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REVIEW PAPERS

Structure and Role of Microbial Communities in Southern Taiga Soils

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Abstract—General regularities in the structure of the microbial communities of southern taiga soil ecosystems and taxonomic differences between the microbial communities of soils with different hydrothermal characteristics are discussed with reference to the main types of soils of the Central State Forest Biosphere Reserve.

Key words: microbial diversity, spatial structure, monitoring, ecological functions.

Investigation of the ecosystems of reserves as ecologically unaltered areas is very important for environmental management, including the protection of soils and the preservation of their biological diversity.

The Central State Forest Biosphere Reserve (CSFBR) may serve as a standard for forest ecosystems of the central part of European Russia, whose stability is due to its position in a forest watershed region some distance away from large industrial centers [1].

Investigations of the reserve soil biota were started in the 1990s by the researchers of the Departments of Soil Geography and Soil Biology of the Faculty of Soil Science of Moscow State University, the Laboratory of the Ecological Functions of Soils of the Severtsov Institute of Ecology and Evolution, and the Institute of Soil Science of Moscow State University and the Russian Academy of Sciences. The main goal of these investigations, which were guided by academician G.V. Dobrovol'skii, was to elucidate the regularities of soil functioning in the unimpacted southern taiga landscapes and to determine the role of macro- and microfauna in the ecological functioning of soils.

The results of the analysis of the structure and dynamics of micro- and nanofauna in the CSFBR soils were published earlier [2, 3]. In the present paper, we reviewed the data of the six-year investigation of the structure and role of microbial communities in different biogeocenoses of the reserve.

Investigations were performed with reference to six types of soils (Fig. 1) associated with certain land forms, soil-forming rocks, and forest types and differing in the degree of differentiation into genetic horizons, the presence and specificity of eluvial sediments, the morphology of diagnostic horizons, as well as in some chemical characteristics.

The materials and methods used were described in detail elsewhere [3–8].

BACTERIAL COMMUNITIES

To elucidate the structure, dynamics, and diversity of bacterial communities in the soils under study (white podzolic and brown forest soils), we used two approaches: the simultaneous vertical profiling of microbial complexes in all biogeocenotic horizons and the succession approach consisting in the study of temporal changes in the composition of microbial communities. The combination of these approaches allowed a complete characterization of biogeocenoses, including the description of aerobic and facultatively anaerobic epiphytic and saprotrophic bacteria.

The vertical profiling of bacterial communities showed that the bacterial populations of various biogeocenotic horizons are different [7]. The number of prokaryotic microorganisms in both types of forest soils under study increased in the following order: green parts of plants, tree waste, and litter stratum. The soil bacterial population was somewhat higher in the nemoral than in the bilberry spruce forest. The bacterial population of plants varied from 10^7 to 10^{10} colony-forming units (CFU) per 1 g of plant material (the number of bacteria on grasses and mosses was higher than on needles). The bacterial population was maximum (10^9–10^{10} CFU/g) on dead needles and in the upper litter layer (L) of both types of spruce forests. In the fermentation layer (F) and H layer of the bilberry spruce forest litter, the number of bacteria was, respectively, one order and two orders lower. In proper soil horizons, the bacterial population tended to decrease further (by an order or more), the decrease being more pronounced in a less fertile white podzolic soil [7].

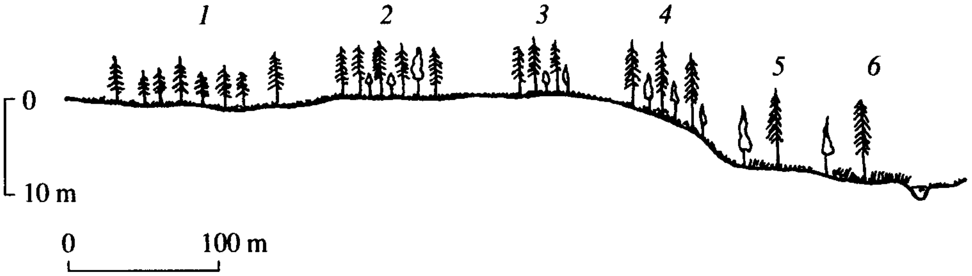

Fig. 1. The CSFBR relief from which soils were sampled: *1*, sphagnous spruce forest on upland peat gley soil; *2*, bilberry spruce forest on white podzolic peaty soil; *3*, crab-apple nemoral spruce forest on pale-yellow soddy podzolic soil; *4*, nemoral spruce forest on burozem soil; *5*, black-alder marsh spruce forest on lowland peaty soil; and *6*, fern–spiraea spruce forest on soddy gley soil.

The number of actinomycetes in litters, which peaked in their fermentation layers, was 3–4 orders lower than that of bacteria. Unlike the bacterial population, the actinomycete population gradually decreased with depth [9, 10].

