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EXPERIMENTAL ARTICLES

Distribution of Microorganisms in the Al–Fe–Humus Podzols of Natural and Anthropogenically Impacted Boreal Spruce Forests

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Abstract—Natural and anthropogenically induced seasonal variations in the abundance and biomass of various groups of microorganisms in the Al–Fe–humus podzols of boreal spruce forests were analyzed. The fungal biomass in these soils was found to be considerably higher than the bacterial biomass. The microbial population was mainly concentrated in a thin surface layer (10–15 cm in thickness), which included the forest litter and the upper mineral root-inhabited soil horizon and greatly differed from other soil horizons in morphology and other properties. This layer was found to be optimal with respect to hydrothermal and nutritional conditions and is characterized by profound seasonal variations in the abundance and biomass of microbiota. The high acidity, typical of the Al–Fe–humus podzols, resulted from the metabolism of their microbial communities. In the polluted podzols, the population of prokaryotes increased and that of eukaryotes decreased.

Key words: forest, soil, anthropogenic pollution, microorganisms, biomass, seasonal dynamics of microorganisms.

The metabolism of heterotrophic soil microorganisms is closely related to plants providing microorganisms with organic nutrients through root exudates and plant detritus. In boreal forests, the main source of organic matter is plant detritus. It is believed that the microbial communities of forest biogeocenoses (BGC) are characterized by (i) the domination of fungi, (ii) the maximum concentration of microorganisms in the upper organogenic soil horizon (forest litter); (iii) stratification of litters and the succession of microbiota related to the conveyor utilization of plant detritus and animal remnants; and (iv) the existence of a correlation between the location, function, succession cycle, and life strategy of soil microorganisms [1–4]. Investigations based on the direct counting of microorganisms by luminescence microscopy led to some reappraisal of the established beliefs. In particular, the distribution of microbiota in the root-inhabited soil horizon is found to be more uniform than it was considered earlier [4].

At present, the functioning of forest BGC is greatly influenced by their pollution with industrial airborne acidic substances and heavy metals [5]. The severe pollution and acidification of some areas of boreal forests can essentially alter the composition, distribution, and productivity of soil microorganisms.

The aim of the present work was to study natural and anthropogenically induced changes in the distribution of microorganisms in the Al–Fe–humus podzols of boreal spruce forests based on the analysis of spatial and seasonal variations in the abundance and biomass of different microbial groups.

MATERIALS AND METHODS

Investigations were performed on shrub–green moss–spruce forest test plots, which were either unpolluted or polluted by airborne wastes from the Severonikel' metallurgical company, which produces copper and nickel. The industrial pollution caused the shrub–green moss–spruce forest to transform to a shrub–grass–spruce forest and then to a light crowberry–spruce forest. The inhibited growth and the enhanced death rate of plants resulted in a decrease in the live phytomass and in the accumulation of dead organic matter. The dominant species of spruce forests (spruce, green mosses, and bilberry), which are susceptible to environmental pollution, were substituted by pollution-resistant species, such as crowberry and grass [6].

Unpolluted spruce forests contained two types of forest parcels: spruce parcels and shrub–green moss parcels. At the stage of defoliation, polluted spruce forests had three types of parcels: spruce parcels, shrub–

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Table 1. Microbial abundance in soils underlying various parcels of the shrub–green moss–spruce forests

Soil horizon, depth (cm)	Bacteria, billion cells/g	Actinomycete mycelium, m/g	Fungal mycelium, m/g	Fungal spores, millions/g
Shrub–green moss parcel				
FH, 0–3	1.5/ND	144/ND	259/ND	2.5/ND
H, 3–6	1.5/2.0	96/109	989/1473	3.7/6.7
E, 6–12	1.7/0.7	120/87	1104/1104	3.8/6.2
B, 12–22	1.2/0.7	80/83	347/336	3.2/3.5
BC, 22–35	0.8/0.5	48/54	91/125	2.5/2.4
Spruce parcel				
FH, 0–4	0.6/1.8	90/170	763/3533	5.3/11.0
H, 4–10	2.0/1.4	148/205	869/1392	2.5/4.8
E, 10–15	2.1/0.7	140/145	221/1373	3.2/4.3
B, 15–25	0.8/0.4	80/54	160/672	1.8/3.4
B, 25–40	0.7/0.2	34/25	80/107	1.8/1.4

Note: Data in the numerator correspond to the beginning of the vegetative period (June), and data in the denominator correspond to the end of the vegetative period (August). ND stands for "not determined."

