ISSN 1067-4136, Russian Journal of Ecology, 2018, Vol. 49, No. 5, pp. 406–412. © Pleiades Publishing, Ltd., 2018.
Original Russian Text © V.A. Mukhin, E.N. Patova, M.D. Sivkov, I.V. Novakovskaya, N.V. Neustroeva, 2018, published in Ekologiya, 2018, No. 5, pp. 368–375.

Diversity and Nitrogen-Fixing Activity of Phototrophic Mycetobionts of Xylotrophic Fungi

V. A. Mukhin[a], *, E. N. Patova[b], M. D. Sivkov[b], I. V. Novakovskaya[b], and N. V. Neustroeva[a]

[a] *Institute of Plant and Animal Ecology, Ural Branch, Russian Academy of Sciences, Yekaterinburg, 620144 Russia*
[b] *Institute of Biology, Komi Research Center, Ural Branch, Russian Academy of Sciences, Syktyvkar, 167982 Russia*
**e-mail: victor.mukhin@ipae.uran.ru*

Received February 15, 2018

Abstract—It is shown that the basidiocarps of many wood-decomposing fungi are inhabited by taxonomically and biomorphologically various eukaryotic (Charophyta, Chlorophyta, and Ochrophyta) and prokaryotic (Cyanophyta/Cyanobacteria) algae. They represent widespread eurybiont species and do not include any specialized mycetobionts. The communities formed by them have a host preference and green algae are their basic and obligate component, while other organisms are facultative components. Basidiocarps in which mycetobionts include heterocytic cyanoprokaryotes (*Anabaena* sp., *Calothrix parietina*, *Hassallia byssoidea*, *Nostoc commune*, *N. punctiforme*, *Nostoc* sp., and *Scytonema ocellatum*) are capable of molecular nitrogen fixation. Its activity is 0.044–0.903 mg of $C_2H_4/m^2/h$ in the basidiocarps of *Bjerkandera adusta*, *Cerrena unicolor*, *Gloeophyllum sepiarium*, and *Trametes ochracea* and 0.001–0.008 mg of $C_2H_4/m^2/h$ in the basidiocarps of *Onnia leporina*, *Phellinus chrysoloma*, *Ph. tremulae*, and *Trametes pubescens*. Basidiocarps without algae and those inhabited only by eukaryotic algae have no nitrogenase activity.

Keywords: forest ecosystems, fungi, Basidiomycota, Agaricomycetes, eukaryotic algae, cyanoprokaryotes/cyanobacteria, biodiversity, nitrogen fixation, symbiosis

DOI: 10.1134/S1067413618050090

One of the essential features of wood as a habitat for xylobiont organisms is an extremely low content of nitrogen. According to S.I. Vanin [1], the total content of this element in wood is about 0.1% and the C/N ratio is 500 : 1. According to data from Watkinson et al. [2], the C/N ratio in wood can reach 1250 : 1. According to our estimates [3], the content of mobile (hydrolysable) nitrogen in deciduous and coniferous wood decomposed by xylotrophic basidiomycetes is 0.18–0.57 mg/g, or 0.01–0.05%, and the C/N ratio is 1400 : 1.

Recyclization, the selective use of cell materials in the case of nitrogen deficiency, and the ability to selectively utilize different nitrogen-containing compounds are considered as physiological adaptations of wood-decomposing fungi to the nitrogen regimen of the wood medium [4–6]. These adaptations serve as a basis for the so-called nitrogen-saving strategies of wood-decomposing fungi. The adaptations of wood-decomposing fungi should also include their ability to use various nitrogen sources: plant and animal residues, water extracts from living and dead leaves, as well as nitrogen-fixing bacteria, nematodes, and collembolans [2, 7–11].

Basidiocarps of tens of wood-decomposing fungal species are inhabited by algae, which belong mostly to the Chlorophyta group and less frequently to the Ochrophyta, Charophyta, and Cyanoprokaryota groups [12, 13]. The relationships between fungi and algae can be characterized as a facultative associative symbiosis, in which algae receive some protection from insolation, as well as water, and acquire carbon dioxide formed during fungal respiration, while fungi acquire an additional (other than wood) source of carbon and nitrogen [12].

