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RESEARCH ARTICLE

Relationship between the content of basic chemical elements and ecological and trophic groups of microorganisms in peat oligotrophic frozen soil

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Abstract
The paper analyzed the number of ecological-trophic groups of microorganisms and the elemental composition of the active, permafrost and thawed layers of a typical flat mount frozen peatlands (plateau palsa) in the Nadym-Pur interfluves, Western Siberia, with part of it affected by fire. The number of ecological-trophic groups was found to change after permafrost thaw. The study revealed a relationship between the number of microorganisms and the content of some chemical elements in the soil profile of the plateau palsa in the Nadym-Pur interfluve. A statistically significant relationship was found between the most probable number of microorganisms (CFU/g) in different peat layers and the pH, the ash content and the content of calcium, magnesium, strontium, and iron.

Keywords
Ecological-trophic groups of microorganisms, Western Siberia, plateau palsa, permafrost thaw

Introduction

Peatland ecosystems, with an incomplete cycle of chemical element transformation and a cumulative type of matter and energy transfer, occupy large areas in Siberia and are important for carbon accumulation and formation of the atmospheric gas composition (Vompersky 1999; Liss et al. 2001; Kirpotin et al. 2009, 2011). Wetland ecosystems annually return less organic matter to the environment than they consume, accumulating carbon in peat deposits (Roulet 2000; Chmura 2003).

Several mires in the north of Western Siberia are covered with permafrost; its thermal state is sensitive to changing climatic conditions, in particular, to elevated air temperature and altered snow conditions (Pokrovsky et al. 2010; Zhao et al. 2010). Cryogenic heaving resulted in abundant flat and large palsas that consist of frozen peat mounds and waterlogged depressions between them. Peat soils in these areas are actively transformed due to both changes in soil formation conditions and various cryogenic effects that directly or indirectly determine the nature and intensity of soil formation (Pyavchenko 1955).

The global nature of organic carbon accumulation in mires dictates the need for its microbiological study (Golovchenko and Volkova 2019; Grodnitskaya et al. 2018). The soil microbiome contributes to soil formation and drives key biochemical processes, performing the decomposition and synthesis of various organic substances in peatlands (Will et al. 2010). Recent studies have focused on a detailed exploration of microbial communities in permafrost, since it is inhabited by viable, cold-adapted microorganisms, contains ecologically and biotechnologically attractive genetic resources with new metabolic potential, and apparently potentially pathogenic species of ecological interest (Mackelprang et al. 2011; Legendre et al. 2014; Deng et al. 2014; Frey et al. 2016; Feng et al. 2020).

Studies addressing the microbiological analysis from soils of the permafrost zone in Western Siberia are insufficient; the effect of thawing on the microbial communities of permafrost soils in Western Siberia is poorly studied; little data are available on the relationship between the chemical composition and microflora of the permafrost zone (Lapteva et al. 2017; Aksenov et al. 2021).

The aim of our study was to analyze the relationship between the content of the main chemical elements and ecological-trophic groups of microorganisms in the profile of the permafrost peat soil of the plateau palsa in the Nadym-Pur interfluves, Western Siberia.

Materials and methods

The study area is located in the Nadym-Pur interfluve of the northern taiga in Western Siberia (Yamal-Nenets Autonomous Okrug). A plateau palsa site with part of the active layer destroyed by fire in 2007 was investigated. At the post-fire site, the peat deposit thawed completely. Previously, the site was described in detail (Kolesnichenko et al. 2019; Lojko et al. 2017).

In 2019, undisturbed and disturbed plateau palsa sites were investigated (Fig. 1). Samples were taken using sterile instruments in triplicate from the active, permafrost and thawed layers. Subsequently, the samples were placed in sterile test tubes and stored in a freezer until further analysis.

Field studies were carried out using the equipment of the unique research installation 'System of experimental bases located along the latitudinal gradient' of TSU under the financial support of the Ministry of Science and Higher Education of Russia (RF-2296.61321X0043, 13.UNU.21.0005, contract No. 075-15-2021-672).

The moisture content of the samples was measured by the gravimetric method. The ash content of peat was determined in accordance with GOST 11306-83. The content of the main chemical elements was analyzed by ICP mass spectrometry using the equipment of the Tomsk Regional Center for Collective Use, TSU. The Center is supported by the grant from the Ministry of Science and Higher Education of the Russian Federation No. 075-15-2021-693 (No. 13. TsKP.21.0012).