Table 2. Microbial biomasses (mg/g soil) in unpolluted soils underlying various parcels of the shrub–green moss–spruce forests*

Soil horizon, depth (cm)	Bacteria	Actinomycete mycelium	Fungal mycelium	Fungal spores	Total
Shrub–green moss parcel					
FH, 0–3	0.03/ND	0.006/ND	0.52/ND	0.03/ND	0.59/ND
H, 3–6	0.03/0.04	0.004/0.004	2.10/3.60	0.06/0.13	2.19/3.77
E, 6–12	0.03/0.01	0.005/0.003	2.12/2.70	0.05/0.09	2.21/2.81
B, 12–22	0.03/0.01	0.003/0.003	0.46/0.65	0.04/0.05	0.53/0.72
BC, 22–35	0.02/0.01	0.002/0.002	0.15/0.29	0.04/0.03	0.21/0.33
Spruce parcel					
FH, 0–4	0.01/0.04	0.004/0.006	1.73/8.65	0.09/0.25	1.84/8.94
H, 4–10	0.04/0.03	0.006/0.008	1.58/2.76	0.05/0.10	1.68/2.90
E, 10–15	0.04/0.01	0.006/0.006	0.45/2.26	0.04/0.06	0.54/2.34
B, 15–25	0.02/0.01	0.003/0.002	0.49/0.93	0.03/0.05	0.54/0.99
BC, 25–40	0.02/0.00	0.002/0.001	0.25/0.28	0.03/0.02	0.30/0.30

*For notes, see Table 1.

grass parcels, and grass parcels. At the final stage of severe pollution, the polluted spruce forests had spruce parcels, crowberry parcels, grass parcels, and parcels completely devoid of vegetation. Soil was profiled in all parcel types at the beginning (June) and at the end (September) of the vegetative period from the major soil horizons (O, E, B_{hfa}, and BC). The litter horizon was subdivided into the FH and H horizons. The morphogenetic and nutritional characteristics of podzols were described in detail elsewhere [7, 8].

Available elements were determined by extracting soil samples with 1 M CH_3COONH_4 (pH 4.65) [9–11]. The soil-to-substituent ratio was taken to be 1 : 25 for organogenic horizons and 1 : 10 for mineral horizons. The concentration of cations was determined by atomic absorption spectrophotometry and that of sulfur, NO_3, NH_4, and phosphorus was evaluated colorimetrically.

The concentration of nutritionally important elements in ground waters was determined for three soil horizons (O, B_{hfa}, and BC) using 12 lysimeters for each of the BGC states [12]. Aluminum, iron, calcium, magnesium, potassium, manganese, zinc, nickel, and copper cations were assayed by atomic absorption spectrophotometry; SO_4 and NO_3, by ion-exchange chromatography; NH_4 and P, colorimetrically; and carbon, by the bichromate method.

Table 3. Microbial abundance in soils underlying various parcels of the defoliating shrub–green moss–spruce forests*

Soil horizon, depth (cm)	Bacteria, billion cells/g	Actinomycete mycelium, m/g	Fungal mycelium, m/g	Fungal spores, millions/g
Shrub–green moss parcel				
Od, 0–2	1.3/ND	122/ND	125/ND	1.9/ND
H, 2–7	3.0/1.8	144/135	1104/1080	4.3/12.5
E, 7–14	1.3/1.9	119/135	979/25	3.8/44.5
B, 14–30	1.0/1.0	112/97	331/22	2.7/37.4
BC, 30–45	0.9/0.7	19/58	230/60	2.4/15.8
Spruce parcel				
FH, 0–3	1.6/1.9	160/155	538/1421	5.3/8.6
H, 3–9	2.3/1.5	140/126	802/1181	5.8/4.8
E, 9–18	1.5/0.8	116/93	1910/984	4.3/4.8
B, 18–25	1.4/0.5	96/70	355/740	3.5/2.9
BC, 25–38	0.7/0.3	39/50	407/154	1.4/2.9
Grass parcel				
Od, 0–2	3.1/3.7	158/193	442/1113	4.8/12.0
H, 2–4	3.2/2.7	173/122	394/892	3.2/16.3
E, 4–11	2.2/1.4	130/97	542/700	2.4/16.8
B, 11–25	0.9/1.3	83/112	451/434	2.9/26.4
BC, 25–40	0.4/1.0	58/58	504/504	1.6/31.2

* For notes, see Table 1.