The use of symbiotic algae by fungi as a source of carbon nutrition has been experimentally confirmed [12, 14], while their use as a source of nitrogen is only an assumed probability or a working hypothesis that is based on the presence of nitrogen-fixing cyanoprokaryotes among mycetobionts. To validate this hypothesis, one should establish the presence of the nitrogen-fixing activity in basidiocarps with mycetobionts and show its correlation with the presence of or no cyanoprokaryotes and other groups of phototrophic mycetobionts.

MATERIAL AND METHODS

The taxonomic and biomorphological composition of mycetobiont communities and their nitrogenase activity were analyzed using 43 samples of basidiocarps inhabited by 21 species of xylotrophic basidio-

mycetes (Basidiomycota group, Agaricomycetes class), which were collected on September 12–14, 2017, in middle-taiga old-aged mixed forests in the northeastern part of the Russian Plain (the suburbs of the city of Syktyvkar, the Republic of Komi, 61°34′ N, 50°36′ E). With respect to biological and ecological characteristics, the study group of xylotrophic fungi is quite various and representative: white and brown rot agents, deciduous and coniferous wood destructors, and fungi with perennial and annual basidiocarps. Their species identification was performed using traditional anatomical and morphological methods of determining basidial fungi [15–17]. The nomenclature of fungi and algae is given according to MycoBank DataBase [18] and Algaebase [19], respectively.

To compare the values of the nitrogen-fixing activity of basidiocarps of xylotrophic fungi and lichens, we also collected the thalli of cyanobiont nitrogen-fixing lichen *Lobaria pulmonaria* (L.) Hoffm in the sites where the basidiocarps were sampled.

The nitrogenase/nitrogen-fixing activity was assessed immediately on the day when basidiocarps were collected under the conditions of their natural field moisture using the acetylene reduction technique [20]. Before the analysis, basidiocarps were cleaned from foreign organic residues (needles and leaves) and small (21.5 mm in diameter) sample parts were cut out and put into sealed 130 mL flasks (exposure chambers) closed with rubber plugs for gas sampling. Ten mL of air was sampled from each chamber flask using a 10 mL syringe and 13 mL of 100% acetylene was then introduced into each flask to reduce its concentration to 10%. The duration of sample exposure in the chambers was 24 h: 16 h covered by the light period (the intensity of photosynthetic active radiation was 50 μmol/m^2/s (Sylvania F8W/T5/Gro plant lamp) and 8 h covered by the dark period. The chambers were exposed at a constant temperature of 21°C; the temperature was recorded using a DS 1923 hygrochron (Dallas Semiconductor, United States).

Air mixture samples were collected from the chamber flasks after 1 h and 24 exposure hours. Gas samples with a volume of 0.8 mL were collected in each measurement and immediately studied on a gas chromatograph. The samples of basidiocarps that exhibited nitrogenase activity were additionally measured in the acetylene-free air medium to identify possible natural extraction of ethylene by them; as a result, ethylene was revealed in none of these samples. The presence of ethylene was analyzed using a Tsvet-800 gas chromatograph (Russia) with a flame-ionization detector and Porapak N 80/100 sorbent in a 2-m packed metal column with an external diameter of 4 mm. Helium was used as a carrier gas. The chromatograph was calibrated using standard LindeGaz mixtures (Russia). The nitrogenase activity was calculated in mg of C_2H_4/m^2/h. with one replication, which seemed to be sufficient for achieving the main goal of the study, i.e., detecting the nitrogen-fixing activity and assessing its expression.

Upon completion of gas analysis, samples were extracted from the exposure chambers and examined under a Nikon Eclipse80i microscope (×1000 magnification) with a system of differential interferential contrast and video fixation of images. Direct microscopic examination without using culture techniques makes it possible to reveal the actively vegetating and dominant species of phototrophic mycetobionts. Algae and cyanoprokaryotes (blue–green algae) were identified according to Russian and foreign guides [21–23]. Some species, the identification of which requires observations on development and reproduction stages, were identified only to a genus.