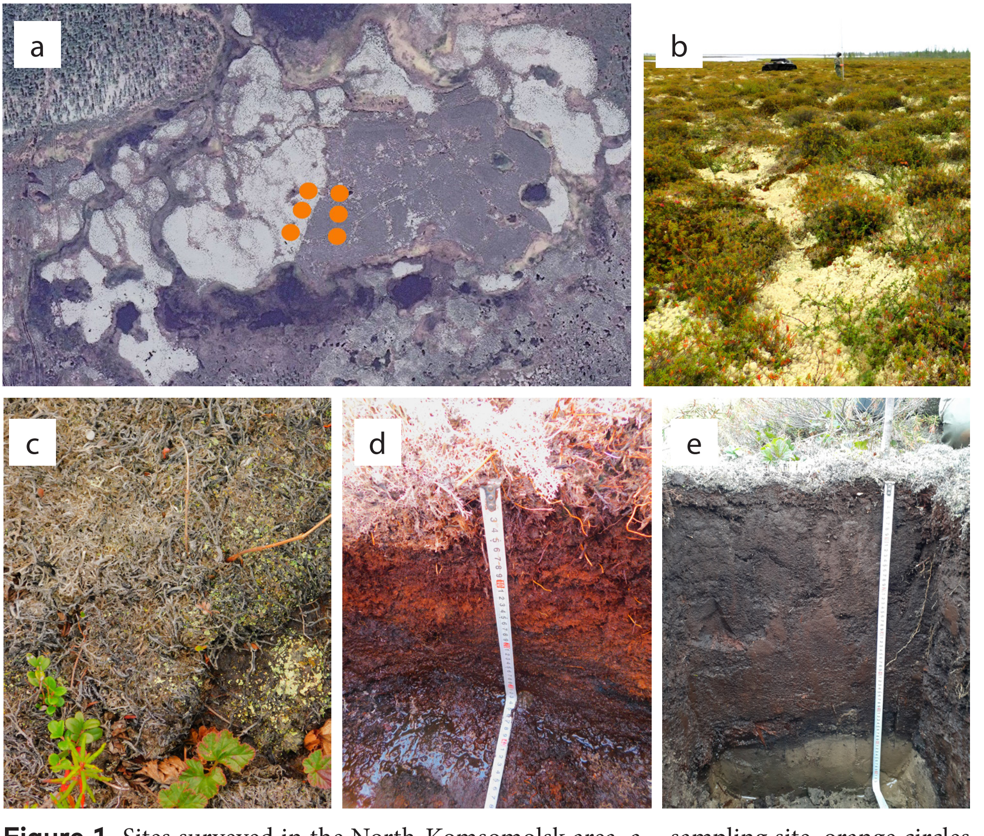

Figure 1. Sites surveyed in the North-Komsomolsk area. a – sampling site, orange circles – soil selection points; b – vegetation cover of the undisturbed plateau palsa; c – disturbed plateau palsa; d – soil sections in undisturbed plateau palsa; e – disturbed plateau palsa.

The microorganism abundance estimated by direct counting throughout the profile shows actual reproduction of a part of the microbial complex not only in the upper, but also in the lower peatland layers (Golovchenko et al. 2005; Golovchenko et al. 2008; Dobrovolskaya et al. 2012; Golovchenko et al. 2013). Therefore, the Koch method was employed to determine the number of microscopic fungi and ammonifying, amylolytic, humus-destroying, and oligotrophic microorganisms in permafrost peat soils by direct microbiological inoculation in elective media. The contribution of the microbial community of permafrost peat soils to the nitrogen cycle was evaluated with respect to the number of ammonifying microorganisms, which transform nitrogen-containing organic compounds to ammonium, and amylolytic microorganisms that decompose nitrogen-containing inorganic substances. The contribution of the microbial community to the carbon cycle was assessed with respect to the number of humus-destroying microorganisms, oligotrophic microorganisms, and microscopic fungi. The total number of bacteria was evaluated in colony forming units (CFU) per 1 g of dry soil.

The abundance of ammonifiers was evaluated in fishmeal hydrolyzate broth from the State Scientific Center for Applied Microbiology and Biotechnology.

The abundance of amylolytics was evaluated on starch-ammonia agar (SAA): 10 g starch, 2.0 g $(NH_4)_2SO_4$, 1.0 g K_2HPO_4, 1.0 g $MgSO_4$, 1.0 g NaCl, 3.0 g $CaCO_3$, 20 g agar, 1000 ml H_2O_{dist}.