Bacteria isolated from various substrates were represented by spirillas; myxobacteria; cytophages; gram-negative bacteria of the genera *Flavobacterium, Pseudomonas,* and *Xanthomonas*; coryneforms; bacilli; and streptomycetes. The vertical distribution of bacteria in the bilberry and nemoral spruce forests was similar to that in other types of forests [11, 12].

The difference between the bacterial complexes of various soil strata manifested itself in the domination of different bacterial taxa. The domination frequency was defined as the ratio of samples in which a given taxonomic group comprised more than 30% of the bacterial population to the total number of samples examined. All of the spruce forest soil strata were dominated by hydrobionts represented by spirillas. The domination frequency of other bacterial groups depended on the inhabited substrate. The bacterial populations of plants were dominated by coryneforms and gram-negative bacteria of the genera *Flavobacterium, Pseudomonas,* and *Xanthomonas.* The second dominant group of forest litters was represented by gliding bacteria, while forest soils were dominated (along with spirillas) by bacilli and streptomycetes. The latter were represented by the sections and series typical of taiga biogeocenoses, such as *Cinereus Achromogenes, Cinereus Chrysomallus, Albus Albus, Albus Albocoloratus, Helvolo-flavus Helvolus,* and *Imperfectus* [9, 10].

Among the five dominant species of spore-forming bacteria, the facultative anaerobes *Bacillus circulans* and *B. cereus* were most abundant. The six dominant species of the genus *Cytophaga* included the rare facultatively anaerobic species *Cytophaga succinicans* [4].

The succession approach allowed a wider range of bacterial taxa to be elucidated in forest soils [4]. In addition to the aforementioned taxonomic groups, the brown forest soil (burozem) contained azospirillas, facultatively anaerobic proteobacteria of the families *Enterobacteriaceae* and *Vibrionaceae*, and the actinobacteria *Promicromonospora* and *Micromonospora*, which were detected at different stages of succession. The latter actinomycete was more abundant in the white podzolic soil than in burozem; this can be explained by the adaptation of micromonosporas to the excess moisture content of white podzolic soil due to the hydrophilicity of their spores and the microaerophilicity of their mycelium [13].

Bacterial diversity, estimated as the Shannon index, was maximum in the fermentation layer of both types of litters. However, the range of bacterial dominants was wider in the burozem than in white podzolic soil [4, 7].

The differences in the bacterial complexes of proper soil horizons were due to their different organic profiles. For instance, bacterial diversity in the soil stratum of burozem, which contains a humus-accumulating soil horizon beneath its litter stratum, was higher than in the white podzolic soil, whose horizon beneath its litter stratum is low in humus.

The illuvial horizons of the soils under study differed in the generic composition of coryneforms, which are typical inhabitants of these horizons. In the burozem, coryneform bacteria, which were represented by arthrobacters (87%), rhodococci, and micrococci, were most diverse. Instead of arthrobacters, the white podzolic soil contained yellow coryneforms, which were not identified at the generic level. The number of such coryneforms was about the same as that of other actinobacteria.

The variance analysis of the seasonal [7, 14] and annual dynamics of soil bacterial complexes allowed us to estimate the influence of various factors, such as the type of soil or soil horizon (substrate) and the year of observation, on the number and diversity of bacteria. This analysis showed the significant (at a significance level of 0.9) effect of the substrate type on the number of saprotrophic bacteria. The bacterial population density tended to decrease in a downward direction from the litter strata to the illuvial soil horizons against the background of insignificant seasonal and annual variations.

The taxonomic composition of bacterial complexes depended (in order of decreasing influence) on the year of observation (the effect of this factor was determined by the amount of precipitations in a given year), the substrate type, and the soil type. The Shannon index in all of the biogeocenotic horizons of burozem and white podzolic soil was minimum in the driest year, which was also characterized by the most pronounced differences in the Shannon indices of different soil types and horizons. In wet years, these differences were lower against the background of the higher bacterial diversity.

Moisture content also determined the vertical distribution pattern of bacteria. During wet periods, when soils were almost completely saturated with water, bacteria were distributed continuously over the whole 0.5-m soil depth, including the litter strata. At the same time, during relatively dry periods, when the moisture content of soils was less than their total moisture capacity, bacterial taxa were distributed discretely, i.e., the bacterial communities of the litter strata and soil horizons differed distinctly in the generic composition. In this case, the litter strata were dominated by gliding bacteria (cytophages and myxobacteria), whereas soil horizons were dominated by bacilli and coryneforms.

The composition of the bacterial complex of the white podzolic soil in wet and dry years is shown in Fig. 2. The wet soil was dominated by spirillas, which are typical hydrobionts, whereas the relatively dry soil was dominated by myxobacteria (the content of bacilli increased by as much as tenfold). As the soil moisture content decreased under the laboratory conditions (drying in the air), the fraction of bacilli increased to 40%, so that this bacterial group became dominant, together with an increasing content of coryneforms and streptomycetes. Similar dynamics of actinobacteria and bacilli were observed during the laboratory drying of the soddy gley soil samples from the CSFBR [5] but not in the field experiments. At the same time, in the case of the sandy podzolic soils from the Oka Biosphere Reserve in the Ryazan region, which are characterized by good mechanical properties and better warming in the summer, the aforementioned dynamics of bacterial complexes, i.e., the prevalence of drought-resistant actinomycetes and bacilli, was observed in both laboratory and field experiments [15]. Therefore, the insignificant variation in the taxonomic structure of the bacterial complexes of the CSFBR soils in relation to the year and season of observation is explained by the fact that these soils are always wet.