The similarity/difference in the taxonomic composition of algal groups associated with basidiocarps of different xylotrophic fungal species was estimated according to the Sorensen–Czekanowski index. The results of the analysis were visualized in the form of a hierarchic cluster analysis using the group mean method in ExcelToR [24].

RESULTS AND DISCUSSION

Algological analysis of basidiocarps shows that xylotrophic fungi can be divided into two groups. The fungi of the first group (seven species) do not have mycetobiont algae in their basidiocarps: *Abortiporus biennis* (Bull.) Singer, *Daedaleopsis confragosa* (Bolton) J. Schröt., *Fomes fomentarius* (L.) Fr., *Fomitopsis betulina* (Bull.) B.K. Cui, M.L. Han & Y.C. Dai, *F. pinicola* (Sw.) P. Karst., *Ganoderma applanatum* (Pers.) Pat., and *Rhodofomes cajanderi* (P. Karst.) B.K. Cui, M.L. Han & Y.C. Dai. The second group includes fungi (14 species) with mycetobionts in their basidiocarps; in addition, their mycetobionts are characterized by quite a high diversity (Table 1). Most of them (74%) are eukaryotic algae (Chlorophyta, Ochrophyta, and Charophyta); cyanoprokaryotes are considerably exceeded in diversity. In terms of biomorphology, these are mainly trichal (15 species, 48%) and coccoid (11 species, 35%) algae. Colonial coccoid species (*Coenocystis* sp., *Desmococcus olivaceus*, *Neocystis* sp., and *Sporotetras polydermatica*) occur rarely and monad species (*Chlamydomonas* sp.) are recorded even more rarely (see Table 1). There are no obligate mycetobionts. For instance, all algae that occur most frequently in basidiocarps represent widespread and eurybiont species: pedobionts and hydrobionts (*Chlamydomonas* sp.), epiphytes (*Desmococcus olivaceus*), and aerophytes and lichen photobionts (*Pseudococcomyxa simplex* and *Stichococcus bacillaris*) [25, 26].

Table 1 shows that basidiocarps are inhabited by two (*Phellinus igniarius*) to 13 (*Trichaptum fuscoviolaceum*) algal species (on average, about seven species). None of the species occurs in the basidiocarps of all the 14 fungal species. Few of the mycetobionts

Table 1. Taxonomic composition of mycetobiont symbiotic algae of xylotrophic algae in old-aged middle-taiga forests of the Komi Republic

Mycetobiont alga	Symbiont fungus													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Cyanoprokaryota														
Anabaena sp.[II]				+				+						
Calothrix parietina Thuret ex Bornet et Flahault[II]	+	+												
Hassallia byssoidea Hassal ex Bornet et Flahault[II]										+				
Nostoc commune Vaucher ex Bornet et Flahault[II]										+				
N. cf. *punctiforme* (Kützing ex Hariot) Hariot[II]	+									+				
Nostoc sp.[II]	+	+			+	+								
Phormidium sp.[II]				+										
Scytonema ocellatum Lyngbye ex Bornet & Flahault[II]										+	+			
Ochrophyta														
Bumilleriopsis sp.[II]											+			
Characiopsis cf. *acuta* (A. Braun) Borzì[I]		+												
Characiopsis sp.[I]	+	+							+	+		+		
Tribonema vulgare Pasch.[II]				+										
Vischeria helvetica (Vischer&Pascher) D.J. Hibberd[I]												+		+
Chlorophyta														
Chlamydomonas sp.[IV]	+	+	+						+	+	+	+		+
Coenocystis sp.[III]	+								+				+	
Desmococcus olivaceus (Persoon ex Acharius) J.R. Laundon[III]	+	+	+			+		+	+		+	+	+	+
Dictyochloropsis sp.[I]			+									+		+
Elliptochloris sp.[I]												+		+
Elliptochloris subsphaerica (Reisigl) Ettl & Gärtner[I]			+				+		+			+		+
Interfilum terricola (J.B. Petersen) Mikhailyuk, Sluiman, Massalski, Mudimu, Demchenko, Friedl & Kondratyuk[II]					+					+	+			
Leptosira sp.[II]		+								+		+	+	+
Mychonastes homosphaera (Skuja) Kalina et Puncochárová[I]											+	+		
Myrmecia sp.[I]													+	
Neocystis sp.[III]		+												
Pseudococcomyxa simplex (Mainx) Fott[I]	+	+	+		+				+	+	+	+	+	+
Sporotetras polydermatica (Kützing) I. Kostikov, T. Darienko, A. Lukesová, & L. Hoffmann[III]	+					+				+	+	+		+
Stichococcus bacillaris Nägeli[II]		+	+		+	+	+	+	+	+	+	+	+	+
Trebouxia sp.[I]		+	+									+	+	+