Saccharolytic micromycetes were grown in Czapek medium (OOO SPC Biokompas-S, Russia).

The abundance of microorganisms was evaluated in Vinogradskogo agar medium Vinogradskogo for autochthonous microflora: 5 g of $K2_2HPO_4$; 2.5 g of $MgSO_4 \times 7H_2O$; 2.5 g NaCl; 0.05 g $FeSO_4$; 10 ml of ammonium humate (1%); 1000 ml of H_2O_{dist}.

Oligotrophs were grown on peat agar prepared as follows: 200 g of peat was poured into 500 ml of tap water and boiled over low heat for 2 h. After being cooled, the extract was filtered and 2% agar-agar was added.

Petri plates inoculated were incubated for 5–14 d in a thermostat at 25 °C. After incubation, the grown colonies were counted and the most probable number of CFU per 1 g of peat was calculated with 95% confidence interval.

Statistical data were processed and graphical models were constructed using Microsoft Excel and Statistica 8.0 (method of nonparametric statistics (Spearman rank correlation coefficient, Kruskal-Wallis and median test, regression analysis).

Result

The studied peatlands, at both undisturbed and disturbed sites, are submerged in sands and are composed of shrub and woody-shrubby peat with rare herbaceous inclusions, and the degree of decomposition varies from 30% to 70%. Table 1 summarizes the main physical-chemical characteristics and the concentration of some elements in the sections of permafrost and thawed peat.

Table 1. Main characteristics and elemental composition of the peat in the profile of permafrost and the thawed peat soil

Sampling depth, cm	Peat type	Degree of decomposition, %	pH	Na	Mg	K	Ca	Ba	Fe	Zn	Mn
				Permafrost peat soil (section 2)							
0–5	Active layer, shrubby	43	3.73	291.6	349.6	712.3	1131.3	47.0	1829.1	12.0	10.8
10–15	Active layer, shrubby	55	3.68	132.3	163.7	293.8	911.0	54.1	1940.2	8.0	5.0
20–25	Active layer, shrubby	65	3.66	139.3	93.2	294.5	436.1	59.8	1825.9	5.4	4.3
30–35	Active layer, shrubby	>70	3.59	159.0	74.8	300.7	318.6	57.1	1080.3	8.6	5.0
38–43	Suprapermafrost layer, woody-shrubby	40	3.67	41.0	54.0	149.7	315.1	37.6	958.1	4.8	3.7
43–53	Permafrost layer, woody-herbaceous-shrubby	53	3.62	510.6	156.4	1396.5	429.6	92.4	1447.6	455.1	18.2
53–63	Permafrost layer, herbaceous-woody	>65	3.88	70.6	107.1	155.8	763.0	63.5	2124.1	195.1	13.0
63–73	Permafrost layer, woody-herbaceous-shrubby	58	4.11	44.8	69.2	112.0	783.9	59.9	1523.2	238.6	15.8
93–103	Permafrost layer, woody-shrubby	?	5.24	1918.4	386.2	5214.3	643.3	220.0	2055.1	85.6	60.0
103–113	Permafrost layer, woody-shrubby-herbaceous	50	4.44	35.6	127.9	82.4	1480.0	68.2	2393.7	39.9	48.8
143–153	Permafrost layer, woody-herbaceous	60	4.63	88.3	287.3	168.6	3446.8	86.9	5923.0	53.6	123.0
				Thawed peat soil (section 5)							
0–5	Thawed layer, shrubby	40	4.04	390.6	269.6	927.0	950.8	82.1	1684.4	14.4	18.2
10–15	Thawed layer, woody-shrubby	63	4.00	112.2	65.4	267.4	180.9	56.7	1525.3	4.7	5.9
20–25	Thawed layer, woody-shrubby	63	3.83	56.8	43.1	168.5	202.4	56.5	1275.0	3.7	4.4
30–35	Shrubby	55	3.84	48.3	43.0	131.4	202.5	52.0	990.7	11.0	5.4
40–45	Thawed layer, woody-shrubby	62	3.92	58.5	75.0	167.9	372.0	54.4	758.0	6.2	11.9
50–55	Thawed layer, woody-shrubby	58	4.02	202.1	211.0	526.4	490.7	55.4	1342.3	5.5	18.3
60–65	Mineral	–	4.92	2657.9	490.7	2497.0	1525.3	233.3	2919.8	34.4	104.3

