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SOIL BIOLOGY

Dynamics of Zoomicrobial Complexes upon Decomposition of Plant Litter in Spruce Forests of the Southern Taiga

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Abstract—Comparative studies of the composition and abundance of soil-dwelling invertebrates (microarthropods, nematodes, and testate amoebas) and micromycetes in the course of leaf and needle litter decomposition were conducted in two types of spruce forests on white-podzolic and brown forest soils in a field experiment. The analysis of the destruction dynamics has revealed a correlation between the rate of the litter mass loss and the abundance of microarthropods and testate amoebas in the decomposing plant residues. The highest amplitude of the seasonal fluctuations in the number of invertebrates was found for the micromycetes and nematodes as compared to that for the testate amoebas and microarthropods. In the complexes of micromycetes and invertebrates, changes in the dominants were revealed at the different stages of the decomposition. The litter's composition was found to be the main factor affecting the composition and abundance of the zoomicrobial complex of the destroyers. The type of biogeocenosis less influenced the abundance of pedobionts, but it determined their taxonomic composition to a greater extent. A significant inverse correlation was revealed between the number of micromycetes and that of small soil invertebrates.

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INTRODUCTION

In taiga forests, the needle and leaf litter is decomposed completely during 3 to 10 years and longer [4, 25, 26]. The destruction and biochemical transformation of the organic residues is accompanied by succession changes in the composition of the soil organisms taking a direct part in these processes. The succession regularities of the saprophilic zoomicrobial complex were investigated in detail using the example of the activity of microscopic fungi and soil invertebrates in the course of the decomposition of organic material [2, 6, 15, 20, 22, 23, 27, 28]. In nature, hard-to-decompose lignin–cellulose plant substances are mainly decomposed by basidio- and ascomycetes, especially at the late stages of their decomposition [21]. At the initial stages, micromycetes and invertebrates actively participate in the process of the decomposition. Their interaction has been poorly studied until the present and is of interest for understanding the functional structure of the trophic network in the soil. The micromycetes taking part in the transformation of organic residues are a nutrient source for many groups of soil invertebrates–microbophages [1, 12, 17]. Therefore, revealing of the regularities of utilization of plant residues by micromycetes and invertebrates allows determining the function of the whole soil saprophilic block.

The studies of the organic residues' decomposition in natural conditions that were conducted in the southern taiga spruce forests of the Central Forest Reserve during some years have resulted in the detection of the main trends and sequence in the biochemical transformations of organic residues [10, 19]. The dynamics of some groups of pedobionts in the course of the plant litter decomposition were also studied [8, 9, 14]. However, the functional interactions between the main groups of organisms participating in the detritus trophic chains were not considered in the works mentioned. In particular, an integrated analysis of the changes in the number of micromycetes and invertebrates in the course of plant residues' decomposition in soils under different forests has not been performed.

The aim of this work is a comparative analysis of the changes in the key groups of biodestroyers (micromycetes and invertebrates) in the course of the plant litter decomposition in forests on different soils. The determination of the spatial–temporal alterations in the soil saprophilic block will allow revealing the biotic mechanisms for regulating the activity of the myco- and zoobiota at different stages of the plant litter decomposition and to assess the weight of such modifying factors as the soil conditions and kinds of plant residues.

OBJECTS AND METHODS

The work was conducted on test plots selected for complex biogeocenotic investigations of the struc-

tural–functional organization of southeastern forests at the Central Forest Nature Biosphere Reserve (Tver oblast) [18]. Two model areas distinctly different in their vegetation and soils were chosen for the field test on the biogenic litter decomposition.

One plot (SB) was located in a sphagnum–green moss–bilberry spruce forest of the boreal type. At the Reserve, spruce forests of this type occur predominantly on white-podzolic soils. In the spring and autumn, these soils are waterlogged for a long time. In the greater part of this plot, peaty–white-podzolic soils are spread; they are waterlogged to a greater extent. The profile of the white-podzolic soil comprises the thick (up to 15 cm) peaty litter and podzolic horizon; a humus horizon is absent. The decomposition of the needle and leaf litter was studied on two test plots—SB_n and SB_l, respectively.

Another plot (SN) was located in a nemorose archangel–oxalis spruce forest characteristic of the burozems in this region. The podzolic horizon is practically absent in these soils because of the predominance of the lateral runoff, hence, the absence of water stagnation. The soil profile is weakly differentiated. The litter (4 cm thick) and humus (5–8 cm) horizons are well pronounced; a light-colored horizon is absent. The decomposition of the needle and leaf litter was studied on two test plots—SN_n and SN_l, respectively.

