

REVIEW

Xylotrophic and Mycophilic Bacteria in Formation of Dystrophic Waters

G. A. Zavarzin^a and A. G. Zavarzina^{b, 1}

^aWinogradsky Institute of Microbiology, Russian Academy of Sciences,
pr. 60-letiya Oktyabrya 7, k. 2, Moscow, 117312 Russia

^bFaculty of Soil Science, Moscow State University, Moscow, 119992 Russia

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Abstract—The microbial communities developing in ultrafresh stagnant water originating from rainfall comprise the group of ombrophiles. The microorganisms of the myco–bacterial community developing on coarse woody debris are involved in formation of humus-enriched dystrophic waters in the watersheds of forested wetlands. Oligotrophic acidophilic dissotrophs participate in the transformation of organic matter in such waters. The scheme of trophic interactions in the microbial community is proposed.

Key words: ultrafresh waters; dystrophic waters, xylotrophs, myco–bacterial community, ombrophiles, dissotrophs.

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Acidic ultrafresh waters with a low primary production and high content of recalcitrant organic matter comprise a significant part of the water flow drained to the rivers of the northern part of European Russia. Such waters are designated as dystrophic (Table 1). These humus-enriched, ultrafresh waters are common on lowland plains, mainly in forest–wetland ecosystems. Their formation results from excessive supply of rainwater with low mineral content and from terrestrial destruction of the dead plant biomass.

The goal of this review is to present an overall picture of involvement of the microbiota in the formation of dystrophic waters and to develop a conceptual scheme of trophic interactions within the microbial community. The abundance of available information from various fields of knowledge prevents the detailed description of all the stages of the process. The review is therefore limited to the generalizations dealing mostly with the territory of Russia.

FORMATION OF DYSTROPHIC WATERS: SCALE OF THE PROCESS

The humid climate of the boreal zone implies a significant supply of rain water during the vegetation period and predominance of precipitation over transpiration, so the washing out water regime is developed. Rainwater has a conductivity of tens μS ; these values correspond to tens to hundreds mg/l of mineral compounds [1]. The microorganisms developing under conditions of an abundant supply of low-mineral, ultrafresh

water are designated as ombrophiles (from the Greek ομβροζ, rain, cloudburst) [2]. They do not depend on soil water and have an advantage in autonomic landscapes with ombrotrophic (hydrol.) nutrition. Ombrophilic communities are typical for lowland plains and comprise a necessary component of the continental orographic profile. The cold climate of the boreal zone suggests that the microbiota should consist of the psychrophilic or psychrotolerant organisms, i.e., those developing at $\sim 15^\circ\text{C}$. An accidental increase in temperature to 30°C means a heat shock for most of them, while low temperature and frosts are within the physiological reaction norm.

In the north of the Russian Plain, the watershed basin consists of lakes, ombrotrophic bogs, and forested wetlands (Fig. 1). Ombrotrophic *Sphagnum* bogs play a significant role in the initial drainage formation as sort of “water tanks” with specific acidophilic microbiota [3–6]. This microbiota includes many unknown and difficult-to-isolate microorganisms, members of such poorly studied phylogenetic groups as the *Acidobacteria*, *Verru-*

Table 1. C_{org} content and trophicity of water bodies [18]

Trophicity	Net primary production, $\text{g } C_{\text{org}}/\text{m}^2/\text{day}$	Dissolved organic carbon, $\text{g } C_{\text{org}}/\text{m}^3$
Dystrophic	<1	>10
Oligotrophic	<1	0.5–3
Meso- and eutrophic	1–4	5–10
Hypereutrophic	4–6	>10

¹ Corresponding author; e-mail: zavarzin@inmi.host.ru

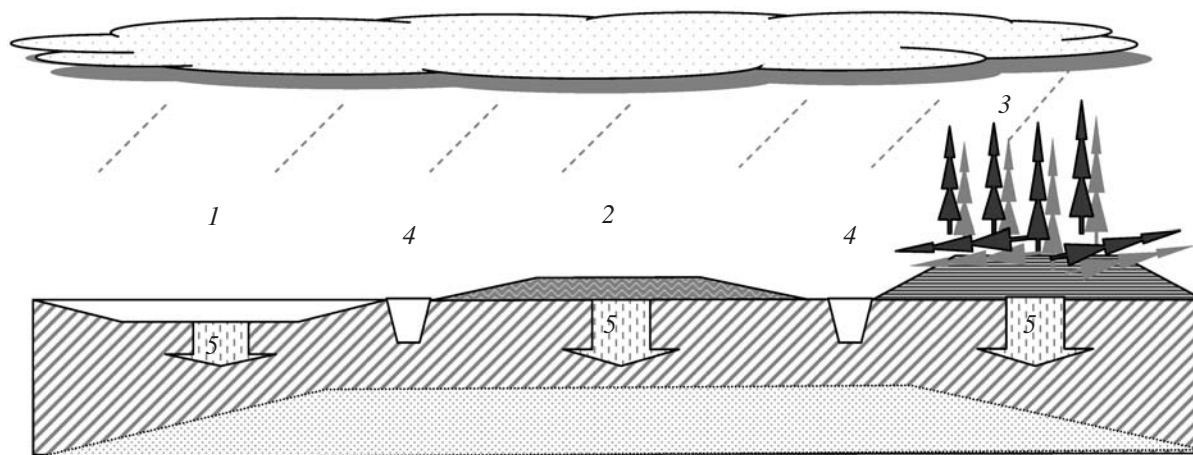


Fig. 1. Schematic representation of the major biocenoses of a lowland plain in the boreal zone of humid climate at the site of watershed area and development of ombrophilic communities. Lakes and meadows (1), *Sphagnum* bogs (2), forested wetlands (forest-wetland watershed area) (3), water flows (4), vertical water percolation resulting in ground water formation (5).

comicrobia, *Planctomycetes*, etc.; over 50% of them are not identified by the presently known molecular probes [7]. Decomposition of the *Sphagnum* mosses results in formation of acidic fulvate-type dystrophic waters [8]. Our estimation of the water volume for bogs and wetlands of Russia gives 740 km³ for the acrotelm (the aerobic upper layer of a peat bog) and 4000 km³ for the catotelm (anaerobic peat layer underlying the acrotelm). For calculations of the acrotelm's water volume, we assumed that the acrotelm layer is 20 cm thick, peat thickness is >10 cm, and peatland area is about 3700 km². For the catotelm's water calculation, the average peat's layer depth of 1.72 m was taken (peatland areas and depths were as estimated by [9]).