Table 4. Microbial biomasses (mg/g soil) in soils underlying various parcels of the airborne waste–impacted light spruce forest*

Soil horizon, depth (cm)	Bacteria	Actinomycete mycelium	Fungal mycelium	Fungal spores	Total
Shrub–green moss parcel					
Od, 0–5	0.04/ND	0.003/ND	0.52/ND	0.11/ND	0.67/ND
H, 5–8	0.06/0.03	0.004/0.007	0.48/1.50	0.04/0.16	0.59/1.69
A2, 8–10	0.03/0.03	0.006/0.007	0.51/1.02	0.04/0.08	0.59/1.13
B, 10–17	0.02/0.02	0.004/0.006	0.52/0.35	0.07/0.06	0.61/0.49
BC, 17–35	0.01/0.02	0.002/0.006	0.15/0.10	0.02/0.03	0.19/0.15
Spruce parcel					
FH, 0–5	0.08/0.04	0.004/0.005	0.96/0.45	0.10/0.38	1.15/0.88
E, 5–7	0.02/0.02	0.007/0.004	1.23/0.58	0.03/0.05	1.29/0.65
B, 7–18	0.02/0.01	0.004/0.003	1.12/0.12	0.07/0.02	1.21/0.15
BC, 18–35	0.01/0.00	0.002/0.002	0.29/0.06	0.05/0.02	0.36/0.09
Grass parcel					
Od, 0–2	0.12/0.04	0.010/0.008	1.14/2.40	0.12/0.23	1.39/2.68
H, 2–5	0.04/0.03	0.008/0.005	0.61/1.50	0.10/0.09	0.76/1.62
E, 5–7	0.03/0.03	0.006/0.006	1.05/1.50	0.20/0.10	1.27/1.64
B, 7–15	0.02/0.03	0.002/0.004	1.35/0.40	0.06/0.08	1.43/0.51
BC, 15–30	0.01/0.02	0.002/0.004	0.14/0.35	0.01/0.05	0.16/0.42
Wasteland					
0–2	0.05/0.02	0.007/0.005	0.69/0.96	0.06/0.41	0.81/1.39
2–5	0.02/0.02	0.003/0.005	0.62/0.37	0.01/0.09	0.65/0.48
5–15	0.02/0.01	0.003/0.002	0.56/0.24	0.04/0.08	0.62/0.33
15–30	0.02/0.00	0.003/0.001	0.35/0.02	0.06/0.02	0.43/0.05

*For notes, see Table 1.

Table 5. Content (in mg/kg soil) of mobile compounds extractable with 1 M CH_3COONH_4 (pH 4.65) in different horizons of soils underlying various parcels of unimpacted (background) and impacted biogeocenoses

Parcel, sampling size	Soil horizon	Ca	Mg	K	P	S	Ni	Cu
Background								
SGM (n = 26)	O	459	155	70	19	55	0.7	0.2
(n = 2)	E	17	4	13	1.0	3	0.01	0.01
(n = 26)	B	74	16	27	16	38	0.6	0.6
SP (n = 47)	O	2815	462	1081	247	153	4.0	4.4
(n = 3)	E	491	5	12	2.0	6	0.3	0.11
(n = 40)	B	122	20	34	19	48	0.6	1.1
Defoliating parcel								
G (n = 8)	O	1876	211	702	78	104	242	255
(n = 6)	E	69	13	49	9.7	9	7.3	3.3
(n = 6)	B	67	13	37	13	59	5.0	2.1
SP (n = 8)	O	1639	181	574	71	117	141	331
(n = 10)	E	52	9	27	8.8	12	8	12
(n = 10)	B	59	10	30	19	58	8.3	10
SG (n = 26)	O	2054	290	593	77	113	145	109
(n = 9)	E	34	9	42	5.8	10	2.4	0.4
(n = 9)	B	33	6	18	15	59	1.6	0.5
Impacted light forest								
WL (n = 5)	O	1414	159	225	25	138	586	655
(n = 3)	E	81	13	20	5.5	22	31	4.8
(n = 3)	B	60	10	20	6	102	17	3.2
SP (n = 8)	O	883	131	269	30	172	587	1205
(n = 3)	E	107	13	30	4.0	32	55	31
(n = 3)	B	133	9	31	6	109	35	9
SG (n = 5)	O	2546	296	306	46	140	640	404
(n = 3)	E	203	19	33	2.5	24	2.9	20
(n = 3)	B	128	19	30	4	108	7.0	0.7
G (n = 3)	O	1995	336	438	54	135	633	200
(n = 3)	E	130	23	46	3.9	29	27	4.5
(n = 3)	B	117	14	41	6	130	16	1.6

Note: SGM, shrub–green moss; SP, spruce; SG, shrub–grass; G, grass; WL, wasteland; O, organogenic horizon; E, elluvial horizon; B, illuvial horizon.