The dynamics of soil population were studied using the method of the "litter isolation" [16]. Needles of *Picea abies* and leaves of *Tilia cordata* were used for the experiment. Dry needles (5 g) and leaves (1 g) were put into flat bags made of nylon mesh material; the top part (wall) of these bags was made of a net with a 2-mm mesh; their lower part had a 0.5-mm mesh. The mesh of the upper wall allowed small invertebrates, including juvenile earthworms, to easily penetrate inside; the smaller diameter of the mesh in the lower wall kept the needles in the bags. The bags with the substrates were placed into the fermentative litter layer under the boreal spruce forest; in the soils of the nemorose spruce forest, they were arranged at the contact of the fermentative litter and the humus layers. Sixty standard bags with litter were used in each of the four sample plots. The litter mass's losses and the changes in the composition of the fungal and animal populations were determined every 1, 8, 9, 13, 20, and 24 months from September of 2002 to September of 2004. On every date of the counting, 10 bags were taken out and analyzed. In all the terms, soil samples were also collected in order to detect the composition of some animal groups and their seasonal dynamics.

The isolation, counting, and identification of the micromycetes were carried out using traditional mycological methods [5]. Water suspensions of the soil and the experimental litter (1 : 100 and 1 : 1000 dilutions) were inoculated on acidified (to inhibit the growth of bacteria) Czapek's medium. The counting of the fungal colonies (three replicates) was performed on the 5th–7th days. The number of fungi was expressed in CFU/g (number of colony-forming units per 1 g of air-dry weight of the sample).

For the counting of the number of testate amoebas and nematodes, 1 g of litter from the bags was put into a beaker (150 ml), water was added, it was carefully mixed, filtered through a 0.25-mesh sieve, and left for several hours. The supernatant was poured off, and water was added to the remaining water suspension of the filtered substrate up to a volume of 10 ml in the same beaker. The suspension obtained was stained with carbolic erythrosine (5–8 drops) for not less than a day. Then, 1 ml of the stained substrate was placed in a Petri dish, where an area of 2 × 2 cm was marked. The substrate was diluted to the needed volume, and the suspension was uniformly distributed over the dish's bottom. In the area marked, the number of stained testates and that of nematodes was counted. This number was calculated per dish area and per 1 g of air-dry weight. Only living individuals of testates were taken into account.

For the counting of the microarthropods, plant residues from the bags were placed on thermoeclectors for two days; then, they were fixed with 70° ethanol. Their composition and abundance were identified under an MBS-10 binocular microscope. The counting of the microarthropods in the litter of the reference soils was carried out in samples (125 cm^3) using the traditional method [3]; they were also isolated on funnels. The number of invertebrates was calculated per 1 g of air-dry material.

To measure the mass losses, the litter before its weighing was dried and carefully cleaned of soil particles. The rate of the plant material's decomposition was calculated as the loss of its mass in a particular period as referred to the mass obtained in the preceding term of the counting (in percent) [24]. The statistical processing of the results was performed using the Microsoft Excel and Statistica-6 programs.

RESULTS AND DISCUSSION

The dynamics of the litter's mass loss. For the two years of the experiment, the loss of mass comprised more that 50% in all the test variants (Fig. 1). According to the literature data, this type of decomposition corresponds to the weakly inhibited type of plant residues decomposition characteristic of the taiga zone [4]. More than 40% of the litter mass was lost during the first year. The rate of the decomposition altered in the course of the decomposition. In the nemorose spruce forest, the mass of the needle and leaf litter was lost somewhat faster, and, by the end of the experiment, the difference in the loss of both litter kinds did not exceed 10%.

The rate of the decomposition was relatively high during the first autumn–winter period; it was drastically lower in the spring time, probably, due to the excessive moistening of the soils (Fig. 2). In the summer, the rate of the litter's decomposition was maxi-

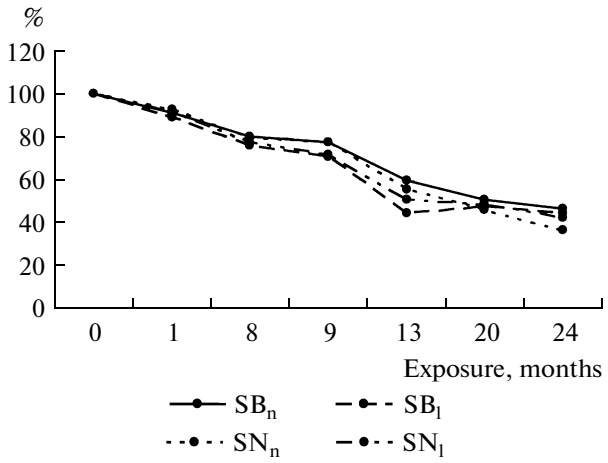

Fig. 1. Dynamics of the litter mass losses in the experiment. The designations here and in Fig. 1 and Fig. 2: SB_n—boreal spruce forest (needle litter); SB_l—boreal spruce forest (leaf and needle); SN_n—nemorose spruce forest (needle litter); SN_l—nemorose spruce forest (leaf litter).