Unlike ombrotrophic bogs with *Sphagnum* as the major source of dead organic matter, the hydrochemistry of dystrophic waters in forest-wetland catchment areas depends mostly on destruction of lignified woody vegetation. Wood decomposition is one of the most large-scale processes of carbon turnover in the boreal zone. The estimated volume of wood in Russian forests is about 70×10^9 m³ at the average apparent density of 0.4 t/m³. Wood constitutes 50 to 60% of the tree mass. The minimal estimated forest growth in Russia (as stem wood) is 240 Mt C_{org}/year [10]. In forest ecosystems, one should differentiate between litter fall (leaves, conifer needles, and small branches on the topsoil), which form forest litter and coarse woody debris (large-size stem wood and stumps). Woody debris is usually subdivided into the following groups [10]: (1) *dead trees*, with the roots anchored to the soil – they remain standing for 20–30 years; (2) *dead fallen trees*, trees and semi-decomposed trunks on the surface, resulting from windbreak and forming windows in the forest canopy where young growth occurs (most typical of spruce); in Middle Russia, large-size deadfallen trunks take over 30 years to

decompose; (3) *attached debris* of dead branches coming to the litter; and (4) *underground tree debris* (stumps and root residues). Woody debris is characteristic of climacteric forests; in the boreal zone, it comprises usually 20–60 t/ha, sometimes up to 200–300 t/ha; the annual input is 0.8–4 t/ha. According to Zamolodchikov [10], the annual C_{org} input as woody debris on forested territories of Russia is 254.87 Mt C_{org}. The estimated woody debris reserves are 5530.95 Mt C_{org}. The woody debris (11062×10^6 m³ over the area of 733.15×10^6 ha) provides local habitats for the microbiota. Leaf debris is the source of organic compounds for the microbial community colonizing the forest litter [11, 12]. Organic matter is supplied from the leaf mortmass and its transformation depends significantly on the hydrothermal conditions and is expressed as the ratio between C_{org} of the litter fall and C_{org} of the litter, and this ratio decreases from north to south. In cold environments (e.g., in the tundra), organic matter remains in the solid phase despite the low primary production; in southern regions, the decomposition potential may exceed the annual supply [13]. Unlike the heterogeneous forest litter, coarse woody debris is a more homogeneous system with lignocellulose as the microbial substrate. Wood decomposition is carried out mostly by fungi during a solid-state fermentation process [14]. Therefore, wood degradation processes have been traditionally of prior interest to mycologists, [15–17], rather than to bacteriologists. The estimated CO₂ emission for Russia resulting from fungal decomposition of the woody debris is 214.26 Mt C/year [10]. Apart from CO₂, humic compounds are the by-products of decomposition. The estimated reserves of humus in forest soils are 100×10^9 t C_{org} [10, 18].

In a cold humid climate, some of the decomposition products are washed out as “brown waters” and enter soil, lakes, and rivers [19, 20]. Aquatic humic sub-

stances play a key role in the C_{org} cycle, being the mobile form of C_{org} [21, 22]. C_{org} removal usually varies from 10 to 100 kg/ha/year with the average value of 56 kg/ha/year. Since xylotrophic fungi remain in the aerated solid phase and the biofilms of micromycetes colonize the surface of submerged wood, a specific bacterial microbiota develops in humus-enriched, often acidic waters [4]. Thus, decomposition of organic matter dissolved in dystrophic waters results mostly from the activity of bacteria, represented by planktonic forms in stagnant water and by biofilms (sometimes containing fungi) in the water flows, [23]. Transport of organic matter from the surface and soil waters into the water flows is controlled by the ecotone barrier represented by lowland swamps and fens in river valleys, where particulate organic matter is precipitated and transformed in the course of microbial aerobic–anaerobic interactions, with the swamp vegetation acting as an additional source of autochthonous organic matter.

Transport of dystrophic waters from the forest–wetlands landscapes into the water flows results in removal of organic carbon. In northern European Russia, the run-off is directed mainly to the Arctic seas. The catchment area of the north-flowing rivers is 12572 km², and the flow volume is 2790 km³/year. The seas of the Arctic Ocean, where 80% of the flow is delivered, act as a sedimentation trap; the sediments are mainly accumulated in the “marginal filter” where river water enters the sea [21, 22]. The annual flow to the Russian Arctic seas is 23.45×10^6 t or 23×10^{12} g C_{org} , i.e., 5% of the world flow to the ocean. The quantitative estimation of C_{org} carry-over by river waters was made considering the catchment area of each of the Arctic seas. Approximately half of it (12.35×10^6 t C_{org}) flows to the Kara Sea (with Ob’ and Yenisei responsible for 75%), while the rivers of European Russia bring 4.8×10^6 t (with Pechora and Northern Dvina responsible for 60%). In the river flow, the soluble form of C_{org} constitutes 86–98%. The estimated underground flow is 0.28×10^{12} g C_{org} [21, 22].