The establishment of the taxonomic position of microorganisms typical of a given biogeocenosis makes it possible to estimate the ecological role of these microorganisms. For instance, the saprotrophic bacteria of the CSFBR soils are represented by the members of diverse ecological and trophic groups—hydrolytics, copiotrophs, and oligotrophs. In turn, hydrolytics are represented by diverse bacterial groups—bacilli, gliding bacteria (myxobacteria and cytophages), and actinomycetes of the genera *Cellulomonas*, *Nocardioides*, *Micromonospora*, and *Streptomyces*.

Bacteria capable of degrading plant polymers, including cellulose, were found in all the horizons of the burozem and white podzolic soil, although their total and relative numbers were higher in the layers where plant residues undergo active degradation, i.e., in the litter strata and the upper humus-containing soil horizons.

At the same time, the burozem and white podzolic soil differed in the taxonomic composition of hydrolytic bacterial complexes in both litter strata and soil horizons. The burozem litter was characterized by a wide range of hydrolytic bacteria and a high frequency of their domination over the whole observation period. The hydrolytic bacteria, dominated by myxobacteria and cytophages, were also frequent in the burozem soil horizons. In the eluvial horizon of white podzolic soil, coryneforms and cytophages were absent, whereas bacilli and streptomycetes were dominant. The population of the latter bacteria in the white podzolic soil decreased with depth more steeply than in the burozem; this was probably due to a higher content of humus in all burozem horizons as compared to the white podzolic soil. The number of hydrolytic bacteria correlated with the fermentation activity of soils. Cellulolytic activity was maximum in the burozem Ahf and Bf horizons and minimum in the white podzolic soil [16].

The succession study of hydrolytic bacteria in the organogenic soil horizons showed that, at the early stages of succession, amylolytic bacteria were represented by cytophages and myxobacteria, while, at the late stages of succession, they were represented by actinomycetes, myxobacteria, and bacilli [4]. The bacillar species *B. cereus* and *B. megaterium* were dominant in a medium with starch, while *B. circulans, B. brevis,* and *B. globisporus* prevailed in a medium with cellulose. In the soils under study, the yeast biomass was utilized by the cytophages *C. johnsonae* and *C. succinicans* and by the bacillar species *B. circulans.* The prevalence of bacilli and cytophages among the hydrolytic bacteria of the CSFBR soils was confirmed by the replicator method [17]. Spore-forming bacteria, represented mainly by facultative anaerobes, were the major degraders of carboxymethylcellulose (CMC), starch, pectin, microbial biomass, lecithin, Tween, and proteins in the white podzolic soil and the upper horizons of peat gley soil. The number of spore-forming bacteria was maximum in a medium with CMC and varied from 10^3 to 10^5 CFU/g in the organogenic horizons. The relative number of hydrolytic bacteria was maximum in the soddy gley soil and burozem, reaching 10^9 CFU/g in the litter strata of these soils. Cytophages were dominant in media with CMC, starch, and pectin, but the inhibition of the growth of gram-negative bacteria led to the prevalence of streptomycetes, cellulomonads, and bacilli. The latter bacteria were also dominant in media used for the enumeration of prokaryotic bacteria capable of lysing the yeast biomass. Spirillas, which are typical inhabitants of waterlogged soils, isolated from the soddy gley soil were able to hydrolyze lecithin

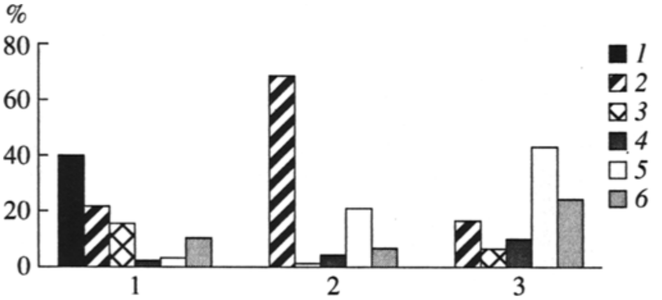

Fig. 2. Effect of soil moisture content on the taxonomic composition of bacterial complexes in white podzolic soil: 1, fresh soil samples taken in wet years; 2, fresh soil samples taken in dry years; 3, air-dried soil samples; *1*, spirillas; *2*, myxobacteria; *3*, cytophagous flavobacteria; *4*, streptomycetes; *5*, bacilli; and *6*, coryneform bacteria.

and Tween, indicating their possible role as lipolytic agents. All these data suggest that the number, taxonomic composition, and role of degrading bacterial complexes depend primarily on the properties of the inhabited soil.