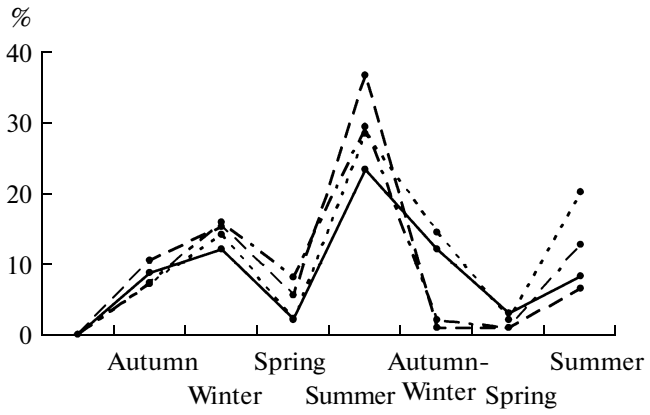

Fig. 2. Intensity of the litter decomposition at different stages of the experiment

mal. For instance, upon the decomposition of leaves in the white-podzolic soil, it amounted to 37%. In the next winter period, the intensity of the decomposition was low, but, in the summer, it rather increased. The rate of the needles decomposition on the burozem was about 20% (Fig. 2). By the end of the experiment, less than 50% of the initial litter mass remained in the samples. After the first winter, the leaves were decomposed faster than the needles. However, during the second spring, the decomposition of the leaves almost fully stopped, and, in the summer, the rate of the leaf litter's decomposition increased more slowly than the rate of the needles' destruction.

The differences revealed are determined by the fact that, during the first year, the leaf tissues, as compared to the needles, were decomposed more intensely. This was observed on both model plots in the spruce forests. In the second year, the losses of the leaf litter mass slowed down: only some residues of conductive tissues (nerves) and leafstalks remained in the bags. These litter components with a high lignin content are slowly decomposed, and, as a rule, it occurs without the participation of animals. At the same time, in the second year, the decomposition of the mesophilic tissues in the needle litter continued. Therefore, at the end of the two-year-long period, the rates of the decomposition of both litter kinds became almost similar.

The dynamics of the number of some pedobiont groups. Micromycetes. At the end of the experiment, a great number of fungi (161.3–764.3 thousand CFU/g) were observed on the plant residues. In the course of the organic material's decomposition, the number of micromycetes drastically decreased (more than by an order of magnitude) (Fig. 3A). This circumstance may be related to the fact that, at the initial stage of the exposure, some epiphytic micromycetes associated with plant substrates disappeared before their entering the soil, as well as the trophic activity of the soil invertebrates populating the litter. In different variants of the test, the total number of micromycetes did not exceed 70 thousand CFU/g, but, in the leaves taken from the white-podzolic soil, it was 6 thousand. The correlation coefficients calculated between the number of micromycetes and that of the invertebrates demonstrate an inverse dependence of the fungi abundance on the number of all the groups of the nano- and microfauna (Table 1). This demonstrates the great importance of animals in regulating the number of biodestroyers.

Testate amoebas. At the initial stages of the experiment, the population of the living testate amoebas was low—800 ind/g of needles and 1100 ind/g of leaf mass (Fig. 3BI). It is noteworthy that, in the litter, a great quantity of empty shells occurs; their share in the taiga soils may be 75% and more of the total number of testate amoebas [13]. The growth of the testate number in the litter samples was observed only a year after the beginning of the test. At this time, in the linden leaf litter samples from both spruce forests, the number of testate amoebas was maximal (5500 ind/g) and exceeded to a greater extent their abundance in the soil (3000 ind/g, Fig. 3BII). The number of testate amoebas was several times less in the needle litter than in the leaf one and did not exceed 2000 ind/g during the whole period of the observations. The number of testates in the needle litter sample from the nemorose spruce forest was higher than that in the boreal one. At the same time, in the samples of the white-podzolic soil, their population was higher than in the burozem samples (Fig. 3BII).

At the final stages of the test, the number of testate amoebas in the linden litter decreased, whereas, on the needle remains, their growth continued. By the end of the test, the abundance of testates reached the level characteristic of the reference soil. Thus, in the second

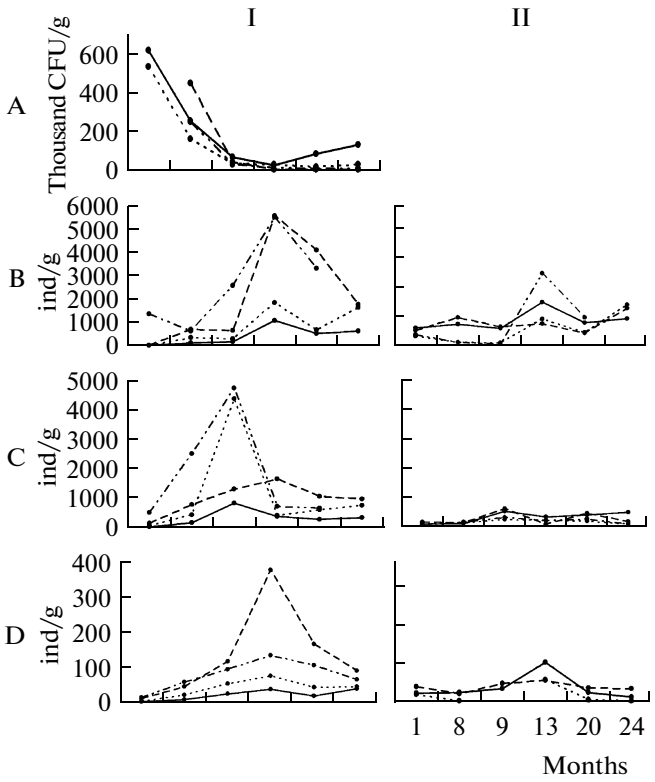

Fig. 3. Dynamics of the numbers: A—micromycetes, B—testate amoebas; C—nematodes; D—micromycetes in the samples of the litter (I) and the soil (II) in the course of the experiment.