Microbial decomposition of wood debris is a large-scale process; for many ecosystems, it should be considered among the most important in the balance of organic carbon. A clear understanding of the microbiological mechanism of the process is therefore required.

MICROBIAL DECOMPOSITION OF WOOD IN THE COURSE OF FORMATION OF DYSTROPHIC WATERS

Since the 19th century, microbial decomposition of plant debris has remained a traditional field of general microbiology and botany. In this paper, we will consider only bacteriology-related issues. A forest may be described as a myco-arboreal system which can be integrated up to the consortium level. Wood decomposition is controlled by humidity, temperature, pH, availability of oxygen, N and P content in water, and the quality of the arriving plant material [16, 24]. The quality implies

both the chemical composition and the mechanical availability; large-size woody debris is less bioavailable and is preserved longer than the rapidly metabolized leaf litter. Moreover, the structural and spatial characteristics of the process are highly important and should also be considered. Fungi spread along the wood layers, using the xylem as guides for hyphal growth [14]. Location of deadfallen wood in a landscape is also important, since it determines the water regime of destruction. The wetted trunks and those in dry locations (e.g., tree trunks broken by windfall and suspended on the stumps) decompose differently. The overall picture is therefore highly heterogeneous.

Microbial processes of wood decomposition in the forest-wetland ecosystems fall into three blocks (Fig. 2):

1. Decomposition of moist wood by xylotrophic fungi (soft-, white-, and brown rot);
2. Decomposition of the mycelium of xylotrophic fungi by the mycotrophic fungi and bacteria;
3. Bacterial transformation of organic matter in dystrophic waters.

While the first two processes are in fact different variants of solid-phase fermentation involving mycelial hydrolytic organisms in the mycosphere, transformation of C_{org} in dystrophic waters is carried out by bacteria.

Xylotrophic fungi and decomposition of wood

Wood decomposition by fungi has been thoroughly studied in the last 3 decades and was described in a number of relevant reviews [14, 17, 25, 26]. Wood decomposition under natural conditions is a solid-state fermentation process with the available surface being a limiting factor for microbiota. Competition for the surface is determined by mycelial growth and the genetically determined mechanism preventing overlapping of colonies [27]. Development of a fungal biofilm forming *xylostroma*, requires sufficient humidity with the possibility of aeration. Such conditions exist in water films and capillary water. Since the moisture supply on the surface of dead wood is associated with rains, this fungal group belongs to ombrophiles. In this respect, they differ from the saprotrophic fungi of the forest litter and from the microorganisms depending on soil water.

The elementary composition of wood differs significantly from the standard Redfield ratio for planktonic algae: $C_{org} : N_{org} : P_{org} = 110 : 16 : 1$. In wood, this ratio is close to (~ 500) : 16 : 1 [28]; due to excessive content of organic carbon, the destruction pathways and microbial groups involved differ considerably from those of aquatic ecosystems. Wood consists of biopolymers (cellulose, hemicellulose, pectin, and protein) submerged into a lignin matrix; their content in the major forest trees varies (Table 2) [14]. The cellulose : hemicellulose : lignin ratio of 50 : 25 : 25 may be accepted as an approximate estimate. For each biopolymer, a specific group of microbial destructors should exist.

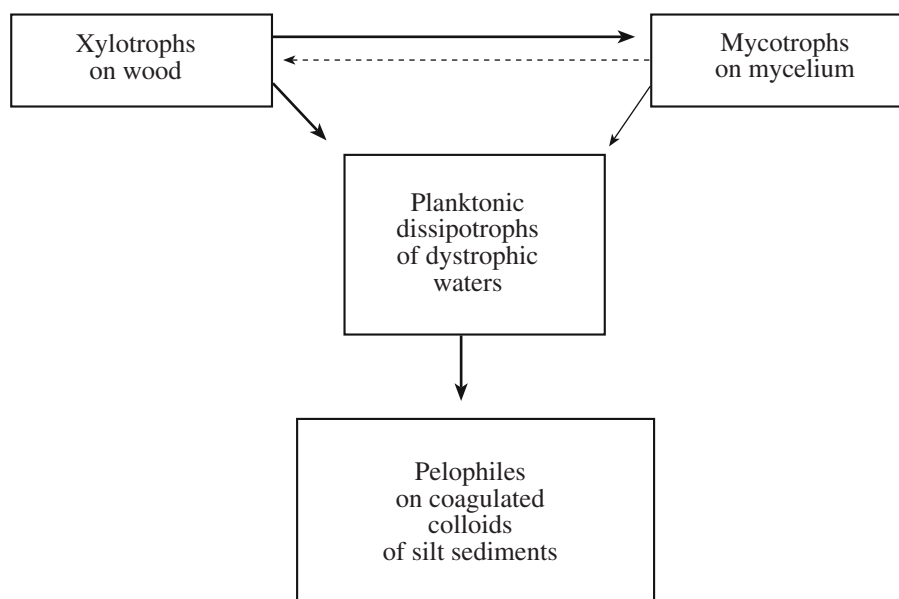


Fig. 2. Schematic representation of the interaction between microbial groups in the course of wood decomposition.

Abundance of food substrates results in a broad variety of xylotrophic fungi (many hundreds of species). Apart from the characteristics of the substrate, a fungal group may gain advantage due to massive inoculation, which ensures predomination of a certain fungal species under highly competitive conditions. Thus, high species diversity exists in fungal biofilms, with the tendencies to the preferential development of a specific group under specific conditions.