In the soils under study, copiotrophs, which are able to utilize only water-soluble monomeric compounds (such as carbohydrates, organic acids, and alcohols), were represented by spirillas, micrococci, and facultative anaerobes of the families *Enterobacteriaceae* and *Vibrionaceae.* The presence of spirillas, which are typical hydrobionts, in these soils and especially their prevalence in some soil horizons are further evidence that these soils are saturated with water.

Oligotrophic bacteria, which are difficult to isolate by plating on solid media, were detected in large quantities at the late stages of succession. These bacteria were mainly represented by prosthecate and budding bacteria [4].

The major chemical elements migrating in the soils of the humid zone are iron and manganese. Fe,Mn-oxidizing bacteria were revealed in all of the horizons of white podzolic soil and burozem in a number which increased with time (succession analysis) and depth (vertical analysis) [4]. These bacteria were mainly represented by bacilli, spirillas, and myxobacteria (i.e., by the dominant bacterial types of the soils under study), whose relative number in the soil horizons was as high as 40%. Fe,Mn-oxidizing bacteria represented by other bacterial taxa were scarce. Therefore, the ability to oxidize iron and manganese is typical of all soil bacteria but not of only some specific bacterial taxa, such as *Pedomicrobium, Galionella,* and *Seliberia,* as was believed earlier [11].

Thus, moisture content, which depends on weather conditions and the hydrothermal regime of soils, is one of the major factors determining the taxonomic composition of soil bacterial complexes. In particular, the moisture content of soil determines (1) the distribution pattern of bacteria over soil horizons (the distribution is continuous during wet periods and discrete during dry periods); (2) the bacterial diversity, which is higher during wet periods than during dry periods; and (3) the proportion of taxa in prokaryotic microbial complexes (spirillas dominate in wet years, while bacilli and actinomycetes dominate in dry years).

The domination of the burozem and white podzolic soil by bacterial hydrobionts and facultative anaerobes of the families *Enterobacteriaceae* and *Vibrionaceae* and the genera *Bacillus* and *Cytophaga* suggests that these bacteria are well adapted to the high moisture content of these soils.

A comparative investigation of the bacterial complexes of the burozem and white podzolic soil, which are characterized by different reliefs and water–air regimes, showed that the bacterial characteristics of these soils strongly differ. In particular,

(1) both the litter and soil strata of the burozem are characterized by a greater bacterial diversity and a higher content of hydrolytic bacteria than the white podzolic soil, which can be explained by the more favorable conditions of degradation of plant residues in the burozem;

(2) the white podzolic soil has a higher population of actinomycetes of the genus *Micromonospora* than the burozem, since these microorganisms are well adapted to the excess moisture content of white podzolic soil;

(3) the illuvial horizons of burozem and white podzolic soil differ in the taxonomic composition of coryneforms, the typical inhabitants of these horizons;

(4) arthrobacters, which grow poorly in highly acidic media, were not detected in any of the horizons of white podzolic soil, although these bacteria were detected in all of the burozem horizons.

FUNGAL COMMUNITIES

To elucidate the composition and role of microscopic fungal communities in the southern taiga soils, the number and diversity of soil fungi and the rate of the fungal mineralization of organic matter were evaluated [8, 18].

The number of micromycetes in the litter strata and humus-accumulating horizons of the soils under study (upland peat gley soil, white podzolic soil, pale-yellow soddy podzolic soil, and lowland peaty soil) comprised hundreds of thousands of CFU/g substrate and was an order of magnitude lower in the illuvial horizons of soils and in the underlying bedrock.

Fungal population densities depended on the season when the soils were sampled rather than on their types. During drought periods, the population of soil microscopic fungi was one to two orders lower than during wet periods.

The taxonomic diversity of soil micromycetes was high: two-year observations made it possible to identify

121 species of micromycetes belonging to 47 genera. The majority of these species were typical saprotrophs of the genera *Acremonium, Aspergillus, Penicillium, Paecilomyces,* and *Trichoderma* from the family *Moniliaceae,* class *Deuteromycetes.* Some fungi belonged to the genera *Alternaria* and *Cladosporium* from the family *Dematiaceae* and to the classes *Zygomycetes* (the order *Mucorales*), *Ascomycetes,* and *Basidiomycetes.* Of frequent occurrence during the microbiological analysis of soils were dark or colorless sterile colonies of the species *Mycelia sterilia.*

The greatest numbers of colonies were isolated from the burozem (61) and white podzolic soil (57), whereas the minimum number, from the upland peat soil (19).

The bacterial diversity depended on the season of observation. The maximum number of fungal species in all biogeocenoses was detected in autumn; this can be explained by the enrichment of litter strata in this season with epiphytic fungi occurring on fresh tree waste. In the summer, the fungal population of soils was minimum, evidently because of the insufficient soil moisture content preventing the growth of fungi.