Soil samples for the enumeration of microorganisms and the evaluation of their biomass were pretreated with a UZDN-1 ultrasonic generator (22 kHz; 0.44 A) for 2 min. The total number of microorganisms was determined by luminescence microscopy. Specimens for the evaluation of bacteria and actinomycete mycelium were stained with orange acridine; they were also stained with calcofluor white for the evaluation of spores and fungal mycelium. The standard deviation $\delta(n-1)$ did not exceed 5% for bacteria and 10% for fungal spores, fungal mycelium, and actinomycete mycelium. The mean density of microbial cells and their water content were taken to be 1 g/cm^3 and 80%, respectively. The dry mass of one bacterial cell 0.1 μm^3 in volume was calculated to be 2×10^{-14} g, and that of the actinomycete mycelium 1 m in length and 0.5 μm in diameter, 3.9×10^{-8} g. Knowing the diameters of fungal spores and mycelium, the masses of one fungal spore and 1 m of fungal mycelium were calculated by the formulas $0.0836r^3 \times 10^{-11}$ g and $0.628r^2 \times 10^{-6}$ g, respectively [4].

RESULTS

Bacteria and Actinomycetes

Under normal conditions (i.e., in the absence of pollution), prokaryotic microorganisms were localized in

Table 6. Content of various ions (in μg-equiv/l) in lysimetric waters from different horizons of soils underlying various parcels of unimpacted (background) and impacted biogeocenoses

Parcel, sampling size	Soil horizon	pH	Ca	Mg	K	NH_4	Al	Ni	Cu	P*	SO_4	NO_3	C*
Background													
SGM (n = 26)	O	4.06	116	65	56	243	80	0.6	0.6	0.29	82	9	55.2
SGM (n = 12)	B	5.55	47	30	15	43	20	0.2	0.3	0.02	84	2	31.5
SP (n = 11)	O	4.24	576	201	329	540	111	3.9	3.6	2.29	748	51	74.2
SP (n = 27)	B	4.89	268	128	138	124	76	0.9	0.5	0.05	535	14	28.8
Defoliating parcel													
SG (n = 21)	O	4.14	147	75	132	229	63	1.8	1.0	0.84	232	24	61.8
SG (n = 13)	B	4.87	128	63	43	31	46	1.6	0.6	0.05	174	4	18.5
SP (n = 24)	O	3.76	435	202	214	301	93	14.2	9.9	0.57	1000	67	40.0
SP (n = 34)	B	4.37	305	140	148	91	142	5.7	1.9	0.15	669	26	28.3
G (n = 15)	O	4.26	71	31	28	93	53	1.3	0.7	0.08	120	3	37.1
G (n = 15)	B	4.88	96	42	48	57	51	1.0	0.3	0.02	171	5	25.0
Impacted light forest													
G (n = 14)	O	4.14	331	136	97	112	66	44	17	0.11	662	39	45.0
G (n = 23)	B	4.59	223	81	32	51	98	26	0.9	0.01	340	189	22.5
SP (n = 17)	O	3.63	287	126	136	115	146	55	74	0.21	846	31	48.6
SP (n = 22)	B	4.61	204	99	47	97	85	44	15	0.02	466	65	30.7
G (n = 10)	O	4.75	132	57	140	219	51	19.5	5.1	0.46	272	141	27.6
G (n = 24)	B	4.76	166	64	76	108	71	21	1.5	0.03	313	211	61.3
WL (n = 15)	O	4.11	341	96	20	168	86	56	8.1	0.19	527	131	41.8
WL (n = 18)	B	4.88	251	85	24	93	48	15	0.9	0.01	276	228	24.1

* P and C concentrations are given in mg/l. For designations, see Table 5.

the upper podzol horizons, namely, in organogenic litter and in the upper mineral soil horizon. The number of bacteria there was as great as 2×10^9 cells/g soil, and the actinomycete mycelium had a length of 200 m/g soil (Tables 1 and 2). In the lower soil horizons, these values were considerably lower. Seasonal variations and variations between parcels were small, except that the length of the actinomycete mycelium in woody (spruce) parcels somewhat increased by the end of the vegetative period.

When in contact with airborne industrial pollution, the number and the biomass of prokaryotic microorganisms tended to increase (Tables 3 and 4). The increase was especially pronounced in the thin spruce forest soils that were polluted, where the bacterial population amounted to 6×10^9 cells/g soil, i.e., three times that observed in the unpolluted soil. The pollution did not considerably affect the vertical distribution pattern of bacteria in soil. The population density of bacteria in the lower layer of the root-inhabited soil horizon was more than 0.5×10^9 cells/g, i.e., higher than under normal conditions.