Decomposition of cellulose and hemicellulose is carried out mostly by soft rot and brown rot fungi. The first group includes predominantly ascomycetes and deuteromycetes, the second group includes mainly basidiomycetes. These organisms produce hydrolases (endo- and exocellulases, hemicellulases, glycanases and glycosidases, and esterases), which decompose the structural polysaccharides of the cell wall (cellulose), and oxidoreductases, which attack the carbohydrate components (glucose oxidases, galactose oxidases, and cellobiose dehydrogenases). Hemicelluloses are relatively easily decomposable compounds; such hydrolases as xylanase and pectinase are required for their utilization [14]. Hemicellulose is responsible for 25% of the wood mass; it acts as a source of soluble polysac-

charides. Soft and brown rot decay results mainly in selective decomposition of amorphous polysaccharides and cellulose, while lignin is only partially modified. Effective lignin decomposition to CO_2 and soluble low molecular weight products is carried out only by the white rot basidiomycetes. This group of fungi produces extracellular lignolytic oxidoreductases (lignin peroxidase, Mn-dependent peroxidase and laccase) which catalyze oxidative destruction of lignin by a free-radical mechanism [14, 29, 30].

Among xylotrophic fungi, a characteristic succession occurs, with a preceding group of organisms preparing the medium for the subsequent ones, [4, 14, 31]. Rapidly growing micromycetes (soft-rot fungi) are the primary colonizers of outer layers of moist wood. They utilize easily available compounds (sugars), cellulose, and hemicellulose and leave the lignin component of the cell walls almost intact (representatives include members of the genera *Aspergillus*, *Trichoderma*, and *Cladosporium*). After 1–1.5 years when easily available substrates on the wood surface are consumed, the white- and brown rot basidiomycetes become predominant. They are capable of utilizing the structural components of wood including those in the middle lamella.

Table 2. Ratio of biopolymers in wood, % [3]

Species	Cellulose	Hemicelluloses	Lignin
<i>Picea abies</i>	40.4–46	31.1–23.6	27.3–28.2
<i>Pinus silvestris</i>	45.5	25.6	26.8
<i>Betula</i> spp.	45.3–48.5	25.1–25.3	19.4–23.1
<i>Populus tremula</i>	49.4	21.2	18.1
<i>Quercus</i> spp.	37.6–40.5	16.3–26.7	22.7–25.7

Among the imperfect fungi accompanying basidiomycetes, numerous *Penicillium* species occur. At this stage, many micromycetes belong to transient species which are active in submerged aquatic environments as well [23]. Yeasts may be possibly involved in destruction of such lignin derivatives as veratryl alcohol [32]. This stage continues for up to 10 years. Saprophytic fungi from the forest litter and soil microbiota carry out the final stage of the process by humification of decomposed wood. Their activity may last for up to 50 years. Soil humus is formed as a result.

The humic substances (HS) resistant to microbial decay are the major by-products of oxidative transformation and hydrolysis of wood by the xylotrophic myco-bacterial community. The HS are described as dark-colored N-containing macromolecular polydisperse compounds of irregular structure and varying composition. HS are operationally divided into low-molecular weight fulvic acids soluble at all pH values (FA, molecular weight 0.3–5 kDa) and high molecular weight humic acids (HA, molecular weight 5–100 kDa), which coagulate at pH below 2 [33, 34]. Humic substances are formed by spontaneous condensation of phenolic compounds (either monomeric or polymeric) with amino acids, proteins, carbohydrates, polysaccharides, etc. [33]. In terrestrial forest ecosystems, modified lignin and the products of its breakdown serve as important source of HS precursors. Synthesis of HS occurs in the mycosphere and is catalyzed by extracellular fungal phenol oxidases, e.g., laccase, as was demonstrated already in early works [35]. Apart from phenol oxidases, the presence of a solid matrix is important for synthesis of high-molecular weight condensation products [36]. Abiotic formation of HS is also possible. Typical examples include: (i) brown-rotted wood when polymeric lignin is slightly modified by OH radicals from the Fenton reaction ($\text{Fe}^{2+} + \text{H}_2\text{O}_2 + \text{H}^+ \rightarrow \text{Fe}^{3+} + \cdot\text{OH} + \text{H}_2\text{O}$)- high molecular weight HA are formed as a product [37, 38]; (ii) abiotic oxidation of soluble phenolic compounds by inorganic soil constituents, containing transition metals such as Fe (III) or Mn(IV). FA- and HA- like products with low molecular weight (up to 10 kDa) are formed as a result [39].

The mycophilic microorganisms and decomposition of the mycelium of xylotrophic fungi

Xylotrophic fungi produce low-molecular products during hydrolysis of wood by extracellular hydrolases and oxidases [14, 40]. Oxalic and citric acids are among the characteristic products of fungal metabolism. Binding of oxalates with metals, e.g., calcium, sometimes results in formation of a mineral film covering the mycelium. Within the xylostroma biofilm, these insoluble derivatives of the metabolic products may be used as a nutrient substrate by bacteria and fungi. A fungal biofilm contains proprietary carbohydrate mucus, which acts as both a habitat and a nutrient source for bacteria. Dead mycelium with chitin (a characteristic

component of the fungal cell wall) and fungal mucus act as a secondary source of C_{org} in the system [41–43]. These substrates provide nutrients for the fungal xylophilic biofilm (xylostroma), which forms a relatively complete trophic system in the mycosphere. The community includes a series of fungi; its trophic structure includes the fungi utilizing the products of hydrolytic fungi in a metatrophic chain, mycophilic fungi (fungi developing on mycelia of other fungi [42]), and polyphagous fungi with a broad substrate spectrum, such as *Trichoderma* spp. [44].

