at site 3 was approximately equal to that at the depth of 75–100 cm at site 2 (13.3 and 12.9 billion cells/g, respectively). An analogous distribution was found for the density of fungal spores. The active part of the micromycetal complex—fungal mycelium—is mainly concentrated in the upper peat layers, because fungi are aerobic organisms, and only few fungal species can develop at greater depths. At the same time, fungal mycelium was detected in the peat layer of 200–250 cm at site 3, though its activity at this depth was 30 times lower in comparison with that in the surface layer. The same regularity was found for the distribution of actinomycetal mycelium in the peat profiles. The activity of microflora in the deep peat layers is explained by different reasons, including the infiltration of oxygen-saturated water down the peat profiles [11]. However, it is known that the migration of water through the peat deposit is a

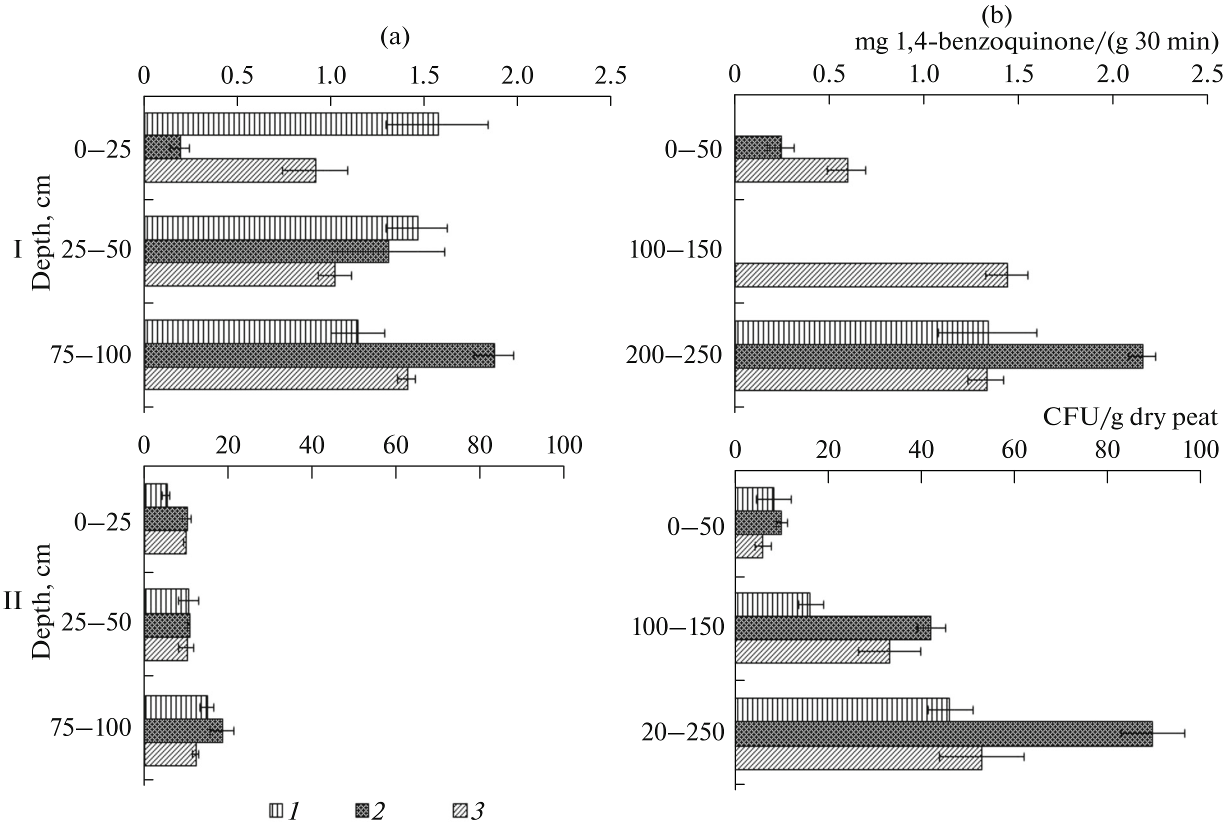

Fig. 1. Dynamics of (I) ammonifiers and (II) actinomycetal mycelium in peat deposits of sites (a) 2 and (b) 3; long-term averages for (*1*) May, (*2*) July, and (*3*) September are shown.

long process (10–20 years) [4], whereas changes in the activity of micromycetal complex can be traced during one growing season.