The thickness of the peat deposit at the undisturbed site was 153 cm, and that at the disturbed site attained 55 cm, since the upper active layer of the peatland was destroyed by fire and part of it compacted. The permafrost boundary at the undisturbed site was found at a depth of 43–45 cm. The soils were acidic and the pH of the water extract varied from 3.04 to 5.24 units, depending on the peat type. The peat soil profile contained two groups of elements: (1) Na, Mg, K, Ca, Ba, and Fe elements with an increased concentration in the thawed layers of the peatland; (2) Zn and Mn elements that show a stable or slightly changed concentration.

The number of microorganisms of the selected ecological trophic groups was counted, and it ranged from 0.12×10^3 to 2.58×10^6 CFU/g in undisturbed peat, and from 0.11×10^3 to 12.25×10^6 in disturbed peat (Table 2).

Table 2. Number of microorganisms (CFU/g, thousand) in the profile of the permafrost and the thawed peat soil

Sampling depth, cm	Groups of microorganisms, thous.				
	Ammonifiers	**Decomposers of nitrogen-containing inorganic substances**	**Oligotrophs**	**Micromycetes**	**Humus-destroying microorganisms**
			Permafrost peat soil		
0–5	1477.7±3.2	1063.0±3.3	1619.7±4.3	20.2±0.44	102.8±1.1
10–15	1025.3±2.5	580.7±2.5	850.3±3.2	7.1±0.24	211.3±1.6
20–25	968.3±1.8	352.0±1.5	273.3±1.4	3.1±0.13	47.0±0.6
30–35	310.0±1.0	45.0±0.6	133.3±1.0	1.6±0.10	16.5±0.3
38–43	163.0±0.9	64.0±0.7	222.0±1.2	0.6±0.06	20.7±0.4
43–53	307.0±1.4	126.7±0.9	151.3±0.8	3.0±0.14	22.4±0.5
53–63	266.5±1.1	53.0±0.9	43.0±0.6	2.0±0.15	19.9±0.5
63–73	259.5±1.1	44.5±0.7	186.5±1.5	1.3±0.12	34.0±0.6
73–83	185.0±0.8	59.5±0.7	88.0±0.9	0.7±0.07	16.4±0.4
83–93	184.0±0.8	24.0±0.4	29.0±0.4	0.2±0.04	2.9±0.1
93–103	16.5±0.2	21.5±0.3	23.0±0.2	0.2±0.03	1.2±0.1
103–113	40.0±0.4	40.0±0.4	10.0±0.2	0.2±0.03	5.0±0.1
113–123	90.0±0.4	30.0±0.3	10.0±0.2	0.1±0.02	5.0±0.1
123–133	90.0±0.4	20.0±0.2	no	0.1±0.02	3.0±0.1
133–143	20.0±0.2	10.0±0.1	10.0±0.1	0.1±0.01	3.0±0.1
143–153	20.0±0.2	10.0±0.1	no	0.1±0.01	no
			Thawed peat soil		
0–5	11886.2±13.3	12258.2±15.3	11538.0±14.6	95.3±1.53	2347.2±6.2
10–15	3134.7±5.5	1050.9±3.5	910.8±3.6	20.8±0.52	83.6±1.0
20–25	3115.2±5.4	593.3±2.3	584.0±2.6	13.4±0.40	67.2±0.9

Sampling depth, cm	Groups of microorganisms, thous.				
	Ammonifiers	Decomposers of nitrogen-containing inorganic substances	Oligotrophs	Micromycetes	Humus-destroying microorganisms
30–35	746.2±2.3	483.6±2.0	242.2±1.5	5.3±0.21	40.8±0.6
40–45	990.0±3.5	622.3±3.0	879.3±3.7	3.4±0.21	56.6±0.9
50–55	414.7±1.2	200.3±0.9	288.3±1.2	1.6±0.08	21.7±0.3
60–65	154.9±0.3	44.4±0.2	44.4±0.2	0.8±0.03	2.3±0.1

Note: no – no growth.

Our data on the number of microorganisms of the main ecological-trophic groups (Table 2) are consistent with those obtained in the studies on Arctic (10^5–10^9), Alpine (10^8–10^{10}) and Antarctic (10^3–10^6) permafrost (Khlebnikova et al. 1990; Ivanova et al. 2012; Blanco et al. 2012; Hu et al. 2015; Goordial et al. 2016).