A bacterial biofilm may also develop on wood. Bacteria utilize available extractive substances rather than relying on the activity of hydrolytic fungi [43]. Bacteria occupy a subordinate position in the fungal biofilm and several limitations exist for them. They should be resistant to the fungal hydrolytic enzymes, to the oxidative stress resulting from the fungal oxidases (which produce reactive oxygen species in the course of lignin decomposition), and to various fungal antibiotics. While the specific effect of antibiotics on bacteria is well known, the unspecific effect of the oxidative stress is poorly understood [29]. All these factors create a highly selective environment for the mycophilic bacterial grouping, and its numbers on a wood surface decrease by three orders of magnitude in the presence of fungi [45]. Existence of bacterial groups should be expected which conform to a certain dominant fungus and its selective action.

Group factors also exist, suggesting certain common characteristics of mycophilic bacteria. Since fungi actively consume oxygen, oxygen deficiency created below the mycelial biofilm limits its further development. In moist wood, rapid oxygen consumption by fungi results in local anaerobic conditions, and thus, in development of anaerobic bacteria up to methane emission from the cores of rotten trunks. Microorganisms utilizing the products of fungal metabolism, primarily organic acids, belong to the typical trophic sequence of product utilization (metatrophic). Organic acids (products of metabolism of xylotrophic fungi) and the products of lignin destruction and transformation create acidic conditions with $\text{pH} < 5$ [46]. The mycophilic microbiota should therefore be acidophilic with optimal growth below pH 5 or at least acid-tolerant. The high $\text{C}_{\text{org}} : \text{N}_{\text{org}}$ ratio is another characteristic feature of the trophic conditions. Nitrogen-fixing bacteria (e.g., *Azospirillum*, *Beijerinckia*, and *Xanthobacter*) should therefore play an important functional role in the xylotrophic biofilm under the conditions of carbon excess and nitrogen limitation.

The mycophilic myco-bacterial community grows along the fungal biofilm (fungal lawn), with the fungal mycelium rather than wood, acting as the initial substrate. It includes the mycophilic fungi, streptomycetes, and bacteria capable of lysing live and dead mycelium [42, 43, 45, 47]. The living mycelium is attacked by mycophagous organisms, while the dead mycelium is

attacked by mycotrophic ones. Fungal mycophagy implies growth of the predatory fungus relative to its host, mycelial winding, secretion of cell-lysing enzymes, penetration into the host cells, and destruction of the cell content [42]. *Trichoderma* is an example of mycophagous fungi, especially interesting due to its universal ability to suppress growth of other fungi and to produce the antibiotic trichodermin [44]. Actinomycetes with chitinases capable of hydrolyzing the fungal cell wall also develop on live and dead hyphae. The role of actinomycetes in the regulation of the density of fungal populations is especially prominent in acidic litter [11]. Among the bacteria colonizing the mycelial surface, members of the genera *Pseudomonas*, *Bacillus*, *Streptomyces*, *Burkholderia*, and *Paenibacillus* were reported. *Pseudomonas fluorescens*, *Achromobacter denitrificans*, *Proteus vulgaris*, *Bacillus mesentericus*, and *B. cereus*, common and numerous organisms isolated on conventional media have been assigned to mycolytic bacteria. The interaction between bacteria and fungi has long been known, especially in the case of pathogens of cultured mushrooms. For example, *Janthinobacterium agaricidoaminosum* attacks the cultured mushroom *Agaricus bisporus* [47]; such examples are rather numerous. Among the mycophagous bacteria an inhabitant of acidic sandy soils, *Collimonas*, attracted attention recently [45]. Myxobacteria also belong to mycophages; however, they have not been studied in detail, although attack of mycelium by myxobacteria has been known since the 1930s. Mycolytic bacteria produce chitinases, glucanases, and proteases degrading the fungal cell wall. Acetylglucosamine and its derivatives are the final products of chitin hydrolysis.

Transformation of organic matter in dystrophic waters and dissipotrophic bacteria

The microbial community developing in dystrophic waters belongs to dissipotrophs [49, 50]. At low levels of primary production, dissolved organic matter (DOM) of terrestrial origin is an important substrate for dissipotrophic bacteria [51]. In the forest-wetland landscapes of the boreal zone, DOM is generated to a significant extent by the xylophagous and xylophilic myco-bacterial communities. Under the washing-out conditions, the products of destruction and transformation of litter and woody debris together with the products of microbial metabolism, are leached to the soil solution and to the flows of the drainage water. DOM may include the carbohydrates from cellulose and products of lignocellulose hydrolysis (soft rot and brown rot decay), low-molecular weight phenolic derivatives of lignin decomposition (white rot decay), and aliphatic organic acids (products of fungal metabolism). Soluble fractions of humic substances can be also eluted into the liquid phase during rainfall.

The molecular masses of the organic compounds of dystrophic waters vary from 1 to 10 kDa [20]. The geo-

biophysical factors of transition from stagnant bog water to flowing river waters are of utmost importance for DOM destruction. The filtration rate with the threshold value of 0.2 cm/h is a determining factor. Bacteria of the water flows utilize primarily the organic compounds with molecular masses below 100 Da [52–54]. Compounds with the masses of 10 kDa and more are degraded at a significantly slower rate [19, 55–57]. Rapid microbial utilization of the low-molecular weight bioavailable compounds (carbohydrates, amino acids, etc.) results in DOM enrichment with the slowly degradable compounds (lignin aromatics, phenolic compounds, and HS) and an increase of the DOM average molecular mass [58]. Labile compounds constitute therefore about 20% of dissolved organic carbon in dystrophic waters [59], while the major part of DOM (60–90%) is represented by HS, which are responsible for the characteristic water color (up to brown) [20]. Humic substances are resistant to microbial degradation, although their bioavailability may be increased due to photochemical oxidation [60, 61]. Enrichment of DOM with resistant fractions may be affected by in situ synthesis of HS and microbial polysaccharides of slime [58]. However, considering the low primary production of dystrophic waters, autochthonous formation of HS from the products of metabolism and destruction of aquatic organisms should be of minor importance. Condensation of HS from autochthonous precursors may be significant in stagnant swamp waters where the conditions develop for accumulation and concentration of organic matter. Thus, the hydrochemistry of flowing dystrophic waters with C_{org} concentration up to 100 mg/l is most probably determined by the autochthonous HS synthesized in the mycosphere and leached out by rainwater. Under solid-state fermentation conditions in wood, the concentrations of both the precursors of HS and the fungal phenol oxidases are higher than in the aqueous phase; the polymerization process is therefore thermodynamically favorable.