year, the biological decomposition of the needles remained active, which is confirmed by the loss of the needle litter mass.

Nematodes. The number of nematodes in the litter was greater than their population in the soils (Fig. 3 BI, BII). The nematode abundance drastically increased at the first stages of the experiment. Their growth was especially pronounced in the leaf litter samples from the nemorose spruce forest. Here, in May of 2003, the number of nematodes reached 4700 ind/g (Fig. 3 BI).

The abundance of nematodes in the needle samples was lower than in the leaves. This difference was also well pronounced in the samples from the boreal spruce forest: the number of nematodes was twice less in the needle litter than in the linden one. By the end of the experiment, in most of the variants, the nematode population decreased, but their number was greater than in the soils of the corresponding plots. An exception was the needle samples from the boreal spruce forest, where the number of nematodes was comparable to that in the reference soils (350 ind/g) (Fig. 3 BII).

Microarthropods. The samples of the needle and leaf litter were colonized by oribatid mites, collembolans, and other very small arthropods, the number of which (irrespectively of the litter kind) gradually increased at the first stage of the test, and, after a year, it reached its maximum (Fig. 3 DII). The highest number of microarthropods was recorded in the linden litter: 350 ind/g in the boreal spruce forest, and 130 ind/g in the nemorose spruce forest. By the end of the second year, in the linden litter, the number of microarthropods gradually decreased, being higher than the background values. In the needle samples, the microarthropod population did not exceed 70 ind/g. In all the periods of the counting, it was greater in the nemorose spruce forest than in the boreal one. On the second year, the number of microarthropods in both forests was similar.

The effect of the different factors on the number of the main pedobiont groups was assessed using a three-factor variance analysis (Table 2). The influence of three factors (the kind of litter, the type of forest, and the season of the sampling) was considered. A significant effect (significance level 0.9) of the litter type on the population density was revealed for all the animal groups. It is noteworthy that the kind of litter (needle or leaves) turned out to be the determining factor for the number of oribatids and nematodes. According to the decrease in the strength of the influence, the rest of the factors form following sequence: testate amoebas—collembolans—other microarthropods.

The type of the spruce forest was the determining factor solely for the number of collembolans and nematodes. The rest of the groups of invertebrates little dif-

Table 1. Coefficients of correlation between the numbers of the biota groups

Micromycetes, site, and litter type		Testate amoebas	Nematodes	Collembolans	Mites	
					oribatids	mesostigmatic
Boreal spruce forest	needles	–0.69	–0.49	–0.3	–0.77	–0.62
	leaves	–0.70	–0.63	–0.77	–0.73	–0.86
Nemorose spruce forest	needles	–0.57	–0.43	–0.71	–0.77	–0.83
	leaves	–0.67	0.08	–0.44	–0.88	–0.76

Table 2. The effects of some factors on the number of the biota groups (results of the three-factor variance analysis)

Factor	Dispersion	Fisher's test	Significance level
Fungi			
Forest type	0.064	0.273	0.6046
Substrate typ	*1.653*	*7.048*	*0.0122*
Season	*2.579*	*10.994*	*0.0022*
Mites			
Forest type	0.280	0.971	0.3267
Substrate typ	*9.574*	*33.212*	*0.0000*
Season	*1.463*	*5.076*	*0.0263*
Collembolans			
Forest type	*1.577*	*7.454*	*0.0074*
Substrate typ	*1.364*	*6.451*	*0.0125*
Season	0.017	0.081	0.7762
Other arthropods			
Forest type	0.037	0.346	0.5575
Substrate typ	*0.919*	*8.650*	*0.0040*
Season	0.083	0.784	0.3777
Nematodes			
Forest type	*0.797*	*4.761*	*0.0361*
Substrate typ	*3.845*	*22.969*	*0.0000*
Season	*1.039*	*6.209*	*0.0177*
Testate amoebas			
Forest type	0.045	0.271	0.6077
Substrate typ	2.049	12.363	0.0020
Season	1.881	11.352	0.0029

Note: The significant values are italicized.

fered in their populations in the boreal and nemorose spruce forests (Table 2).

The season of the sampling had a weak effect, since the seasonal dynamics of the main groups of biodestroyers were mitigated by the succession changes in their abundance. They varied greatly in the different test variants (Fig. 30.