Table 1. (Contd.)

Mycetobiont alga	Symbiont fungus													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Charophyta														
Klebsormidium nitens (Kützing) Lokhorst[II]														+
K. pseudostichococcus (Heering) H. Ettl & Gärtner[II]											+			
Mesotaenium cf. *chlamydosporum* De-Bary[I]				+										
Number of algal species/number of analyzed basidiocarps	9/2	11/2	7/1	4/1	4/1	4/1	2/1	3/1	7/2	11/1	10/1	13/6	7/2	12/5

(1) *Bjerkandera adusta* (Willd.) P. Karst., (2) *Cerrena unicolor* (Bull.) Murrill, (3) *Chondrostereum purpureum* (Pers.) Pouzar, (4) *Gloeophyllum sepiarium* (Wulfen) P. Karst., (5) *Onnia leporina* (Fr.) H. Jahn, (6) *Phellinus chrysoloma* (Fr.) Donk, (7) *Ph. igniarius* (L.) Quél., (8) *Ph. tremulae* (Bondartsev) Bondartsev & P.N. Borisov, (9) *Stereum subtomentosum* Pouzar, (10) *Trametes ochracea* (Pers.) Gilb. & Ryvarden, (11) *T. pubescens* (Schumach.) Pilát, (12) *Trichaptum abietinum* (Pers. ex J.F. Gmel.) Ryvarden, (13) *T. fuscoviolaceum* (Ehrenb.) Ryvarden, and (14) *T. pargamenum* (Fr.) G. Cunn. Mycetobiont life form: (I) coccoid form, (II) trichal form, (III) colonial–coccoid form, (IV) monad form.

(*Chlamydomonas* sp., *Desmococcus olivaceus*, *Pseudococcomyxa simplex*, and *Stichococcus bacillaris*) were recorded in the basidiocarps of eight to 12 fungi and *Characiopsis* sp., *Elliptochloris subsphaerica*, *Leptosira* sp., *Nostoc* sp., *Sporotetras polydermatica*, and *Trebouxia* sp. were recorded in the basidiocarps of five to six algal species. Algae that were recorded in the basidiocarps of one to two fungal species (*Anabaena* sp., *Bumilleriopsis* sp., *Calothrix parietina*, *Characiopsis* cf. *acuta*, *Elliptochloris* sp., *Hassallia byssoidea*, *Klebsormidium nitens*, *K. pseudostichococcus*, *Mesotaenium* cf. *chlamydosporum*, *Mychonastes homosphaera*, *Myrmecia* sp., *Neocystis* sp., *Nostoc* cf. *punctiforme*, *Nostoc* sp., *Phormidium* sp., *Scytonema ocellatum*, *Tribonema vulgare*, and *Vischeria Helvetica*) are an alternative group for these mycetobionts. *Coenocystis* sp., *Dictyochloropsis* sp., and *Interfilum terricola* occur in the basidiocarps of three fungal species (see Table 1).