Humic substances leave the “water humus” category after their coagulation caused by the loss of surface charge. After coagulation as organo-mineral compounds, very often ferric, HS are carried with the water flow to sedimentation basins (lakes). There they can form bottom deposits—mud, enriched with both allochthonous and autochthonous organic matter. The pelophilic microbiota develops on the mud surface [63]. Filamentous bacteria, with trichomes capable of gliding on the mud surface, constitute its significant part. Among the morphologically peculiar pelophiles described by Perfil’ev and other microscopists [62–65], very few have been cultured.

Decomposition of DOM by a microbial community is an indication of its adaptation to the type of inflowing organic matter and of the specificity of the microbial population [56]. Bacterial numbers in dystrophic waters are not high and are close to bacterial numbers in oligotrophic water bodies (up to 10^7 cells/ml). Microorganisms should have adaptations for ultrafresh condi-

tions of dystrophic waters, and such adaptation implies sensitivity to osmotic stress caused by casual increase in the concentrations of dissolved mineral compounds. In this respect, inhabitants of ultrafresh ombrotrophic waters differ from the organisms of soil solutions, where osmotic characteristics may vary significantly depending on drought or precipitation. Soil organisms should be adapted to drying, and thus, retain viability at increased concentrations of salts. Unlike the mycophilic inhabitants of fungal biofilms, microbial communities of diluted dystrophic waters are not immediately affected by fungi; resistance to antibiotics, for example, is not so essential for them. However, while the factors of direct fungal influence on bacteria are absent in dystrophic waters, the effect of the hydrochemical environment they create remains significant. Ultrafresh waters have a low buffer capacity; therefore, pH of the medium may vary. When organic acids (e.g. oxalate and citrate) produced by the xylotrophic fungi in the course of wood decomposition are washed out, it results in acidification of the medium. The dissimilators of dystrophic waters should therefore be acidophilic or acidotolerant and capable of growth within a wide range of low pH values. In this respect, the bacterial community of the xylophilic group in dystrophic waters differs largely from the inhabitants of *Sphagnum* bogs which leave under conditions of constant acidic pH: *Sphagnum* mosses act as solid buffers due to the ion-exchange characteristics of their surface. Nevertheless, the bacterial community of dystrophic waters shares many properties with the inhabitants of *Sphagnum* bogs which are an important source of lignin-depleted fulvate waters in the region. Apart from low-molecular weight organic acids, the xylotrophic group also generates HS. In spite of their resistance to microbial attack, humic substances are a considerable ecophysiological factor, which creates a selective environment for bacteria inhabiting dystrophic waters [66]. The factors determining the effect of HS on the microbiota are believed to be the following: high concentration in dissolved organic matter; catalytic activity due to quinones and other electron-carriers; formation of complexes with metal ions and interaction with minerals; selective sorption; formation of colloidal micelles; and formation of phenolic compounds and radicals in the course of photochemical oxidation [14, 20, 67, 68]. The quinones of HS are a stress factor for aquatic organisms, and they affect cyanobacteria to a greater degree than algae. A more specific effect was recently reported, which was related to the role of humic acids in the metabolism of iron-reducing bacteria as electron shuttles in the course of reduction of iron oxides [69, 70]. Since interaction with iron hydroxide is an important factor removing humic acids from the water, coupling of the iron cycle with the fate of humic acids is especially important for dystrophic waters [71–74].

Since ombrophilic microorganisms are exposed to such ecological factors as osmotic conditions of ultrafresh water, acidic pH, high content of HS, a spe-

cific set of substrates, and effect of fungal antibiotics, they might have been assigned to extremophilic microorganisms, as opposed, for example, to soil organisms. However, the ecosystem of the scale ubiquitous to the lowland plains can not be classified as unique or extreme. On the contrary, this is the most typical forest-wetland ecosystem of the humid boreal zone. In spite of all the stress factors, this community probably includes widespread and banal forms. This community may be expected to act as a natural reservoir for well-known cultivated microorganisms. In any case, this is true for the fungal component of the community, since the fungal species are numerous, widespread, and well known [5]. Aerobic organotrophs, moderate acidophiles, oligotrophs, psychrophiles, or psychroactive bacteria should be present; these are usually slow-growing inhabitants of climacteric systems. Since available nitrogenous compounds may be quickly consumed within the biofilm and are not leached to the washing water, conditions in dystrophic waters may be favorable for development of a specific dinitrogen-fixing group of bacteria or for oligonitrophiles.