The length and the biomass of actinomycete mycelium also increased in response to pollution, although the increase was not so great as in the case of bacteria. The contents of actinomycetes in the unpolluted soils and in the soils under defoliating forests were comparable; however, the specific length of actinomycete mycelium in the grass parcels of polluted spruce thin forests was as great as 300 m/g soil. The described differences in the interparcel and vertical distribution of actinomycetes suggest that the most beneficial conditions for their growth are in the upper, organogenic horizons of grass parcels and, to a lesser degree, of spruce parcels. Even in the upper horizons of soils which are devoid of plants, the concentrations of bacteria and actinomycetes were higher than in the other soil horizons.

Fungal Mycelium and Spores

The vertical, interparcel, and seasonal changes in the distribution of micromycetes in the Al–Fe–humus podzols of shrub–green moss–spruce forests had much in common with those of prokaryotic microorganisms. However, under normal conditions, the mycelium

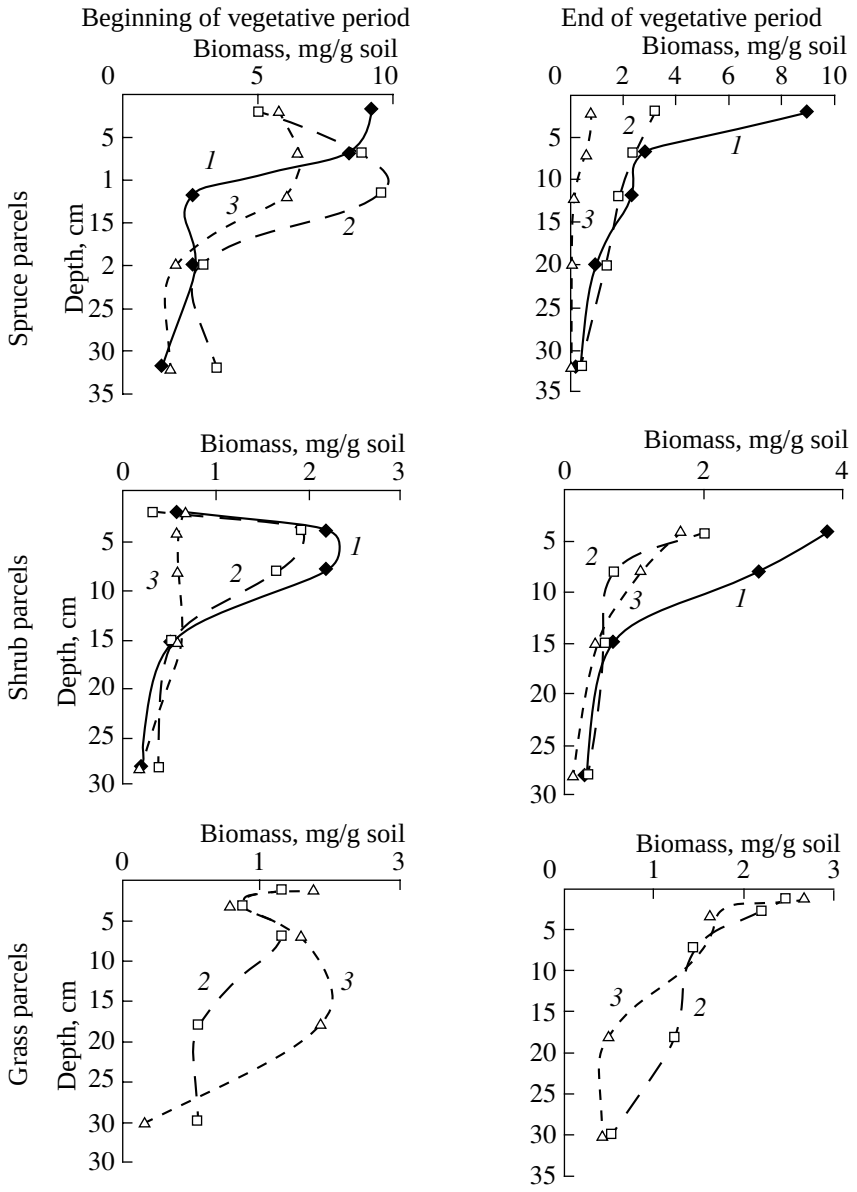

Fig. 1. Vertical distribution of the total microbial biomass in soils underlying various parcels of (*1*) unimpacted forest, (*2*) impacted defoliating forest, and (*3*) impacted light forest at the beginning and end of the vegetative period.

length (1400 m/g soil), the number of spores (11 billion spores/g), the mycelium mass (8.7 mg/g soil), and the spore mass (0.3 mg/g) of fungi (Tables 1 and 2) were considerably greater than the respective values for actinomycetes. The fungal population in the lower soil horizons (the root-inhabited horizons B and BC) was more than 10 times lower than in the upper soil horizons (the organogenic, O, and the eluvial, E, horizons from 10 to 15 cm in thickness). Seasonal variations in the micromycete population were well pronounced, with the amount of the mycelium and spores increasing by the end of the vegetative period.