Thus, the leading factor responsible for the number of the biota components investigated is the kind of litter. In terms of their influence, the season and the type of spruce forest are of minor importance.

Dynamics of the saprophilic block's diversity parameters. Micromycetes. Sixty-six species and 27 genera of micromycetes were identified in the experimental period. Before the placement of the litter samples, the number and species diversity of the micromycetes in the needle and leaves were very different. After 8 months, the species diversity and the total abundance of micromycetes in the litter samples put into the litter in the same type of spruce forests did not differ significantly. The analysis of the dynamics of the species composition showed that the reason for the convergence of these indices was explained by the gradual colonization of the substrates by indigenous soil species and by the elimination of epiphytic species associated with the leaves and needles before their placing in the soils. Table 3 demonstrates the alterations in the composition of the most numerous species of micromycetes in the course of the experiment.

The succession changes in the structure of the micromycete complex were revealed on every model plot. For instance, in the first spring in the boreal spruce forest, *Penicillum miczynskii, P. corylophylum, P. canescens, Umbelopsis ramanniana*, and *Mycelia sterilia* were identified in the decomposing needles. In the middle of the experimental period, *P. janczewskii, P. citrinum*, and *Trichoderma polysporum* appeared, while *Oidiodendron griseum, O. rhodogenum*, and *Phialophora* sp. were identified in the second year. At all the stages, a high abundance of *P. spinulosum* and *P. glabrum* was observed.

In the leaf samples placed in the same spruce forest, a high number of *P. spinulosum* was found at all the stages of the litter decomposition; the composition of the rest of the species changed. In the spring of the first year, the number of *P. janczewskii* and *Cladosporium cladocporioides* was high; later on, it drastically decreased. At the early stages of the decomposition, *Mycelia sterilia, Oidiodendron griseum, P. brevicompactum*, and *P. canescens* were abundant. In the second year of the test, the abundance of almost all the micromycete species decreased. *P. corylophilum, Trichoderma polysporum, Oidiodendron griseum, O. tennuissimum*, and *Mucor circinelloides* were identified.

The species diversity of the micromycetes was higher in the litter of the nemorose spruce forest as compared to that in the boreal spruce forest. The differences in the taxonomic composition were determined by the great number of dark-colored micromycetes (*Botrytis cinerea, Oidiodendron griseum, Thysanophora penicilloides, Cladophualophora* sp., and *Mycelia sterilia* (Dematiaceae)) identified in the litter of the nemorose spruce forest. The share of fast-growing micromycetes was also higher in this forest. Along with species of the *Trichoderma* genus, species of the *Botrytis, Cylindrocarpon*, and *Mucor* genera were identified. With the depletion of the substrate in the course of the litter's decomposition, the taxonomic composition of the mycobiota in the litter residues became close to that of the reference soil, and, at the end of the test, the basis of the dominant micromycete complexes in all the test variants was the species typical for the corresponding soil types of the model plots.

Testate amoebas. At different stages of the decomposition, 24 species of 14 genera and 8 families were identified in the litter (Table 4). The previous studies

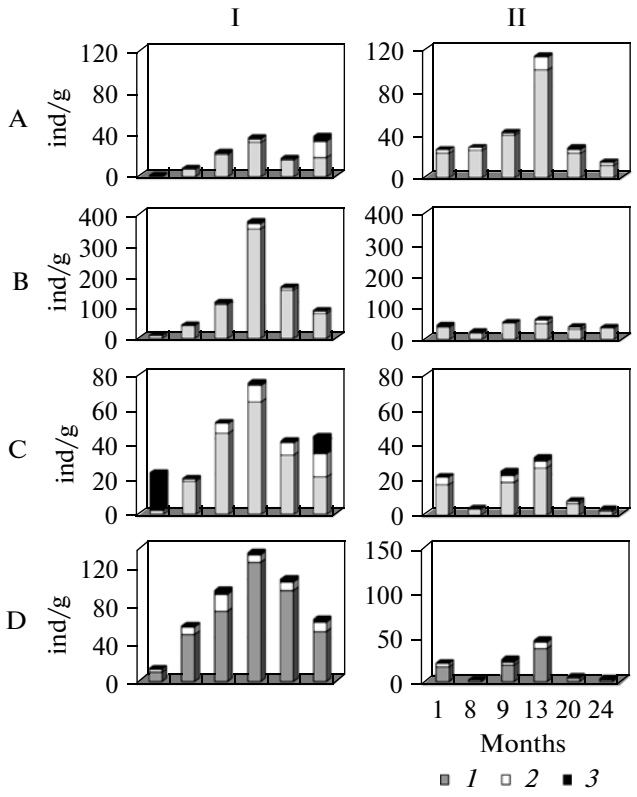

Fig. 4. Proportion between the mites (*1*), collembolans (*2*), and other small arthropods (*3*) in the litter samples (I) and soils (II) in the course of the experiment. A, B—plots in the boreal spruce forest; C, D—plots in the nemorose spruce forest. On plots A and C, bags with needles were placed; on plots B and D, leaf litter was placed.