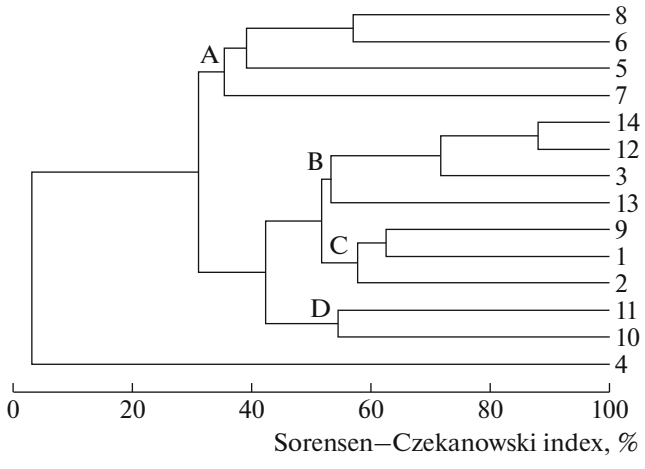

Fig. 1. Similarity of the taxonomic composition of communities of mycetobiont algae inhabiting basidiocarps of different wood-decomposing fungal species ((1)–(14), see the note to Table 1).

Figure 1 presents the results of the cluster analysis of mycetobiont communities associated with basidiocarps of 14 fungal species. It can be seen that they form several groups (clusters). One of them (group A) includes algae that inhabit the basidiocarps of fungi of the genus *Phellinus* (*Ph. chrysoloma*, *Ph. igniarius*, and *Ph. tremulae*) and *Onnia leporine*; group (B) includes algae that inhabit the basidiocarps of fungi of the genus *Trichaptum* (*T. abietinum*, *T. fuscoviolaceum*, and *T. pargamenum*) and *Chondrostereum purpureum*; group (C) includes algae that inhabit the basidiocarps of fungi *Bjerkandera adusta*, *Cerrena unicolor*, and *Stereum subtomentosum*; and group (D) includes algae that inhabit the basidiocarps of fungi of the genus *Trametes* (*T. ochracea* and *T. pubescens*). The mycetobionts of *Gloeophyllum sepiarium* do not include species that are common with other fungi. Therefore, mycetobiont communities have a certain level of host preference and closely related fungal species have maximum similarity.

Mycetobionts associated with separate basidiocarps of the same fungal species are not characterized by the persistence of their composition. For instance, only three of the 13 species of mycetobiont algae associated with *Trichaptum abietinum* (namely, *Chlamydomonas* sp., *Pseudococcomyxa simplex*, and *Stichococcus bacillaris*) were recorded in all the five studied basidiocarps and four species (*Desmococcus olivaceus*, *Leptosira* sp., *Sporotetras polydermatica*, and *Trebouxia* sp.) were recorded in three basidiocarps. The other six species occurred in one to two basidiocarps. The same situation is characteristic of *Trichaptum pargamenum*: only two of the 12 species of mycetobiont algae (*Pseudococcomyxa simplex* and *Stichococcus bacillaris*) occurred in all the five studied basidiocarps; *Sporotetras polydermatica* and *Desmococcus olivaceus* were

Table 2. Nitrogenase activity (NA) of basidiocarps of xylotrophic fungi, mg $C_2H_4/m^2/h$

Symbiont fungus	Symbiotic cyanoprokaryotes	NA
Bjerkandera adusta	*Calothrix parietina*, *Nostoc* cf. *punctiforme*	0.079*
Cerrena unicolor	None	0.0
C. unicolor	*Calothrix parietina*, *Nostoc* sp.	0.044*
Gloeophyllum sepiarium	*Anabaena* sp., *Phormidium* sp.	0.089*
Onnia leporina	*Nostoc* sp.	0.003
Phellinus chrysoloma	*Nostoc* sp.	0.008
Ph. tremulae	*Anabaena* sp.	0.003
Trametes ochracea	*Hassallia byssoidea*, *Nostoc commune*, *Nostoc* cf. *punctiforme*, *Scytonema ocellatum*	0.903*
T. ochracea	None	0.0
Trametes pubescens	*Scytonema ocellatum*	0.008*

* Samples were tested for the natural extraction of ethylene in daily exposure.

recorded in three basidiocarps and the other mycetobionts were found in one to two basidiocarps.