Airborne industrial wastes adversely influenced micromycetes (Tables 3 and 4), the degree of pollution being inversely related with the fungal biomass, mycelium length, and spore number. For instance, the fungal biomass in the soils of unpolluted spruce parcels, defoliating forests, and thin spruce forests was equal to 9, 3, and 1.2 mg/g soil, respectively. A similar tendency was revealed for the soils of the shrub–green moss and shrub–grass parcels (the former parcels transformed into the latter parcels under the action of the industrial pollution). The population of micromycetes was at a minimum (0.8 mg/g) in the soils of the parcels that lost their vegetation as a result of pollution.

Fungal mycelium and spores were also found in the soil horizon B, extending to a depth of 25–30 cm. The number of fungal spores was maximum in the soils of

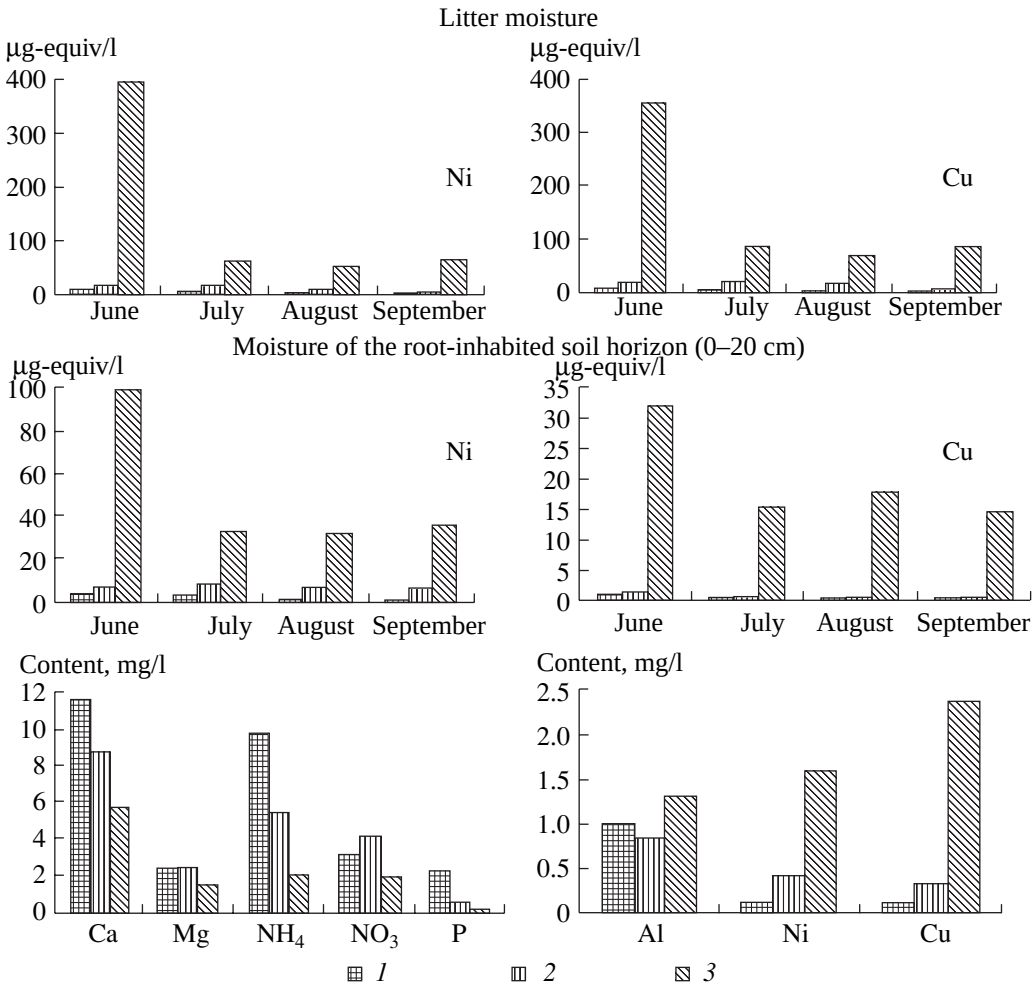

Fig. 2. Dynamics of nickel, copper, and nutritional elements during the vegetative period in the moisture of soils underlying (*1*) unpolluted forest, (*2*) impacted defoliating forest, and (*3*) impacted light forest.

defoliating forests, reflecting the destructive changes in the soil micromycete communities that were induced by the polluted environment. The fungal mycelium length, biomass, and the number of spores decreased by the end of the vegetative period.