We reported a decreased number of microorganisms at increased depth of the peat, at both undisturbed and disturbed sites, where the active layer of the peat deposit (Fig. 2) was optimal for the growth of microorganisms sampled from permafrost and thawed peat of Western Siberia. These data are consistent with the results of the analysis of samples taken from the permafrost peatlands of the Khanymei site in Western Siberia (Aksenov et al. 2021) and the permafrost peatlands of the Bolshezemelskaya tundra (BZT) in the Nenets Autonomous Okrug (Lapteva et al. 2017).

Ammonifying microorganisms were a predominant ecological trophic group throughout the entire depth of the peat deposit (Figure 2), where oligotrophic microorganisms were found to dominate at a depth of 40 cm, and amylolytic microorganisms were most abundant at depths of 0 to 5 cm, in particular, 93 to 103 cm at the undisturbed site and 0 to 5 cm at the disturbed site. The dominance of ammonifying microorganisms was also reported for frozen soddy-meadow gleyic soils in Central Yakutia (Ivanova et al. 2014).

The studied peat horizons are inhabited by numerous eutrophic microorganisms that prevail in number over oligotrophic ones, indicating that peat deposits contain a sufficient amount of nutrient substrate for the vital activity of microorganisms (Fig. 3).

In contrast to the undisturbed site, the disturbed site exhibited an increased number of all ecological-trophic groups, since the permafrost thaw increases bacterial diversity (Fig. 3). The increased abundance and diversity of microorganisms during permafrost thaw were previously reported for forest soils from the Huma River basin in northeast China (Dong et al. 2023), peat bogs in Alaska (Mondav et al. 2017; Woodcroft et al. 2018) and for soil after 10 years of permafrost thaw in the Abisko peatland, Northern Sweden (Monteux et al. 2018). Kallistova et al. (2019)

reported the effect of permafrost degradation on the methanotrophic community, that is, changes in the community structure and its functions. In laboratory experiments, a similar pattern was observed during the thawing of permafrost soil in central Alaska (Mackelprang et al. 2011).

An inverse relationship was revealed between the number of ammonifying organisms and saccharolytic micromycetes and the pH value in the permafrost layer; a direct relationship was revealed between the number of oligotrophic organisms and the pH value in the active layer (Fig. 4). A similar relationship between the number of oligotrophic organisms and the pH value was previously reported for peat soils in the eastern part of the Vasyugan mire (Savichev et al. 2019) and acidic soils in the northeast of European Russia (Shirokikh 2004).

It was found that in the thawed layer, the number of ammonifying and oligotrophic organisms statistically significantly decreases with increased ash content, while in the permafrost layer, the number of oligotrophic organisms is observed to increase (Fig. 5).

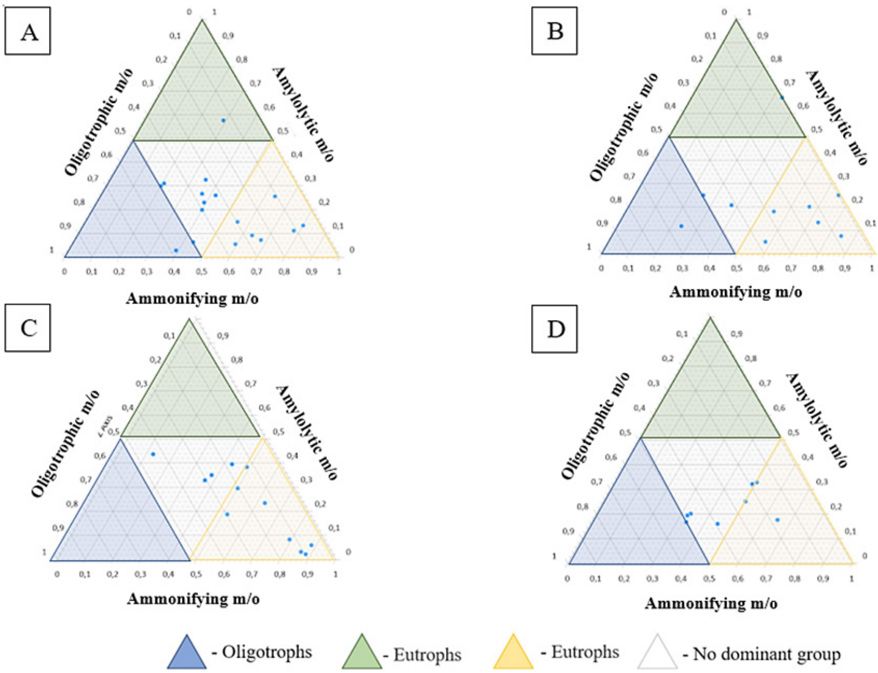

Figure 2. The ratio of eutrophic/oligotrophic microorganisms: Active layer (A), Permafrost layer (B), Thawed layer (C), Deep thawed layer (D).