Thus, the length of the actinomycetal mycelium reaches its maximum values in the upper 50 cm of the peat deposits. However, at the depth of 3 m, the activity of the actinomycetal complex remains relatively high during the entire growing season (Fig. 2). In this layer, the activity of the actinomycetal mycelium is related to the hydrolytic activity and to its participation in the mineralization of the organic matter of peat. It is known that some actinomyces may remain active even in the case of the oxygen concentration in the air of about 2% and less. It is interesting that a higher supply of the peat deposit at site 2 with nutrients and other elements was not the factor of a higher activity of the actinomycetal mycelium; at the depth of 25–50 cm, its activity decreased by two times. However, the activity of the actinomycetal mycelium in this layer increased in September. In other words, the transformation of the organic matter of peat by the soil microflora during the growing season had a pulsating character independently from the degree of the soil waterlogging, as the bog water level was no deeper than 40 cm during the growing season. The uneven pulsating character of the microbiological activity was typical both for aerobic and anaerobic microflora.

A specific feature of the water regime of peat deposits in bog ecosystems is their waterlogged state. However, despite the waterlogging, peat deposits always contain some free oxygen that enters the system through various mechanisms, including the biochemical processes in the peat deposits.

It can be supposed that peat deposits always contain some amounts of the gas phase consisting of not only greenhouse gases (CO_2 and CH_4) but also of free oxygen. It is known that oxygen concentrations in the peat deposits vary from 65–80 to 100–150 g/m^3, or 5–11 vol.% [20].

Among other factors contributing to the production of oxygen in peat deposits, the catalase activity of peat soils should be considered (Fig. 3). Under its impact, hydrogen peroxide forming in other reactions is decomposed to water and free oxygen. In the 3-m-thick peat deposit of site 3, the catalase activity was relatively low and varied from 2.4 to 4.4 mL O_2/g per 2 min; in the upper meter of peat deposit at site 2, it varied from 3.0 to 11.8 mL O_2/g per 2 min and was assessed as moderate. A higher catalase activity in the peat deposit within the transaccumulative part of the