The fungal diversity index varied from 0.16 in the deep mineral horizons of soils to 12.8 in the upper litter layers L and F. It should, however, be noted that, for unbiased estimation, it is necessary to differentiate and determine the abundance of typical, dominant, rare, and occasional fungal species [19, 20]. The ecological role (i.e., functional activity, involvement in the processes of transformation of organic matter, etc.) of these groups of fungi is different, being insignificant for rare and occasional species and essential for dominant species. The species domination index is one of the most representative indices of the taxonomic structure of microbial complexes, which is closely related to the type of ecosystem under examination [21].

The domination index, which is determined by the abundance rate of fungal species, is inversely dependent on their diversity and is maximum when the pressure of bacteria on fungi is minimum. Therefore, high values of the fungal species domination index should be expected in peat gley and white podzolic soils, whose high acidity promotes the growth of fungi but not of bacteria. Among the dominant fungal species of these soils are (in order of increasing abundance rate) *Penicillium verrucosum* Dierckx, *P. spinulosum* Thom, *P. claviforme* Bainier, as well as colored and colorless forms of *Mycelia sterilia.* The latter fungus, together with representatives of the genus *Metarrisium,* prevailed in the peat gley soil.

The high diversity of micromycetes in the lowland peat and pale-yellow soddy podzolic soils, which are favorable for fungi, correlated with the lower values of the domination index. In general, the species diversity index of the soils under study was higher in less acidic soils, showing maximum values in autumn.

Of much interest is the species composition of micromycetes in the nitrogen-rich pale-yellow soddy podzolic soil formed on carbonate rocks. Only this type of soils contained fungi of the genus *Fusarium* (*F. stilboides, F. lateritium* Nees et. Fries, and *F. expansum* Schlecht), whose typical habitats are soils rich in organic matter.

The paired comparison of soils with respect to fungal abundance showed that the most similar (in this respect) soil pairs are burozem–white podzolic soil (the similarity index of Sörensen–Chekanovskii (SI) = 0.51) and pale-yellow soddy podzolic soil–lowland peaty soil (SI = 0.45) (Table 1). The relatively low values of SI for all soil pairs suggest that the mycobiotas of all of the soils under study significantly differ.

This inference was confirmed by the kinetic analysis of soil fungal communities based on measuring the radial rates of colony growth. In the litter strata of burozem and white podzolic soil, micromycete complexes greatly differed even at the early stages of succession. The Shannon diversity index was higher for the litter stratum of burozem (1.55) than for the litter stratum of white podzolic soil (1.1). Irrespective of the season of observation, the burozem litter contained a greater number of fast-growing (and, therefore, capable of an intense colonization of the substrate) fungi than the white podzolic soil litter, whose fungi produced single-type slow-growing colonies with K_r = 0.06–0.10 mm/h. In proper soil horizons, fast-growing micromycetes were more abundant than slow-growing micromycetes in springtime only; the prevalence of fast-growing micromycetes was most pronounced in the burozem and pale-yellow soddy podzolic soil.

It should be noted that the kinetic approach makes it possible not only to rapidly evaluate the biodiversity of various biotopes but also to estimate the succession conversion of substrates, for instance, hydrocarbon fractions [22, 23].

Micromycetes play an important role in heterotrophic microbial communities; therefore, elucidation of the structure and role of micromycete complexes in soils in relation to the transformation of organic matter is of much ecological importance.

In springtime, fast-growing micromycetes, dominated by mucorales of the genera *Cladosporium, Alternaria,* and *Trichoderma,* rapidly colonized the substrate, consuming water-soluble carbohydrates. By the summer season, the succession conversion of organic matter led to an increase in the proportion of poorly metabolizable compounds; this promoted the growth of many slow-growing fungi belonging to the genera *Penicillium, Acremonium, Aspergillus,* etc., which possess a powerful cellulolytic complex. With autumn defoliation, the proportion of fast-growing soil fungi increased again.

The analysis of the Shannon indices and the rates of mineralization of organic matter, K_m, in the litter strata showed that these parameters highly correlated in the fermentation layers of the litters in all seasons and in their humic layers in the summer. In the upper layer of

Table 1. Paired similarity of the CSFBR soils with respect to the abundance of micromycete species as estimated by the Sörensen–Chekanovskii indices

Soil	No.*	1	2	3	4
Peat gleysolic	1				
White podzolic	2	0.27			
Burozem	3	0.29	0.51		
Pale-yellow soddy podzolic	4	0.29	0.37	0.27	
Lowland peat	5	0.26	0.37	0.45	0.27

* The serial number of soil.

Table 2. Correlation between the species diversity of micromycetes (Shannon index) and the mineralization rate of organic matter (K_m) in the soil litters

Subhorizon	Spring	Summer	Autumn
L	0.68	0.07	0.20
F	0.78	0.86	0.61
H	0.41	0.89	0.23

litters, where the activity of microorganisms is strongly influenced by environmental conditions, the correlation between the aforementioned parameters was minimum (Table 2).