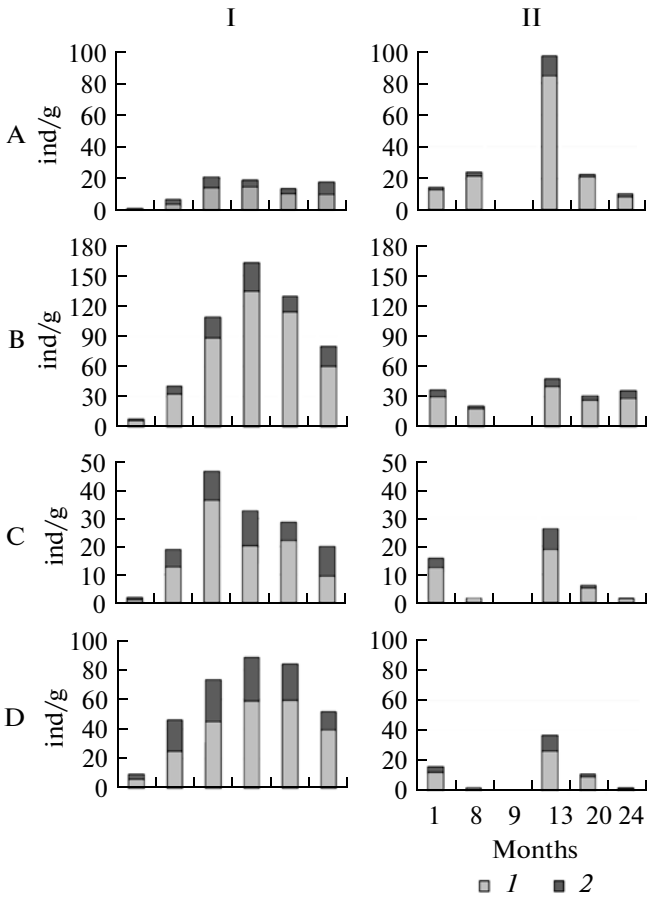

Fig. 5. Proportions between the oribatids (*1*) and the mesostigmatic mite (*2*) populations in the samples of the litter and the soil in the course of the experiment. The designations of the plots are the same as in Fig. 4.

revealed 43 species of testate amoebas of 20 genera and 11 families in the fermentative litter horizons of the same soils at the Reserve [13] taking into account not only the living individuals but also the empty shells. In our samples, only 50% of the testate amoebas were active. Since the majority of the Testacea species develop in the upper litter layers, their empty tests could fall to the bags with the litter due to the rain water or zoochory.

In all the variants, the highest species diversity of Testacea was registered in the second year after the test's beginning. At all the stages of the decomposition, the total diversity of the testate amoebas was higher (18 species in the boreal and 16 species in the nemorose spruce forests) than in the linden leaf litter (12 and 13 species, respectively). In the same habitat and in different kinds of litter, the faunal composition of the animal population little differed in the number of rare species, whereas the complexes of the dominants were similar there.

Significant differences in the composition of the Testacea complexes were revealed in the litter of the different forest types. In the boreal spruce forest, the core of the Testacea group was composed of such species as *Trinema lineare, Euglypha laevis, Nebela militaris, N. bohemica, Trigonopyxis arcula*, and *Trinema complanatum*. In the nemorose spruce forest, the number of *Euglypha rotunda, Trinema lineare, Centropyxis sylvatica, Plagiopyxis declivis, Tracheleuglypha acolla, Trinema complanatum*, and *Valkanovia* sp. was high. The earlier studies showed that the type of forest affected the species composition of the testate amoebas [13].

In the course of the litter decomposition, the ecological structure of the testate amoeba community gradually changed. At the initial stages, the surface-dwelling and eurytopic species that enter the substrate with the water flow from the upper litter horizons were registered. By the end of the experiment, the species proportion changed: the share of species characteristic of the lower layers of the organic horizons increased. This was visually displayed in the litter from the nemorose spruce forest. Here, at the end of the experiment, the typical inhabitants of the lower litter horizon (*Centropyxis sylvatica* and *Plagiopyxis declivis*) predominated. This fact testifies to the changes in the

Table 3. Species composition and number (thousand CFU/g) of the micromycetes in the litter samples under different expositions