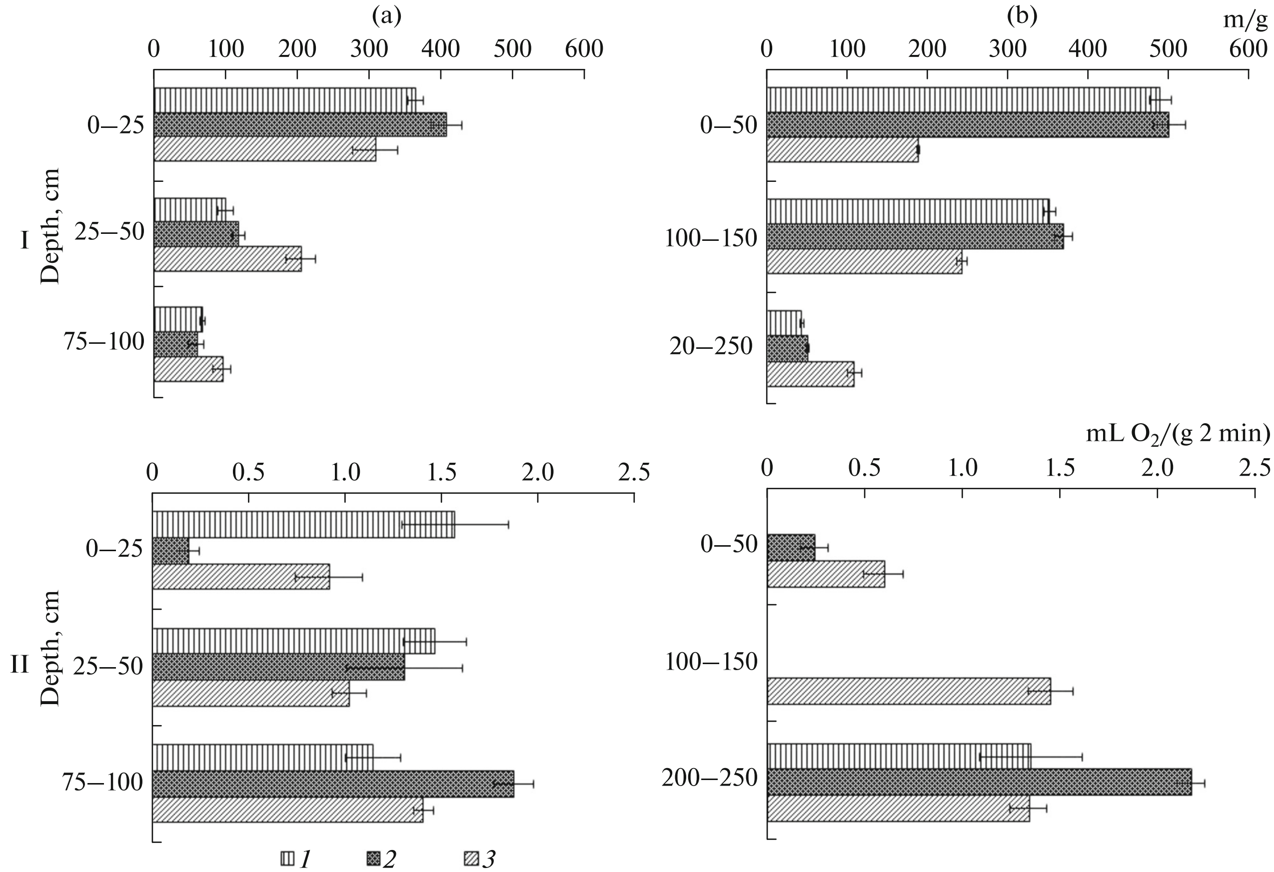

Fig. 2. Dynamics of the (I) catalase and (II) polyphenoloxidase activities in peat deposits of sites (a) 2 and (b) 3 in (*1*) May, (*2*) July, and (*3*) September of 2013.

catena is explained by its specific chemical composition (owing to the lateral inflow of substances from the autonomous part of the catena) and by the bog water level supporting the alteration of aerobic and anaerobic conditions and ensuring progressive swamping of the territory.

Let us consider the dynamics of polyphenoloxidase activity during the growing season. Theoretically, it should decrease upon the high water level, because the oxidation of phenols may only proceed in the presence of oxygen [19]. It is argued that condensed forms of phenol compounds accumulating under anaerobic conditions serve as inhibitors of various enzymes [23, 25]. Experiments have shown that the polyphenoloxidase activity increases by seven times upon an increase in the aeration of the peat. The high values of the polyphenoloxidase activity in the studied peat deposits attest to the absence of obligate anaerobic conditions in them (Fig. 4).

Thus, the micromosaic pattern of aerobic and anaerobic conditions is maintained in the peat profiles. The presence of oxygen in the waterlogged peat is explained by the character of biochemical processes, the botanical composition of the peat, and the presence of macro- and microstructures in the peat material. As a result, even complete inundation of the peat deposits does not create obligate anaerobic conditions in the peat layers. Each surface peat layer, being submerged, retains oxygen in its microaggregates and produces additional oxygen owing to the biochemical processes. The same conclusion was made by other authors [5].

In general, the formation of the peat deposit is a continuous process; the accumulation of peat on the surface is accompanied by the rise in the bog water level bringing elements accumulated in the underlying substrate to the peat layer. These elements are redistributed in the peat profile with a tendency for a gradual decrease in their concentration towards the peat surface. The upper part of the peat deposit corresponds to the modern climatic conditions, whereas the lower peat layers correspond to the climatic conditions of the past. Each peat layer contains the gas phase, including oxygen. Peat layers differing in their botanical composition are characterized by their own regimes of gases and biochemical processes. Thus, the forming peat deposit is a "layer cake," which creates certain difficulties for the industrial use of the peat.