It is not clear whether the main inhabitants of acidic ultrafresh dystrophic waters are capable of growth on conventional laboratory media, especially considering the high salt content in commercially available brands of agar. Such media are probably unsuitable for slowly growing oligotrophs; therefore, direct methods should be extensively used. Direct microscopic investigation revealed considerable numbers of rare and unusual microorganisms in ultra-freshwater environments. Their morphological characteristics attract special attention. Among them, the organisms termed budding bacteria are present [75–77]. Prosthecate bacteria, organisms with cell appendages supposedly increasing the cell area with the transport systems, are a characteristic group of aquatic oligotrophic dissimilators [78, 79]. *Caulobacter* is among the representatives of freshwater microorganisms. It was initially described on slides in lakes. In subsequent early electron microscopic studies, it was revealed as a usual contaminant of laboratory distilled water and was afterwards widely used as a model for investigation of differentiation in prosthecate bacteria. Prosthecate bacteria are mostly planktonic forms, and many of them are carbohydrate-utilizing oligotrophs who respond to low substrate concentrations by switching to high-affinity transport systems. Planktomycetes, which have long been known from microscopical observations in the lakes and have only recently become available for investigation in laboratory cultures, are another characteristic morphological group [80, 81]. Molecular biological approaches based on PCR and 16S rRNA cloning enabled identification of numerous ultra-freshwater organisms not yet obtained in cultures; however, since their functional role remains unknown, they are not considered here. The question should be asked, whether the extreme inhabitants of unique biotopes, belonging to the “rare biosphere” [82, 83] are more important for our under-

standing of environmental processes than the common, "banal" mass forms, which are one of the main routes of carbon turnover in the biosphere. The answer is self-evident. Similar to the few dominant tree species composing Russian forests (Table 2), the widespread microbial forms, culturable or not, are most important. Forest-wetland ecosystems with predominance of a limited number of tree species suggests significant microbial diversity in freshwater due to the wide distribution of the habitat, in contrast to the Thienemann's rule of mass development of few species in extreme ecosystems [84].

TROPHIC RELATIONS IN THE COURSE OF WOOD DECOMPOSITION AND ORGANIC MATTER DECAY IN DYSTROPHIC WATERS BY THE MYCO-BACTERIAL COMMUNITY

The above review of the main processes of wood decomposition make it possible to propose a conceptual scheme of the trophic interactions within the xylophilic myco-bacterial community, a part of the ombrophilic microbial community developing in ultrafresh waters of rainfall origin.

In the ombrophilic community of forest ecosystems, which is responsible for decomposition of wood debris, two major groups of microorganisms may be identified, namely, xylophilic fungi responsible for wood hydrolysis and oxidative transformation, and subordinate dissimilatory freshwater bacteria (Fig. 2). The fungi develop on moist wood and carry out solid-state fermentation of lignocellulose. The process is determined by the extent of the available surface. Bacteria develop in the liquid phase (leachate water) at low concentrations of available nutrients as dissimilatory. A direct trophic link joins both groups, and bacteria in the water phase receive the washed-out products of wood hydrolysis and of fungal metabolism. The above-mentioned group of pelophilic microorganisms of mud sediments forms a separate block; it is, however, especially interesting to hydrobiologists and is listed here merely to complete the picture of the fate of organic matter in sedimentation basins.

The scheme of trophic relations in the xylophilic myco-bacterial communities is presented in Fig. 3. Importantly, each block is a relatively complex dynamic grouping in the state of development with succession of the dominant forms. Wood decomposition determines the main trophic pathway, which is rooted in accordance with the primary carbon-rich nutrient sources (cellulose, hemicellulose, and lignin). The fungal mycelium acts as a secondary source of nutrients, significantly inferior to the main one. The proteolytic pathway is therefore of minor importance for this trophic system. The myco-bacterial consortium acts as a generator of available organic matter, while the dissimilatory bacteria perform its transformation. This myco-bacterial system exists under the conditions of strictly limited mineral supply and excess of not readily

decomposable organic matter. Organic residues accumulate due to the inhibition of microbial destructive activity; low positive values of organic carbon production in an ecosystem are balanced by even lower values for the negative destructive part, and are related to considerable net biome production. The ecosystem is therefore characterized mainly not by the presence of specific bacterial degraders, but rather by their low activity. The dissimilatory of dystrophic waters possess a set of physiological characteristics, which permit their consideration as an ecological group within a broader ombrophilic group. In the humid boreal zone, the characteristics of this community include the following: organotrophy, aerobiosis, oligotrophy, moderate acidophily, low resistance to osmotic stress, and the psychrophilic or psychroactive temperature dependence. Dissimilatory bacteria utilizing the soluble products of wood hydrolysis are mostly saccharolytic oligotrophic aerobes. This group does not include the hydrolytics, such as the cellulose bacteria, developing on suspended organic particles delivered into the water. The microorganisms consuming the products of fungal metabolism, primarily organic acids, belong to acidotrophs. Oxalotrophs are the most important members of this group [85]. Acidotrophs decrease the concentration of organic acids, and the initially acidic medium becomes neutral. Deacidification is a characteristic process determining the microbial succession, which depends upon the balance between production of organic acids by fungi and their consumption by planktonic bacteria. The trophic group of acidotrophic bacteria, which utilize organic acids, is therefore important for the ecosystem as a whole. Since the concentration of the metabolic products in the diluted leaching water is low, the organisms oxidizing organic acids, together with saccharolytic dissimilatory, fall into the category of oligotrophs. Bacteria degrading the cyclic phenolic compounds form a separate group. They play a special role, since the activity of a number of hydrolases is decreased in the presence of phenolic compounds. Inhibition of hydrolases was shown to be ameliorated in the presence of fungal polyphenol oxidases, which remove phenolic compounds from the pore water [86]. Phenol-oxidizing bacteria may possibly cause the same effect. Dystrophic waters contain also quantitatively less significant products, including C-1 compounds, the products of hydrolysis of pectin and lignin not utilized by fungi or utilized but weakly [87], although they are available to yeasts. These compounds promote the development of methylotrophic bacteria. Since dissimilatory bacteria are close to the final step of the trophic chain, they are represented by slowly growing organisms of the climacteric phase of the succession and exhibit a relatively low interdependence.