Micromycete species composition	Boreal spruce forest										Nemorose spruce forest									
	needles					leaves					needles					leaves				
	exposure, months																			
	8	9	13	20	24	8	9	13	20	24	8	9	13	20	24	8	9	13	20	24
Penicillium spinulosum	191	20.2	10.6	6.33	7.64	55.3	1	2.3	0.33	4.04		1.06	0.16	1	3.11					
Penicillium glabrum	37.2	1.73		2.66	0.33						12.6	1.06		1.11	0.11					
Penicillium aurantiogriseum		0.76		0.22	1.13						2.2	4.63	1.33	0.88	3.11	25.5	3.4	1	6.16	
Penicillium miczynskii		8.5		0.11																
Penicillium corylophilum		1.43		0.88					0.5	0.39										
Penicillium janczewskii			3.33	0.22	1.5	4	8.4			0.36	5.1	4.3	1.16	2.11	5.77	172		4.2	1.5	
Trichoderma polysporum			9.22	7.67	2.97			0.7	0.33	0.17	5.9	3.66	15.33	1.22	5.22	2.9		5.5	1.33	3.62
Penicillium citrinum			0.22	0.22																
Oidiodendron griseum				23.1	95.8	12.4		0.5					3.33	2.22						
Phialophora sp.				38.9	22.2															
Cladosporium cladosporioides						2.1	8.4	0.2		0.42										
Mycelia sterilia						5.3	3.4		0.5	0.11										
Penicillium brevicompactum						354.5			0.16		14.9	1.53				9.1	1	0.7	0.16	1.67
Penicillium canescens						7.1			0.16											
Oidiodendron rhodogenum								0.3	0.83	0.08										
Mucor circinelloides								0.3		0.22										
Oidiodendron tenuissimum									1.83	0.23										
Umbelopsis ramanniana											0.3	11.8								
Thysanophora penicilloides											5.6		5.33					0.2		0.41
Geomyces pannorum														6.66	5.22					
Penicillium raistrickii														0.33	0.11					
Penicillium verruculosum														0.55	0.66					
Trichoderma harzianum																13.1	0.4		1.6	0.71
Paecilomyces carneus																	1.6	0.2		
Trichoderma koningii																	0.4		0.66	
Penicillium sp.												0.33	3.67	0.22	2.77					

Table 4. Species composition and the dominant complex (%) of the testate amoebas under the different expositions

Testate species composition	Boreal spruce forest												Nemorose spruce forest										
	needles						leaves						needles						leaves				
	exposure, months																						
	1	8	9	13	20	24	1	8	9	13	20	24	1	8	9	13	20	24	1	8	9	13	20
Trinema lineare		67	50	17	+	12		75	10	+	+	12			18	38	10	+	+	67	39	+	+
Euglypha laevis		33		12	11	+		25			+	+											
Nebela militaris			25	+	31	43			42	22	39	32				+		+					
Plagiopyxis sp.			25			+									+	21	13	10			17	+	12
Trinema penardi				12	+												+		+				
Centropyxis sylvatica				10	15						+					14	16	39	+		28	13	12
Nebela bohemica				17	+	+			19	21	31	+			+			+					
Trinema complanatum				19	+				10			+			30		+	+				17	16
Trigonopyxis arcula				+	+	+																+	
Valkanovia sp.					+	14				50	+	+					15	+				10	+
Corythion dubium				+																			
Cyclopyxis eurystoma				+												21		+					
Assulina muscorum					+				19					25		+		+					
Tracheleuglypha acolla					+							+			+		26	+					+
Euglypha ciliata					+					+	14	28									+		
Arcella sp.					+										+								+
Trinema enchelys						12												+					
Assulina seminulum						+																	
Heleopera sylvatica												+											
Placocista spinosa											+	+											
Euglypha rotunda														50	18		10	14	+	33	11	47	29
Nebela lageniformis														25									
Heleopera petricola																		+					+
Phryganella acropodia																							+

Table 5. Species composition and the dominant complex (%) of the mites under the different expositions

Mite species composition	Boreal spruce forest										Nemorose spruce forest									
	needles					leaves					needles					leaves				
	exposure, months																			
	1	8	13	20	24	1	2	3	4	5	1	8	13	20	24	1	8	13	20	24
Oribatei																				
Oppiidae	38	41	33	33	21	41	67	15	13	19	15	53	20	35	20	14	19	9	16	21
Nothridae	6	6	+	25	24	11	7	+	53	50	7	+	+	26	9	26	17	7	39	42
Hypochthoniidae	12	+	+	–	+	8	+	+	+	+	+	+	+	–	+	7	+	9	+	–
Ceratozetoidea	+	+	+	+	+	+	+	+	+	+	19	+	+	–	+	+	9	+	+	+
Phthiracaridae	+	–	+	–	+	–	+	+	–	+	+	+	+	+	5	5	+	+	+	+
Malaconothridae	+	–	5	–	–	–	–	19	–	–	+	+	+	+	+	–	–	20	–	–
Nanhermanniidae	+	+	+	+	+	–	+	+	+	+	–	+	+	+	–	+	+	+	–	–
Camisiidae	+	–	+	–	–	–	+	+	+	+	+	+	+	–	+	–	+	+	+	+
Brachychthoniidae	–	–	–	–	+	+	–	–	–	–	–	+	–	–	–	+	–	+	–	+
Eulohmanniidae	–	–	–	+	–	–	–	–	–	–	–	+	–	+	–	–	–	–	+	–
Damaeidae	–	–	–	–	–	–	–	–	–	–	–		+	–	+	–	+	–	+	+
Mesostigmata																				
Veigaiaidae	+	14	7	8	19	14	+	+	+	5	10	11	8	10	–	16	8	+	+	6
Zerconidae	+	20	+	9	10	+	9	+	+	9	5	12	7	5	32	7	30	8	19	9
Trachytidae	–	+	+	+	+	+	+	+	+	10	8	8	+	+	16	5	+	9	+	8
Uropodidae	–	+	+	–	–	–	+	–	–	–	+	+	+	–	+	–	+	+	+	–

ecological structure of this community in the course of the litter's decomposition.