DISCUSSION

Natural Conditions

The spatial (interparcel and vertical) and seasonal characteristics of the soil microbial population of spruce forests show that fungi are the main edificators of the heterotrophic microbiocenoses of the podzols studied (Tables 1 and 2). Indeed, the biomass of fungal mycelium amounted up to 90% (up to 97% together with spores) of the total microbial biomass of these soils. These data are consistent with the accepted view that the micromycetes of the boreal forest soils are capable of an almost complete mineralization of the lignocellulose complex [4]. The mycelium length and the biomass of actinomycetes were less than those of soil fungi by one and three orders, respectively. The bacterial biomass was also considerably lower than the fungal biomass.

The microbial population of the spruce forest podzols was primarily concentrated in a thin surface layer (10–15 cm in thickness), which included the forest litter and the upper mineral root-inhabited soil horizon and greatly differed from other soil horizons in morphology and other properties. This root-inhabited zone is optimum for the life of heterotrophic soil microorganisms, although most of them probably occur in a dormant state [2–4].

Boreal forests are characterized by an abundance of overground plant debris which accumulates on the soil surface. Organic substances and nutritional elements also accumulate in the upper, organogenic soil horizons (Table 5). Taking into account these observations, it would be reasonable to suggest that soil microorganisms must be especially abundant in the upper, organo-

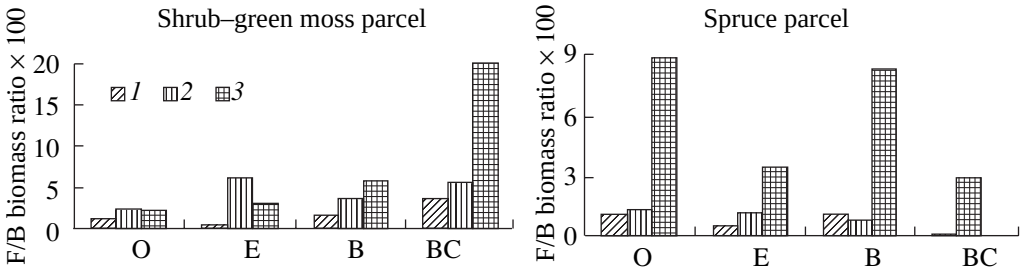

Fig. 3. The fungi-to-bacteria biomass ratio (F/B biomass ratio) in different horizons of soils underlying (*1*) unpolluted forest, (*2*) impacted defoliating forest, and (*3*) impacted light forest: O, organogenic horizon; E, elluvial horizon; B, illuvial horizon, and BC, transitional horizon.

genic soil horizons (forest litter) and scarce in the lower, mineral, root-inhabited soil horizons.

However, the results presented above show that there is not a drastic decrease in the abundance and the biomass of microorganisms in the lower horizons of the Al–Fe–humus podzols. The abundance and the biomass of microorganisms decrease only in the soil horizon B of the shrub–green moss parcels, whereas these parameters are almost the same in the podzolic horizon and in the lower layer of the organogenic horizon. In spruce parcels, the appreciable decrease in the microbial population was observed only beneath the illuvial horizon. In this case, the abundance and the biomass of microorganisms were maximum in the upper litter horizon (FH layer), especially at the end of the vegetative period.

Statistically significant differences in the microbial populations of different parcels were observed only for the upper layer of the organogenic horizon: in this layer of the spruce parcel, the biomass of fungal mycelium was considerably greater than in the other parcels studied. This leads us to the question as to why the microbial biomasses in the neighboring fertile organogenic and nonfertile mineral soil horizons are almost the same? One possible answer to this question may be the descending migration of litter waters rich in organic carbon and soluble biogenic compounds, which are readily utilizable by microorganisms, to the lower mineral horizons (Table 6). The supply of this root-inhabited horizon, which is characterized by the fine granulometric composition of the soil and the beneficial hydrothermal conditions, with nutrients makes it suitable for the growth of microorganisms.

In the shrub–green moss parcels, the maximum density of soil microorganisms was observed in the lower part of the optimum zone for heterotrophic microorganisms. Presumably, this was related to the inhibition of their growth by certain metabolites of green mosses incoming from above. This suggestion is confirmed by the fact that the maximum concentration of microorganisms in the soils of spruce parcels, where the growth of green mosses is usually inhibited, is observed in the upper part of the organogenic horizon.

Seasonal variations in the abundance and the biomass of the soil microbiota of spruce parcels were maximum in the optimum zone for microbial life, where benign hydrothermal and nutritional conditions led to a notable increase in the micromycete biomass by the end of the vegetative period.