The relationship between the species diversity of micromycetes and the intensity of transformation of organic matter in soils is, undoubtedly, complex and depends on many factors. For instance, the rate of degradation of organic matter by fungi decreases with the increasing number of fungal species, probably due to their competition [24]. This inference was confirmed by measurements of the organic matter mineralization rates in the humic layer of the H litter stratum of white podzolic soil containing different numbers of micromycete species. These measurements showed that the mineralization rate was higher when this layer contained one micromycete species than when it contained several species.

Thus, analysis of the structure of fungal communities in the spruce forest soils showed that their litter strata are characterized by maximum values of fungal population and diversity, as well as by a high correlation between the diversity index and the rate of mineralization of organic matter.

The season of observation exerted an influence on

(1) the fungal population density (the density was higher during wet periods);

(2) the proportion between fast- and slow-growing soil fungi (the number of fast-growing fungi was greater in the spring and autumn, while that of slow-growing fungi, in the summer);

(3) the abundance of micromycetes and their diversity (these parameters were higher in autumn).

The spruce forest soils differed in the diversity of micromycetes and dominant species. The fungal diversity was higher in neutral soils rich in organic matter.

YEAST COMMUNITIES

The yeast population of forest biogeocenosis, which differs from that of tundra and desert biogeocenoses [25], is composed of the epiphytic yeast complex involving the inhabitants of phylloplane, the litter complex involving hydrolytic yeasts, and the soil complex involving specific yeast species adapted to life in mineral soil horizons.

The taxonomic structures of yeast communities were studied with reference to the three types of spruce forests (bilberry, peat moss, and nemoral spruce forests) of the CSFBR, which occur at different landforms and are characterized by hydromorphically different soil types (white podzolic, peaty gleysolic, and burozem soils, respectively) [6, 26].

The yeast population density varied from 10^2 CFU/g on the green parts of plants to 10^6 CFU/g in the mineral soil horizons. The maximum yeast population density was in the moss and litter strata of the spruce forests, and the minimum was on the rhizoplane of trees, bark, decaying wood, and the mineral soil horizons. The mean yeast population density on the green and dead overground parts of plants in spruce forests (10^3–10^4 CFU/g) is lower than that in other types of forest biogeocenoses (10^5 CFU/g) [21, 27, 28].

Yeasts of the biotopes studied comprised 36 species belonging to 14 genera. The species diversity of yeasts decreased in the following order: the green parts of plants, dead parts of plants, litter, organogenic soil horizons, and mineral soil horizons. For instance, five–six yeast species could be isolated from one sample of mosses or the green parts of vascular plants, whereas only one–two species were isolated from one sample of mineral soil horizons.

The species composition of the yeast communities on plant and soil substrates is shown in Fig. 3.

The yeast population of mosses was dominated by *Leucosporidium scottii* and *Cryptococcus laurentii* (the latter is a common inhabitant of the overground parts of plants). On the green and dry unlignified parts of vascular plants, the dominant yeast species were *C. laurentii, Sporobolomyces roseus*, and *Rhodotorula minuta.* On bark and wood, the dominant yeast species were *C. laurentii* and species of the genus *Pichia* (the latter yeasts are the associants of xylophagous beetles). The litter yeast complex involved the typical litter inhabitants *C. podzolicus* and *Trichoderma pullulans.* The yeasts of soil strata were dominated by *C. albidus* and *C. podzolicus.*

The significance of the relationship between substrates and inhabiting yeast species was confirmed by the two-factor variance analysis of data, where one factor was the type of substrate with three gradations

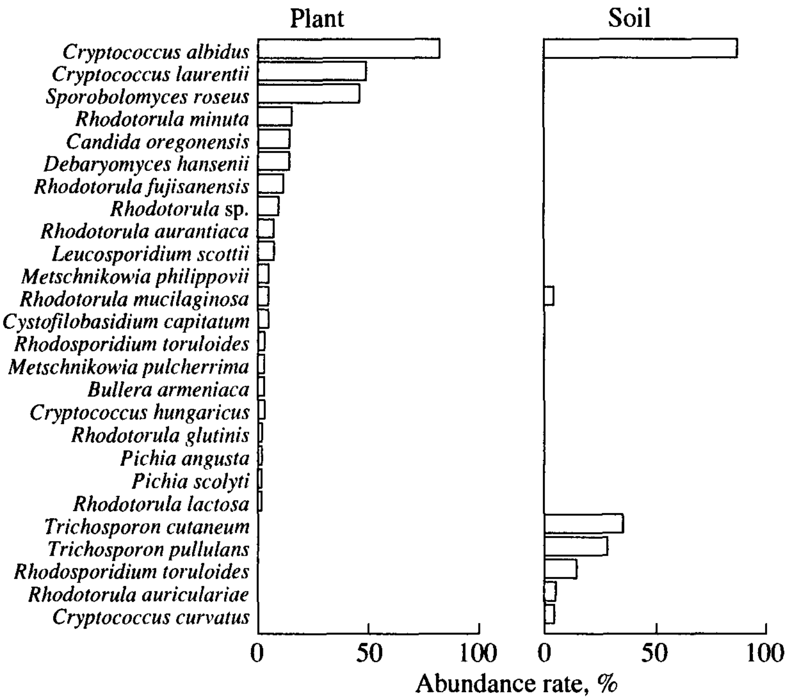

Fig. 3. Species abundance of yeasts on plant and soil substrates.