At all the stages of the litter decomposition, oribatid mites predominated among the microarthropods—50–95%. (Fig 4). Collembolans comprised 5–30%; the number of other fine arthropods did not exceed 5% of the total microarthropod number.

The litter samples were actively colonized by oribatids and predatory mesostigmatic mites, among which Gamasidae and Uropodidae mites predominated. Representatives of the Trachytidae family were also found. Figure 5 shows the proportion between the oribatid and predatory mesostigmatic mites at the different stages of the decomposition (with oribatids being the dominant species). As compared to the reference soils, in the litter samples, the share of predatory mesostigmatic mites was always much higher. It was especially obvious in the samples from the nemorose spruce forest, where, sometimes, they comprised more than 40% of the total number of mites.

The oribatid mites were represented by 10 families (Table 5) with species of the Opiidae, Northridae, Northridae, Hypochthoniidae, and Malaconothridae as the dominant ones. In addition, in the plot for the nemorose spruce forest, at one of the decomposition stages, the species of Ceratozetoidea and Phthiracaridae were recorded. According to their morphological and ecological features, these groups belong to inhabitants of the contact zone between the litter and the mineral soil horizons. Evidently, this zone was a source for colonization of experimental substrates.

In the course of the decomposition, the dominating groups of oribatid mites interchanged. At the early stages, Hypochthoniidae and Nothridae representatives predominated and, in the nemorose spruce forest, Ceratozetoidea and Phthiracaridae species prevailed. In the middle of the test, the number of Malaconothridae species increased; at the final stages, the number of Northridae species was higher. In addition, in all the samples and at all the stages of the decomposition, the Opiidae (typical representatives of the lower litter layers) species predominated. In the oribatid complexes, the Nanhermanniidae, Camisiidae, and Brachychthoniidae species occurred; they were not among the dominants. In the nemorose spruce forest, single Damaeidae individuals were present. Among the predatory mesostigmatic mites, representatives of two families—Veigaiaidae and Zerconidae—predom-

inated. The latter were especially numerous in the nemorose spruce forest. In the same samples, representatives of the Trachytidae family were also abundant.

CONCLUSIONS

The results of the field experiment showed that the activity of the key representatives of the soil saprophilic block was high at the contact of the litter and mineral horizons. In the linden leaf litter, as compared to the needle one, the successions of invertebrates and micromycetes alternated more intensely. Along with the significant differences in the quantitative indices characterizing the abundance of the pedobionts that colonize the litter in the course of the succession, the rates of the losses of the needle and leaf litter masses differed to a great extent. In the leaf litter, the decomposition of the blades was completed towards the end of the first year, which was in good agreement with the high abundance of invertebrates in the leaves, which was several times higher than in the needles. In the needle litter, in the second year, the active decomposition continued, and the abundance of invertebrates remained at a high level.

It is noteworthy that, in the spruce forests investigated, the potential activity of the soil biota was high. This was especially well pronounced in the waterlogged white-podzolic soil (plot SB_1), where the number and diversity of the biodestroyers in the leaf litter was not lower than in the burozem, and, at some succession stages, they exceeded those in the soil under the nemorose spruce forest (Fig. 3). Despite the clear distinctions in the edaphic–vegetation conditions, the low rates of the biological cycle in the boreal spruce forests cannot be explained by the lower activity of the saprophilic zoomicrobial complex. The same fact was also found by other specialists [7, 8, 19]. This is also proved by the results of the three-factor analysis that confirmed the major effect of the kind of litter on the population of biodestroyers.

At the contact of the litter and mineral horizons, the alterations in the species composition and the abundance of the dominant invertebrate groups were pronounced not so clearly as in the top litter horizon, as was show from the example of the microarthropod successions upon the leaf and grass litter decomposition [20, 22, 23].

The rates of the succession changes in the complexes of the micromycetes and invertebrates in the litter turned out to be close, probably, due to the relatively stable habitat conditions at the contact of the organic and mineral horizons. At the very early stages of the test, the active colonization of the litter samples by micromycetes was replaced by the intense development of nematodes; by the end of the first year of the decomposition, the activity of the microarthropods and Protozoa was maximal. The fine invertebrates populating the litter mostly referred to microphytophages [11, 12, 17]. This fact can explain the decrease in the number of microscopic fungi in the litter samples in the middle of the experiment. In the decomposing plant residues, the invertebrates actively consume micromycetes. By the end of the test, in all the test variants, the abundance and diversity of the zoomicrobial population decreased and approached the indices characteristic of the soil population; this change indicated the termination of the active phase of the decomposition.

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