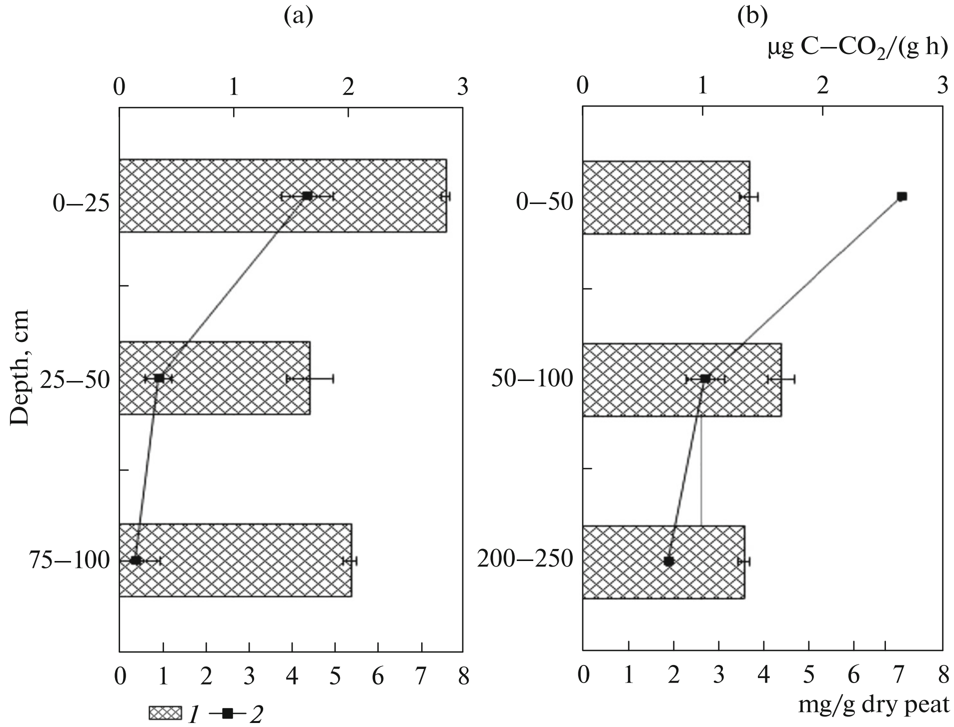

Fig. 3. Changes in the (*1*) rate of microbial respiration and (2) microbial biomass in the peat profiles of sites (a) 2 and (b) 3.

It is interesting to trace the relationships between the microbial biomass and its respiration activity (as measured by the method of substrate-induced respiration) as reliable indications of the activity of soil microflora (Fig. 5) [1, 22, 27]. The highest values of the microbial biomass are typical of the upper peat layer of both sites; the average values for the growing season are equal to 4.37 and 7.10 μg/g for the low and high ryams, respectively. In the deeper layers, the microbial biomass decreases by about three times. At the same time, the rate of basal respiration of the microorganisms changes insignificantly along the soil profile. Thus, in the surface layers, the transformation of organic matter of peat is mainly due to the activity of aerobic microflora, whereas in the deep layers, it is ensured by the activity of anaerobes or facultative anaerobes.

With an increase in the thickness of peat deposits, redox conditions in the deep layers are shifted towards the predominance of anaerobic processes. Therefore, the biological activity of microflora, including that determined by the method of substrate-induced respiration, decreases.

The analysis of these characteristics allows us to suppose that the notions of the active and inactive peat layers (acrotelm and catotelm) should not be applied to the biochemical and gas regimes of the peat deposits, because the transformation of the chemical composition of peat in the facultatively anaerobic layer does not stop. In the deep layers of peat, the contents of water-soluble and easily hydrolyzable compounds decrease, whereas the content of humic acids increases. These phenomena are interrelated, because the synthesis of humic acids takes place in the course of transformation of some easily hydrolyzable components of peat. In other words, in the deep peat layers, the aerobic microbiological processes (mainly, hydrolysis of substances) are replaced by other biochemical processes favoring the transformation of the organic matter of peat and the production of humic acids. In this context, the notions of the active and inert peat layers should only be applied to the specific features of the water regime in the upper and lower parts of peat bogs [6, 12].