The biotic relationships in the biofilm are crucial for the microorganisms of the myco-bacterial community. They include the relationship with fungi: resistance to antibiotics and to oxidative stress, dependence upon the position in the biofilm at the submillimeter level (which

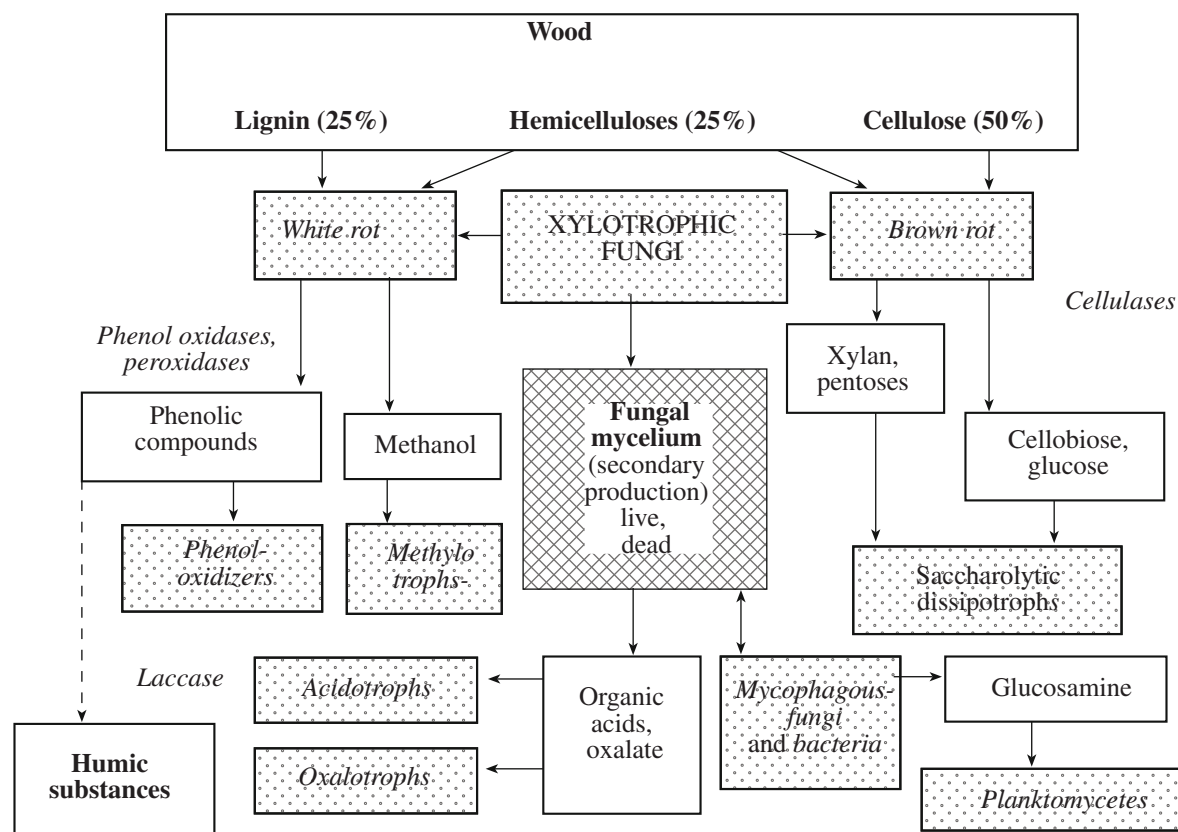


Fig. 3. Schematic representation of the expected trophic relations in a xylotrophic myco-bacterial community.

may result in oxygen limitation in the deep layers of decomposed wood), competition for the substrates, ability to utilize fungal mycelium as a nutrient substrate, and resistance to drying (sporadic xerophytes). The xylotrophic fungal community produces humic substances, unavailable to bacteria, which determine the hydrochemistry of dystrophic waters. Since fungal succession was established, and since the source material in the environment (wood) is changing at the rate of years, variations in the characteristics and composition of the bacterial community depending on the stage of the process should be expected.

CONCLUSION

The system of wood decomposition under washing with rainwater is a classical system with hydrolytics and dissipotrophs, where the hydrolytics are mostly mycelial organisms (xylotrophic fungi), while the dissipotrophs are planktonic aquatic bacteria. The following stages may be found in wood decomposition. (1) Fallen trees are colonized by microfungi, consuming easily degradable compounds and leaving the cell walls almost intact. (2) Cellulolytic (brown rot) or ligninolytic (white rot) fungi develop together with deuteromycetes as satellites. At this stage, formation of organic acids in the course of fungal metabolism results

in acidification of the medium. Humic and fulvic acids are formed as by-products of the xylotrophic group. (3) The dead mycelium is decomposed by the mycophilic microorganisms, and bacteria in the water phase consume organic acids. (4) Wood decomposition results in its maceration and consequent development of mosses and pileate fungi and mushrooms, and organogenic forest soil develops. The water-soluble fraction of the humic substances resulting from wood decomposition is washed off with rainfall and enters the water flows. The water then may be clarified due to coagulation of organo-mineral colloids; otherwise, humus-enriched, brown dystrophic waters are formed, which are typical of some regions in northwestern European Russia.

This ecosystem can be simulated under laboratory conditions. For this purpose, microscale lysimeters were made out of plastic water bottles, with a piece of wood supported on a mesh in the upper section and distilled water in the lower one. In the upper section, a moist camera is formed, where mycelial growth occurs on the surface of wood and organic matter is generated by the xylotrophic myco-bacterial biofilm. During wood decomposition, water-soluble degradation products, including humic substances, are accumulated in the lower section of the microlysimeter where dissipotrophic bacteria develop. This simple experimental setup made it possible to observe the interaction

between the xylotrophic and dissipotrophic groups and resulted in detection of a variety of microorganisms [81, 88].

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