The relationship between the number of microorganisms and the content of the main chemical elements in the permafrost peat soil was analyzed (Fig. 6).

A significant direct relationship was revealed between the number of ammonifying microorganisms (r = 0.59) and oligotrophic microorganisms and the calcium content. Savichev et al. (2019) reported a similar pattern in the study on peat samples from the Vasyugan mire. A significant relationship was found between magnesium content and ammonifying microorganisms (r = 0.58), oligotrophic (r = 0.73), ammylolytic (r = 0.54) and saccharolytic micromycetes (r = 0.61) in the active layer of permafrost peat soil ($p<0.05$). In the active layer, a significant relationship was found between the number of ammylolytic (r = 0.55) and oligotrophic (r = 0.53) microorganisms and the content of strontium ($p<0.05$). A relationship was also found between the number of saccharolytic micromycetes and the iron content of the peat in the thawed layer (r = 0.51, $p<0.05$).

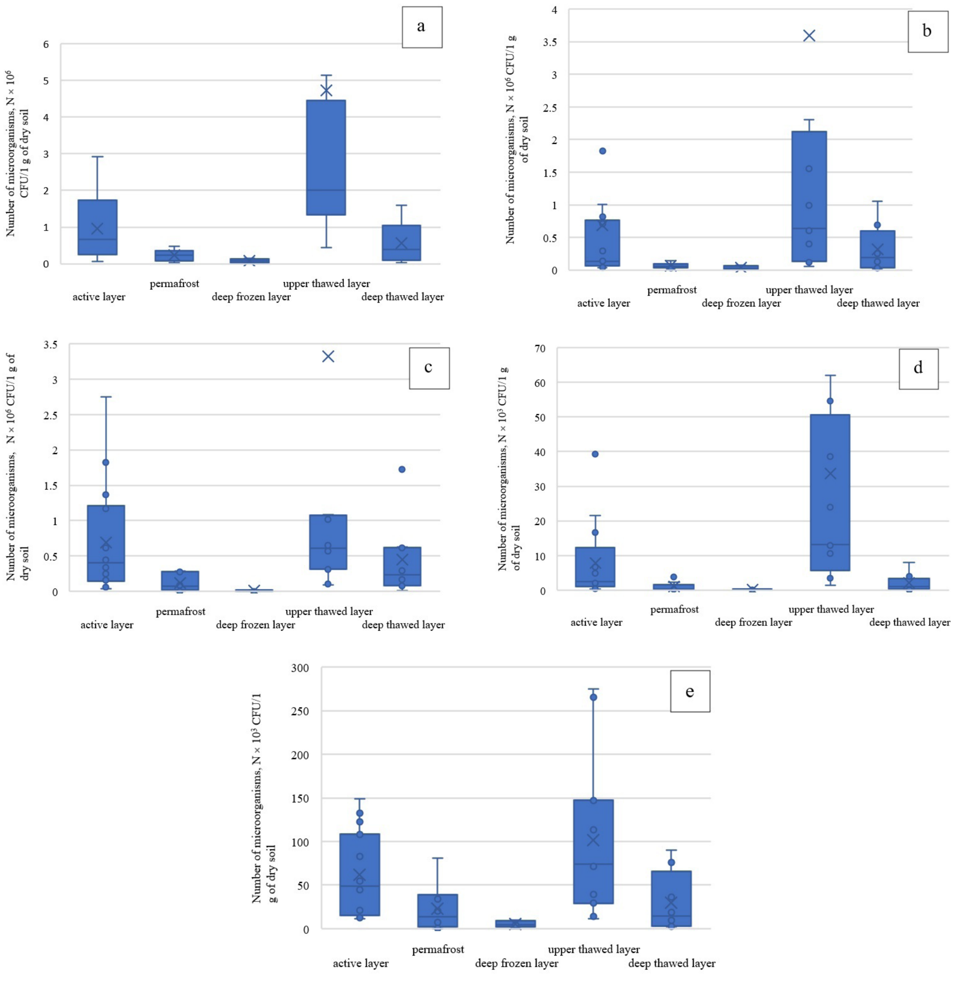

Figure 3. Number of microorganisms of various ecological and trophic groups in the active, frozen and thawed soil layers: ammonifying (a), amylolytic (b), oligotrophic (c), saccharolytic micromycetes (d), humus-destroying (e).