Let us consider redox conditions in the peat deposits of the catena averaged for many years. Their dynamics are clearly correlated with the dynamics of the bog water levels (Table 3). The positive value of the redox potential is only maintained in the layer that gets free of gravitational water upon a decrease in the bog water level. The lower part of the peat deposits is characterized by permanently negative values of the redox potential. Formally, this index supports the idea about the subdivision of the peat deposits into the active (aerobic) and inert (anaerobic) parts. It should be noted that artificial drainage of peatlands is accompanied by gradual changes in the redox conditions. In the profiles of drained peatlands, the layers with oxidative, transitional (oxidative–reducing), and reducing conditions can be distinguished. Strongly negative values

Table 3. Values of redox potential

Depth, cm	Kind of peat; type of peat layer	$\frac{R}{A}$	May	June	July	August	September
			Site 2				
10	Pine–cotton grass–sphagnum; oligotrophic	$\frac{45}{6.5}$	615	644	564	621	342
20	"	$\frac{45}{6.5}$	744	794	749	804	742
40	"	$\frac{45}{6.5}$	–135	351	416	256	164
80	Woody–cotton grass; transitional	$\frac{55}{8.0}$	–158	–168	–175	–167	–180
100	"		–168	–174	–181	–171	–182
			Site 3				
10	Fuscum; oligotrophic	$\frac{5}{3.7}$	667	642	708	679	609
20	"	$\frac{5}{2.7}$	391	253	533	576	403
40	"	$\frac{5}{2.7}$	–75	–80	–71	–59	–62
60	Medium; oligotrophic	$\frac{5}{2.1}$	–88	–92	–84	–72	–74
100	"	$\frac{5}{2.1}$	–46	–47	–45	–35	–38
160	Pine–cotton grass–sphagnum; transitional	$\frac{50}{6.0}$	–117	–121	–112	–98	–98
200	Sedge; eutrophic	$\frac{45}{4.3}$	–122	–122	–108	–91	–89
250	"	$\frac{45}{4.3}$	–160	–171	–176	–168	–179
300	Sedge–fern; eutrophic	$\frac{45}{10.1}$	–178	–187	–192	–184	–196

R is the decomposition degree, %; *A* is the ash content, %.

of the redox potential are not typical of them. A different situation is observed for peat bogs in their natural state However, characteristics of their biological regimes (Figs. 1–3) and physical properties of the peat bog soils indicate the presence of oxidative conditions in the natural bogs. What are the factors that favor the development of oxidation processes in these bogs?

Stationary observations over the redox potential in the studied peat soils for several years indicate that the boundary of the transition from positive ORP values to negative values is very sharp at site 2 and less distinct at site 3. This may be related to the specific transaccumulative landscape position of the high rayam (site 2).

It is known that oxidation and reduction reactions in the peat soils usually take place in the presence of oxygen contained in the heterogeneous multiphase peat medium even in the waterlogged state. However, in native bogs, reducing conditions predominate from the depth of 20–40 cm. The predominance of strongly reducing conditions in the peat thickness against the background of the high biochemical activity attests to the need to revise traditional approaches to the assessment of ORP values. It should be taken into account that the organic matter of peat contains up to 40% of humic substances that have the strong reducing capacity. Hence, the known estimates of the ORP values are not quite suitable for the peat deposits, because they overestimate the parameters of the reducing conditions. We argue that a traditional ORP value of 200 mV that is considered the boundary between reducing and oxidizing conditions in the mineral soils should be lowered for the peat soils. We suppose that the boundary of the transition to the reducing conditions in the peat soils should be set at 0 mV as suggested in [13].

Certainly, this is a preliminary assumption; to confirm it, additional studies, including model experiments, are necessary.