The results of testing the basidiocarps of xylotrophic algae for the nitrogenase/nitrogen-fixing activity showed it is not present in *Abortiporus biennis*, *Daedaleopsis confragosa*, *Fomes fomentarius*, *Fomitopsis betulina*, *F. cajanderi*, *F. pinicola*, and *Ganoderma applanatum*, which did not have mycetobiont algae in their basidiocarps, nor is it present in the basidiocarps of fungi that are inhabited only by eukaryotic algae: it was not revealed in any of the 15 studied basidiocarps of *Stereum subtomentosum*, *Trichaptum abietinum*, *T. fuscoviolaceum*, and *T. pargamenum*, which were inhabited by these algae.

The nitrogenase activity was revealed only for basidiocarps of a small group of species: *Bjerkandera adusta*, *Cerrena unicolor*, *Gloeophyllum sepiarium*, *Onnia leporina*, *Phellinus chrysoloma*, *Ph. tremulae*, *Trametes ochracea*, and *T. pubescens* (Table 2): its level was 0.001 to 0.903 mg of C_2H_4 m^2/h. The highest nitrogen-fixing activity (0.044–0.903 mg of C_2H_4 m^2/hr.) was recorded for basidiocarps of *B. adusta*, *C. unicolor*, *G. sepiarium*, and *T. ochracea*. It was significantly lower in basidiocarps of *O. leporina*, *Ph. chrysoloma*, *Ph. tremulae*, and *T. pubescens*: 0.001–0.008 mg of C_2H_4 m^2/h.

All basidiocarps with the nitrogenase activity contained cyanoprokaryotes (Fig. 2) and the level of nitrogen fixation positively depended on their diversity: two to four cyanobacterial species were recorded at high nitrogenase activity, while, at low nitrogenase activity, only one species was found. When there is no cyanoprokaryotes, basidiocarps lose their nitrogen fixation ability, as can be seen from the example of *Cerrena unicolor* and *Trametes ochracea* (see Table 2). This also indicates the facultative pattern of correlations between cyanoprokaryotes and fungi.

The level of nitrogenase activity is almost 30 times higher in the basidiocarps of xylotrophic fungi than in the thalli of the nitrogen-fixing epiphytic lichen *Lobaria pulmonaria* (3.191 mg of $C_2H_4/m^2/h$) that were collected in the same areas as the basidiocarps under study. However, it is quite comparable to the nitrogenase activity of cyanoprokaryote–moss associations in the moss cover of forest communities with a range of 0.01 to 0.75 mg of C_2H_4 m^2/h [27, 28] and in biological soil crusts (with the dominance of cyanoprokaryotes) in arctic and mountain areas (0.03–1.3 mg of C_2H_4 m^2/h) [29].

CONCLUSIONS

In the old-aged middle-taiga forests of the northeast of the Russian Plain, a significant part of wood-decomposing fungi is symbiotically associated with algae inhabiting their basidiocarps. All of them are nonspecialized mycetobionts; in turn, widespread eurybiont phototrophic eukaryotic (Chlorophyta, Ochrophyta, and Charophyta) and prokaryotic (Cyanoprokaryota) algae are symbiotically associated mainly with trichal and coccoid thalli. Mycetobiont communities differ in the number and composition of species and have a host preference and their maximum similarity is usually recorded for closely related fungal species, i.e., species of the same genus.

Basidiocarps without mycetobionts and those that contain them, but only in the form of eukaryotic algae, have no nitrogenase/nitrogen-fixing activity. This activity is inherent only in mycetobiont communities that contain prokaryotic algae (cyanoprokaryotes): the higher their content in mycetobionts, the higher the level of nitrogenase/nitrogen-fixing activity being recorded. Its level is lower than that in the thalli of nitrogen-fixing lichens; however, it is comparable to the levels that are characteristic of cyanoprokaryote–moss associations in the moss cover in boreal and mountain forests and in biological soil crusts in arctic and mountain areas.