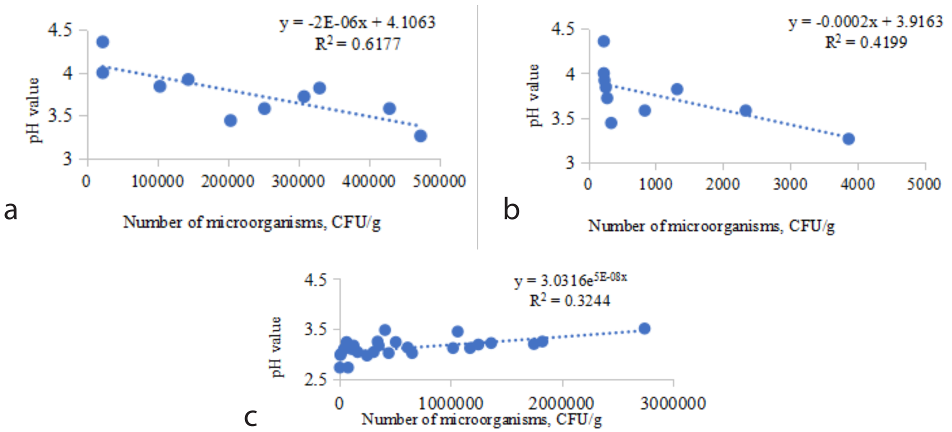

Figure 4. The relationship between the number of ammonifying microorganisms (a), saccharolytic micromycetes (b) in the permafrost layer, and oligotrophic microorganisms (c) in the active layer of peat with the pH value.

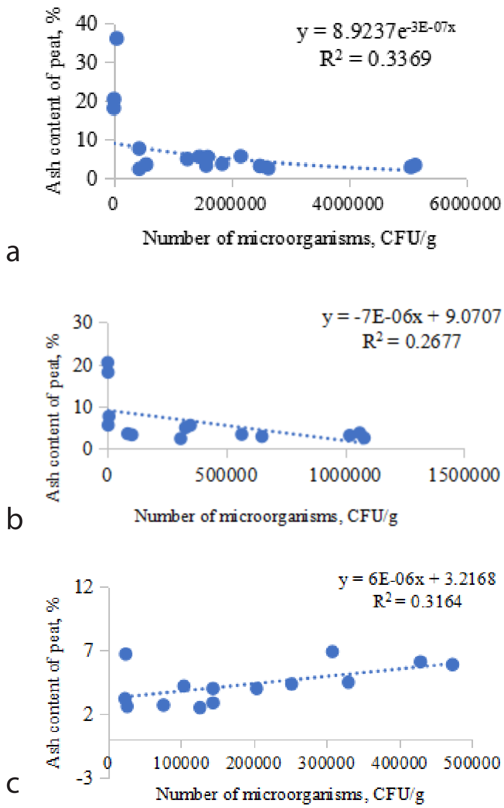

Figure 5. The relationship between the number of ammonifying (a) and oligotrophic (b) microorganisms in the thawed layer of peat and oligotrophic microorganisms in the permafrost layer of peat (c) with ash content.