(overground parts of plants, litters, and mineral soil horizons) and the other factor was the season of observation (spring and autumn). The analysis showed a high fidelity of *C. laurentii, S. roseus*, and *R. minuta* to plant substrates: the abundance rate of the first two yeast species on plants was 60–90%, and that of the third species was 20–40%, whereas the abundance rate of these species in soils and litters was no more than 5%.

The rare species *Bullera armeniaca* and *C. heveanensis* and the psychrophilic species *Leucosporidium scottii* were detected only on plant substrates. The yeast-like fungi *Trichosporon pullulans* and *T. cutaneum* were isolated from half of the litter samples examined, whereas they were rarely detected in soils and never on plants.

The effect of the season of observation on the taxonomic composition of soil yeasts was found to be insignificant.

The yeasts isolated from the spruce forest plants and soils contained a large proportion of colorless species of the genus *Rhodotorula* (*R. fujisanensis, R. bogoriensis*, and *R. foliorum*). Frequent isolates were also imperfect parasitic fungi of the order *Taphrinales*, which were classified into the anamorphic genus *Lalaria* [24] and anamorphic fungi of the genus *Tremella*.

A more detailed study of the yeast communities of the white podzolic soil and burozem [26] showed that, irrespective of the season of collection, all the samples of these two soils contained yeast cells in amounts from tens to hundreds of thousands of CFU/g substrate (the yeast population of burozem was higher than that of white podzolic soil). The litter strata of these soils contained much greater numbers of yeast cells than proper soil horizons.

The yeast communities of the litter strata of these soils were similar in dominant species but differed in minor species. The dominant litter species was *Cryptococcus albidus*, which amounted to 63.6% of the total number of yeast species in burozem and 70.2% of yeast species in white podzolic soil. The minor species of burozem were represented by *Debaryomyces hansenii, R. fragaria, R. hylophila, R. toruloides*, and *R. mucilaginosa*. In the white podzolic soil, the minor species were *C. curiosus, R. auriculariae, R. toruloides*, and *R. mucilaginosa*. Proper soil horizons were inhabited by a single yeast species *Lipomyces starkeyi* (in all seasons, the burozem was more inhabited by this species than white podzolic soil [26]).

Thus, an analysis of the vertical distribution and taxonomic composition of yeasts in the spruce forest soils allowed the following inferences to be made: (1) yeasts are concentrated in the litter strata, (2) yeast species show a high fidelity to particular substrates, and (3) forest soil yeasts are dominated by imperfect basidiomycetes of the genera *Cryptococcus* and *Rhodotorula*. Some of the yeast species isolated (*C. albidus, C. laurentii, R. minuta*, and *S. roseus*) are frequently encountered not only in forests but also in other types of ecosystems, whereas *C. podzolicus* is a specific yeast species of forest biogeocenoses.

The yeast communities of the spruce forest ecosystems have the following specific features:

(1) the yeast population of the green and dead overground parts of plants is low;

(2) the yeast communities of spruce forests contain a considerable proportion of the ascomycetes *Candida–Pichia*, some of which are known as the associants of the xylophagous beetles of spruce forests;

(3) these yeast communities also contain a great number of colorless species of the genus *Rhodotorula* (*R. fujisanensis, R. bogoriensis*, and *R. foliorum*);

(4) frequently encountered species in these biogeocenoses are imperfect parasitic fungi of the order *Taphrinales.*

Contrasting spruce forest soils exhibited no distinct differences in the yeast population density and species composition, except that the soil yeast population of the nemoral spruce forest was somewhat higher than the yeast population of the other soils studied and that their litter strata slightly differed in the composition of minor yeast species.

Some assumptions can be made concerning the role of soil yeasts. For instance, epiphitic yeasts can act as detritivores, consuming the organic substances of dead leaves. Some researchers reported a high oxidative activity of phyllosphere yeasts, which reduces the partial pressure of oxygen in the intercellular space and promotes the nitrogen-fixing activity of bacteria [12]. Phyllosphere yeasts can also affect the activity of diazotrophic bacteria, which utilize the polysaccharides excreted by yeast cells [30]. Yeasts in the litter strata may contribute to the degradation of tree waste, especially during cold and wet periods, when the competition pressure of other microorganisms of the biota is low. Due to their high content in the litters, yeasts may serve as food for numerous soil microscopic invertebrates. As for the forest soil lipomycetes, they may represent an important trophic element in the nutrition of soil invertebrates and, on the other hand, may form associations with the main degraders of organic matter, i.e., fast-growing mycelial fungi. The ability of lipomycetes to synthesize and excrete polysaccharides suggests that they play a role in the formation of the water-resistant soil texture [12].