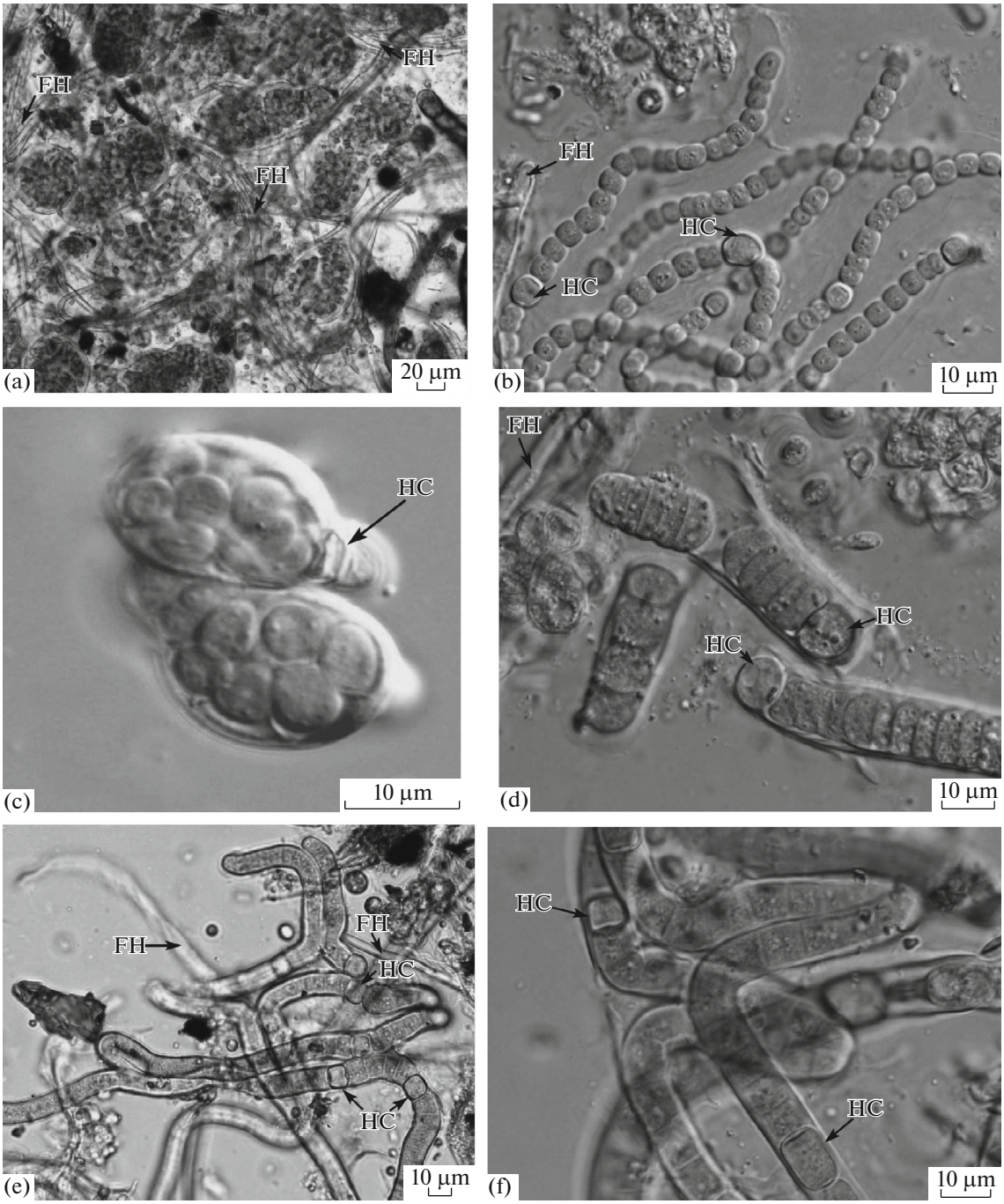

Fig. 2. Nitrogen-fixing cyanoprokaryotes inhabiting the basidiocarps of xylotrophic fungi: (a) *Nostoc commune* colonies among fungal hyphae; (b) filaments of *Nostoc* sp. With heterocytes; (c) *Nostoc punctiforme*; (d) *Hassallia byssoidea*; (e), (f) filaments of *Scytonema ocellatum* at different magnifications; FH, fungal hyphae, HC, heterocytes. Scale size: (a) 20 μm, (b)–(f) 10 μm.