CONCLUSIONS

Natural processes taking place in the geochemically linked landscapes of an oligotrophic bog are specified by the position of the particular landscapes in the catena. In the transaccumulative position of the peat deposits (the high ryam site), the excessive spring moistening of the bog takes place owing to the inflow of water from the autonomous position. During the growing season, the accumulation of various mineral, organic, and organomineral compounds carried by the lateral water flows takes place in the transaccumulative position. As a result, the peat of transitional type is gradually accumulated there; the thickness of the peat deposit in this landscape is about 1 m. It is characterized by a higher biochemical activity in comparison with the 3-m-deep peat deposit of the autonomous part of the catena (the low ryam). Annual inundation by the snowmelt stimulates the expansion of the bog-forming process. The ongoing development of the bog is proved by data on the carbon budget.

Differently directed biochemical processes are active in the entire peat profiles down to the underlying mineral substrates. However, their nature and activity vary in the profiles. In the lower peat layers, these processes are retarded. The process of aerobic decomposition of the peat material gradually shifts upwards in parallel with the growth of the peat deposit. In general, the entire stratigraphic profile of the peat deposit passes through the stage of bog pedogenesis. The biochemical activity in the particular peat layers depends on their physical properties; differently directed biochemical processes are arranged in the micromosaic pattern with alternating anaerobic and aerobic conditions. Oxidizing conditions may exist in microloci even in the waterlogged lower part of the peat deposit. The activity of the biochemical processes even below the bog water level is confirmed by the existence of the microzones containing gas phase, including free oxygen, below the water-saturated layer. These microzones accumulate oxygen, carbon dioxide, and methane produced in the course of biochemical processes.

The notions of the active and inert layers of the peat deposits should only be applied to their water regimes. All the considered biochemical properties of the peat deposits in the system of geochemically linked landscapes of oligotrophic bogs (low ryam–high ryam) confirm the fact that a mosaic pattern of oxidizing and reducing conditions is formed in the peat thickness under the water-saturated upper peat layer; this thickness contains the gas phase, including oxygen. This is explained by the formation of difficultly permeable for water microstructures in the lower peat layers in the course of transformation and polymerization of the products of decomposition of plant tissues. Oxidizing conditions are formed in these structures under the impact of biochemical processes. To prove the existence of aerobic conditions in the peat thickness, special studies of the concentration of oxygen in it and its redox potential should be conducted. It is important to measure the redox potential not only in the bulk peat mass but also in the peat microstructures.

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REFERENCES

1. N. D. Ananyeva, *Microbiological Aspects of Self-Purification and Sustainability of Soils* (Nauka, Moscow, 2003) [in Russian].
2. N. D. Ananyeva, E. A. Susyan, and E. G. Gavrilenko, "Determination of the soil microbial biomass carbon using the method of substrate-induced respiration," Eurasian Soil Sci. **44** (11), 1215–1221 (2011).
3. E. T. Bazin, V. D. Kopenkin, and V. I. Kosov, *Technical Analysis of Peat* (Nedra, Moscow, 1992) [in Russian].
4. V. K. Bakhnov, *Biogeochemistry of Mire Formation* (Nauka, Novosibirsk, 1986) [in Russian].
5. M. P. Volarovich, I. I. Lishtvan, and A. A. Terent'ev, "State of the fine-dispersed fraction of peat according to electron microscopy data," Kolloidn. Zh., No. 2, (1969).
6. P. K. Vorob'ev, "Analysis of the physical characteristics of active horizon of undrained mires," Tr. Gos. Gidrol. Inst., No. 126, 65–69 (1965).
7. A. V. Golovchenko, T. G. Dobrovol'skaya, and L. I. Inisheva, "Structure and stocks of microbial biomass in oligotrophic peat bogs of the southern taiga in Western Siberia," Eurasian Soil Sci. **35** (12), 1296–1301 (2002).
8. A. V. Golovchenko, T. G. Dobrovol'skaya, and D. G. Zvyagintsev, "Microbiological analysis of peat-bog as the soil profile," Vestn. Tomsk. Gos. Pedagog. Univ., No. 4(78), 46–53 (2008).
9. A. V. Golovchenko, A. V. Kurakov, T. A. Semenova, and D. G. Zvyagintsev, "Abundance, diversity, viability, and factorial ecology of fungi in peatbogs," Eurasian Soil Sci. **46** (1), 74–90 (2013). doi 10.7868/S0032180X13010036
10. T. G. Dobrovol'skaya, A. V. Golovchenko, O. S. Kukharenko, A. V. Yakushev, T. A. Semenova, and L. I. Inisheva, "The structure of the microbial communities in low-moor and high-moor peat bogs of Tomsk oblast," Eurasian Soil Sci. **45** (3), 273–281 (2012).
11. V. A. Dyrin and E. P. Krasnozhenov, "Activity of microflora in virgin and reclaimed peatbog soils," Vestn. Tomsk. Gos. Pedagog. Univ., No. 6, 33–38 (2007).