CONCLUSION

The comprehensive microbiological investigation of the CSFBR soils showed that the populations of fungi and actinomycetes in these soils make up hundreds of thousands of CFU/g substrate and that their bacterial population comprises tens of millions of CFU/g. The microbial diversity of these soils was studied using various ecological indices characterizing the taxonomic composition of soil communities and by creating laboratory culture collections that included representatives of the main groups of microorganisms. Tens of yeast and bacterial species and hundreds of fungal species that were isolated from soil samples demonstrate high species diversity of the microbial complexes of the reserve soils.

Novel methodological approaches developed by us [31] made it possible to characterize the microbial complexes of taiga forest soils and to determine the specific features of their structure and role in particular soils during different seasonal periods.

Of much interest are the data showing that the composition of soil microbial complexes is governed by the soil moisture content and the amount of tree wastes. Both the population density and the diversity of different groups of microorganisms in the soils were higher during wet periods. The moisture content of soils also determined the bacterial distribution pattern over soil horizons, which was continuous during wet periods and discrete during dry periods. The proportion between fast- and slow-growing fungi, which was high in the spring and autumn and low in the summer, also depended on the soil moisture content. The high diversity of micromycetes observed in autumn was related to the formation of new tree waste during this seasonal period.

The adaptation of microorganisms to wet environmental conditions typical of the majority of CSFBR soils can be exemplified by the prevalence in bacterial soil complexes of motile proteobacteria (typical hydrobionts), which were dominated by facultatively anaerobic species adapted to low concentrations of dissolved oxygen and by microaerophilic actinomycetes with hydrophilic spores concentrating in wet litters resembling mors in many properties. The proportion of such bacterial forms increases in highly wet habitats, so that the content of "aquatic" prokaryotes is maximum in bog ecosystems [32].

Differences in the diversity and composition of the microbial complexes of the CSFBR soils were mainly due to the different hydrothermal conditions of these soils, determined, in turn, by their relief features. Comparing the mesomorphically contrasting soils (burozem and white podzolic soil) showed that the microbial diversity of burozem was considerably higher than that of white podzolic soil, which has worse water–air conditions than burozem. The type of phytocenosis and hence the quality of tree waste, as well as the soil acidity, can also affect the taxonomic composition of soil microbial complexes. In soddy gleysolic soils, which are formed below areas covered with herbaceous and deciduous plants and have a neutral reaction, dominant bacteria are hydrolytics. At the same time, hydrolytic bacteria in podzolic and peat soils are scarce, while fungi are the main degraders of polymers in these habitats. In spite of the fact that fungi dominate in acidic soils, their species diversity is higher in less acidic soils with an elevated content of organic matter. Some bacterial genera, such as *Arthrobacter* and *Azotobacter*, can be considered as indicators of high soil acidity, since they are frequent in soddy gleysolic soil and burozem but are not detected in acidic podzolic and peat soils.

On the other hand, the yeast-like fungus *C. podzolicus* inhabits only podzolic soils and, hence, can be an indicator of the formation of such soils.

The ecological role of soil microorganisms is diverse. Thus, the main ecological function of soil fungi is the degradation of plant residues. Due to their powerful hydrolytic enzymatic apparatus, soil fungi can hydrolyze a wide range of polymeric compounds and are active at all of the stages of degradation of plant residues. On the other hand, yeast-like fungi are active only at the early stages of this degradation, utilizing simple water-soluble compounds. For this reason, they are typical inhabitants of plants and the upper layers of litters.

Along with fungi, different ecologotrophic groups of soil bacteria, whose taxonomic composition was described above, are also involved in the degradation of plant residues. Furthermore, they contribute to the conversion of chemical compounds containing iron, manganese, aluminum, and other chemical elements that are present in soils. Bacterial species involved in the oxidation of iron and manganese were described above. It should be noted that slime bacteria (myxobacteria, spirillas, and others), which are dominant in wet soils, as well as polysaccharide-excreting lipomycetes, may be involved in the formation of soil texture.

The ecological role of soil microorganisms should be considered with allowance for their relationship with other soil inhabitants. As mentioned above, some soil bacteria can lyse other soil bacteria and yeasts; on the other hand, all soil microorganisms (fungi, bacteria, and yeasts) can serve as food for soil invertebrates. These factors regulate the density of soil microbial populations and affect the degradation rate of organic matter. As shown in laboratory experiments, the degradation rate of organic matter decreased with increasing the number of micromycete species introduced into soil, evidently due to species competition. On the other hand, the species diversity of micromycetes highly correlates with the rate of mineralization of plant residues in the fermentation layer of litters. These results show that the relationship between various ecological indices characterizing the microbial diversity of soils and the rate of various processes occurring there is complex and ambiguous.

The high abundance and diversity of soil microorganisms suggests that they can duplicate each other when performing particular ecological functions under varying environmental conditions.

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