Airborne Industrial Wastes

Airborne industrial wastes greatly affect the whole biogeocenosis. The considerable intake of acidic substances and heavy metals from the atmosphere to the soil brings about severe alterations in the forest biocenosis, such as [12] (i) an increase in the amount of plant detritus due to the defoliation of coniferous trees and the death of pollution-susceptible plant species, particularly green mosses; (ii) the accumulation of heavy metals and the exhaustion of nutritional elements in the plant detritus and litter; (iii) the substitution of the nutritional elements of the soil absorbing complex by acidic cations; and (iv) the release of aluminum from clay minerals and its accumulation in the soil. Analysis of these alterations shows that nutritional conditions for soil microorganisms become unfavorable primarily due to the increased content of toxic compounds, such as heavy metals, in soil [13] and the decreased content of organic matter and nutritional elements.

Nutritional disorders that soil microorganisms have to face in polluted spruce parcels are related to the intense intake of acidic substances and heavy metals from the atmosphere to the soil, which leads to the leaching of basic cations from plant debris and organogenic soil horizons; the accumulation of copper, nickel, and aluminum in litter and soil; and the depletion of the utilizable sources of carbon, magnesium, potassium, phosphorus, and nitrogen. The shrub parcels also had similar problems. The nearly normal content of calcium in the soils of undercrown and intercrown forest parcels was due to its high content in the fallen needles of spruce and the fallen leaves of bilberry and mountain cranberry.

At a low degree of pollution typical of defoliating forests, the biomass of fungal mycelium in the organo-

genic and mineral soil horizons of spruce parcels is comparable with its background value (Table 3 and Fig. 1). It is known that the mobile compounds of nickel and copper are toxic to microorganisms, especially to fungi [14, 15]. The drainage of soils polluted by heavy metals by water from melting snow in the spring partially removes toxic compounds, thus providing conditions more beneficial for the growth of soil microorganisms (Fig. 2). However, by the end of the vegetative period, the amount of fungal mycelium in the polluted soils becomes considerably lower than in the unpolluted soils. This fact can be explained by a gradual increase in the content of the toxic mobile compounds of nickel and copper in soil and ground waters. The accumulation of toxic compounds in soil induces changes in its microbial complex in favor of hydrolytic bacteria, which are more resistant to heavy metals than fungi.

At the beginning of the vegetative period, the abundance and the biomass of microorganisms in the soils of the intercrown and shrub–grass parcels, which are relatively resistant to heavy metal–pollution, corresponded to those in the unpolluted soils. However, by the end of the vegetative period, the population of soil microorganisms tended to decrease, obviously for the same reasons as in the case of the spruce parcels (see the previous paragraph).

The resistances of prokaryotic and eukaryotic microorganisms to heavy metals are different. As a result, the population of bacteria and actinomycetes, unlike that of fungi, tended to increase in polluted soils (Fig. 3). One of the possible reasons for this can be the ability of prokaryotic microorganisms, particularly bacteria, to evolve into species which are resistant to heavy metals. A similar tendency of the prevalence of bacteria in the soils polluted by heavy metals was revealed by Fritze *et al.* [16, 17], who studied the impact of airborne wastes from a copper-producing plant in Finland on soil microflora.

Thus, the pollution of the Al–Fe–humus podzols by heavy metals affected their microbial complexes toward the prevalence of prokaryotic microorganisms. Micromycetes turned out to be the most pollution-susceptible soil microorganisms. By the end of the vegetative period, the amount of fungal mycelium in the polluted soils decreased because of the substrate deterioration (the accumulation of heavy metals and the depletion of nutrients) (Tables 5 and 6 and Fig. 3) and because dead leaves and needles enter the soil throughout the vegetative period, thus disturbing the succession cycles.

In the soils of impacted light forests, the amount of fungal mycelium decreased even further, obviously because of the severer deterioration of the substrate.

The acidotolerance of the microbiota of the Al–Fe–humus podzols can be considered to be an adaptive response of soil microbiocenoses to the specific conditions of the boreal forest soils. The antibiotic activity of *Bryophyta* in the intercrown parcels of boreal forests may inhibit the growth of microorganisms in the upper part of the optimum zone for microbial life, thus displacing the maximum population density of soil microorganisms down to the lower part of this zone. In the spruce parcels, where the growth of green mosses is inhibited, the population density of soil microorganisms is maximum in the upper layer of the organogenic horizon.

The impact of airborne industrial pollutants, including acidic compounds and heavy metals, augments the relative content of prokaryotic microorganisms in the microbial complexes of the Al–Fe–humus podzols. Micromycetes seem to be the soil microorganisms most susceptible to heavy metals.

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