12. K. E. Ivanov, *Water Exchange in Wetlands* (Gidrometeoizdat, Leningrad, 1975) [in Russian].
13. L. I. Inisheva, "Peat soils: genesis and classification," Eurasian Soil Sci. **39** (7), 699–704 (2006).
14. L. I. Inisheva, T. V. Dement'eva, and N. G. Inishev, "Hydrothermal and redox conditions of the active layer of oligotrophic mires," Vopr. Geogr. Sib., No. 24, 183–189 (2001).
15. L. I. Inisheva, S. N. Ivleva, and T. A. Shcherbakova, *Guide for Analysis of Enzymatic Activity of Peatbog Soils and Peats* (Tomsk State University, Tomsk, 2003) [in Russian].
16. L. A. Karyagina and N. A. Mikhailovskaya, "Activity of polyphenol oxidase and peroxidase in soil," Vestn. Akad. Nauk Belorus. SSR, Ser. S-kh. Navuki, No. **2**, 40–41 (1986).
17. O. L. Liss, L. I. Abramova, N. A. Avetov, N. A. Berezina, L. I. Inisheva, T. V. Kurnishkova, Z. A. Sluka, T. Yu. Tolpysheva, and N. K. Shvedchikova, *Mire Systems of Western Siberia and Their Nature-Protective Significance* (Grif i K, Tula, 2001) [in Russian].
18. *Practicum on Soil Microbiology and Biochemistry,* Ed. by D. G. Zvyagintsev (Moscow State University, Moscow, 1991) [in Russian].
19. O. G. Savicheva and L. I. Inisheva, "Biological activity of peats with different botanical composition," Khim. Rastit. Syr'ya, No. **3**, 41–50 (2003).
20. A. V. Smagin, "Soil-hydrophysical maintenance of the studies of gas functions of West Siberian peats related to the greenhouse effect," Ekol. Vestn. Sev. Kavk. **3** (3), 46–58 (2007).
21. J. P. E. Anderson and K. H. Domsch, "A physiological method for the quantitative measurement of microbial biomass in soils," Soil Biol. Biochem. **10** (3), 314–322 (1978).
22. J. Bouma, "Environmental quality: a European perspective," J. Environ. Qual. **26**, 26–31 (1997).
23. C. Freeman, N. J. Ostle, N. Fenner, and H. Kang, "A regulator role for phenol oxidase during decomposition in peatlands," Soil Biol. Biochem. **36** (10), 1663–1667 (2004).
24. L. I. Inisheva, A. A. Zemtsov, and S. M. Novikov, *Vasyugan Mire (Natural Conditions, Structure and Functioning)* (Tomsk State Pedagogical University, Tomsk, 2011).
25. H. Ling, W. Xiang, and S. Xinating, "Effects of temperature and water level changes on enzyme activities in two typical peatlands: implications for the responses of carbon cycling in peatland to global climate change," in *International Conference on Environmental Science and Information Application Technology* (Wuhan, China, 2009), pp. 18–22.
26. K. Salo, "The composition and structure of macrofungus communities in boreal upland type forests and peatlands in North Karelia, Finland," Karstenia **33**, 61–99 (1993).
27. L. J. Sikora, V. Yakovchenko, and D. D. Kaufman, "Comparison of rehydration method for biomass determination to fumigation-incubation and substrate-induced respiration method," Soil Biol. Biochem. **26** (10), 1443–1445 (1994).
28. M. N. Thormann and A. V. Rice, "Fungi from peatlands," Fungal Diversity **24**, 241–299 (2007).

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