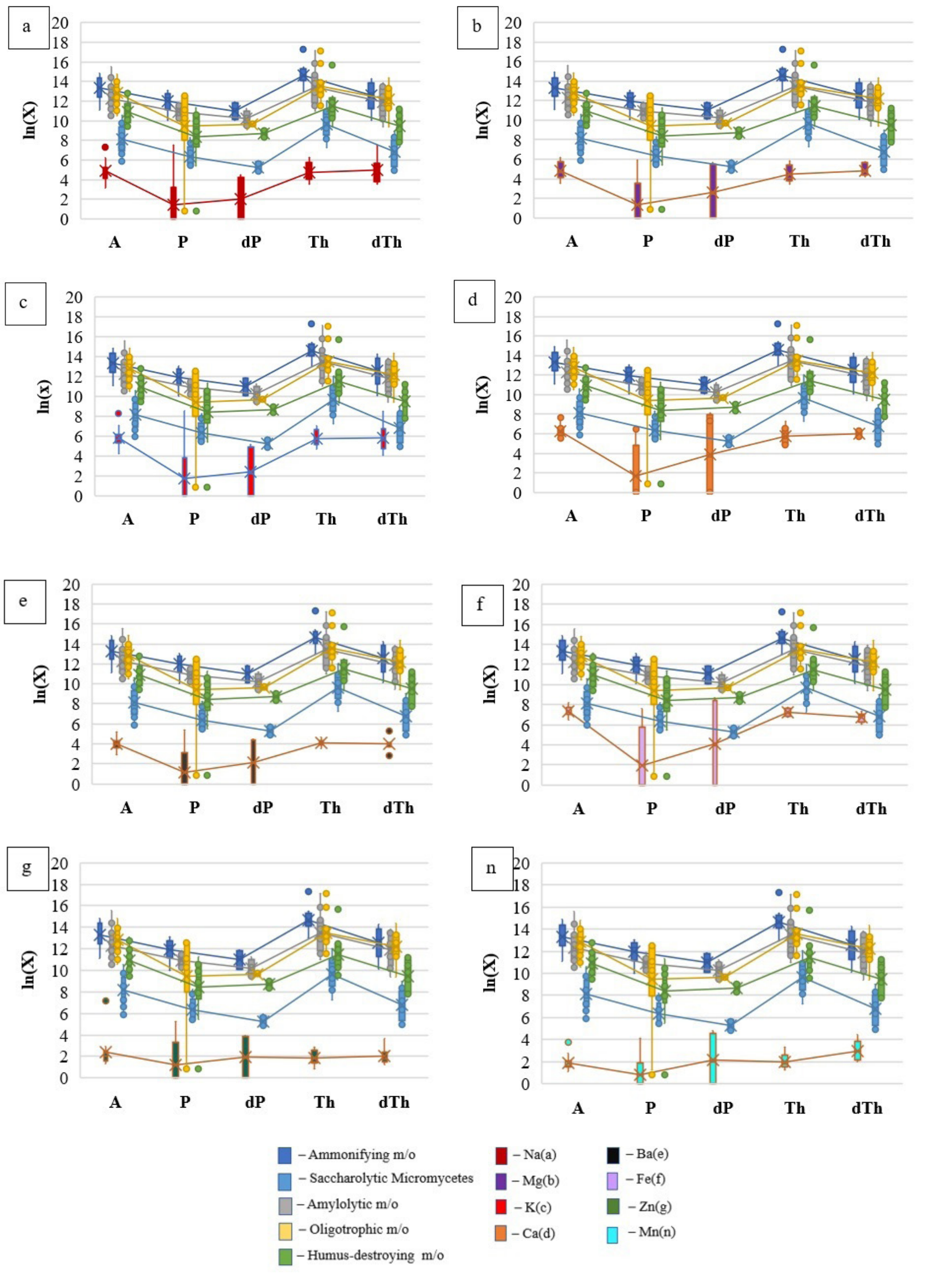

Figure 6. Relationship between the content of the main chemical elements and the number of microorganisms of the main ecological-trophic groups in the profile of the permafrost peat soil.

Conclusions

The number in microorganisms of the selected ecological-trophic groups selected determined by direct counting using selective medium ranged from 0.12×10^3 to 2.58×10^6 CFU/g in undisturbed peat and from 0.11×10^3 to 12.25×10^6 CFU/g in peat after permafrost thaw. The studied peat horizons were inhabited by numerous eutrophic microorganisms that prevailed in number over oligotrophic ones, indicating that peat deposits contain a sufficient amount of nutrient substrate for the vital activity of microorganisms. The amonifying microorganisms were a predominant ecological-trophic group throughout the entire depth of the peat deposit.

A long-term effect of the thawing and degradation on the permafrost peat deposit was revealed. A sharp increase in the abundance of microorganisms of all ecological-trophic groups at the thawed site compared to the undisturbed site indicates that a considerable amount of nutrient substrate is released during permafrost thaw. The analysis showed a statistically significant relationship between the abundance of microorganisms in different layers of the peat and the pH, ash content, and content of calcium, magnesium, strontium and iron ($p<0.05$).

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