The presence of nitrogen-fixing activity in mycetobiont algae makes them, not only an additional source of carbon for wood, but also a source of nitrogen for xylotrophic fungi. In addition, the symbiotic associations of xylotrophic fungi and algae should also be considered as a particular, previously unknown source of nitrogen supply to forest ecosystems, the role and value of which has yet to be determined.

ACKNOWLEDGMENTS

This study was carried out within the state assignment of the Institute of Plant and Animal Ecology, Ural Branch, Russian Academy of Sciences, and was partly supported by the Integrated Program of the Ural Branch of the Russian Academy of Sciences (project nos. 18-4-4-44) and the Russian Foundation of Basic Research (projects nos. 15-04-06881 and 18-04-00643).

REFERENCES

1. Vanin, S.I., *Drevesinovedenie* (Wood Science), Leningrad: Goslestekhizdat, 1934.
2. Watkinson, S., Bebber, D.P., Darrah, P., et al., The role of wood decay fungi in the carbon and nitrogen dynamics of the forest floor, in *Fungi in Biogeochemical Cycles,* Gadd, G.M., Ed., Cambridge: Cambridge Univ. Press, 2006, pp. 151–158. doi 10.2277/0521845793
3. Mukhin, V.A., Diyarova, D.K., Neustroeva, N.V., and Kostitsina, M.V., Mycogenic wood decay: Nitrogen balance, in *Biologiya, sistematika i ekologiya gribov i lishainikov v prirodnykh ekosistemakh i agrofitotsenozakh* (Biology, Systematics, and Ecology of Fungi and Lichens in Natural Ecosystems and Agrocenoses), Minsk: Kolorgrad, 2016, pp. 165–168.
4. Lilly, W.W., Wallweber, G.J., and Higgins, S.M., Proteolysis and amino acid recycling during nitrogen deprivation in *Schizophyllum commune, Curr. Microbiol.,* 1991, vol. 23, pp. 27–32.
5. Caddick, M.X., What's for dinner – what shall I choose?, *Microbiol. Today,* 2002, vol. 29, pp. 132–134.
6. Caddick, M.X., Nitrogen regulation in mycelial fungi, in *The Mycota: 3. Biochemistry and Molecular Biology,* 2nd ed., Brambl, R. and Marzluf, G.A., Eds., Berlin: Springer Verlag, 2004, pp. 349–368. doi 10.1007/978-3-662-06064-3_17
7. Barron, G.L., Ligninolytic and cellulolytic fungi as predators and parasites, in *The Fungal Community: Its Organization and Role in the Ecosystem,* Carroll, G.C. and Wicklow, D.J., Eds., New York: Marcel Dekker, 1992, pp. 311–354.
8. Cromack, K. and Caldwell, B.A., The role of fungi in litter decomposition and nutrient cycling, in *The Fungal Community: Its Organization and Role in the Ecosystem,* Carroll, G.C. and Wicklow, D.J., Eds., New York: Marcel Dekker, 1992, pp. 653–668.
9. Heal, O.W. and Dighton, J., Nutrient cycling and decomposition in natural terrestrial ecosystems, in *Microfloral and Faunal Interactions,* Mitchell, M.J. and Nakas, J.P., Eds., Dordrecht: Springer, 1986, pp. 14–73. doi 10.1007/978-94-009-5173-0_2
10. Klironomos, J.N. and Hart, H.H., Animal nitrogen swap for plant carbon, *Nature,* 2001, vol. 410, pp. 651–652. doi 10.1038/35070640
11. Richter, D.D., Markewitz, D., Trumbore, S.A., and Wells, G.P., Rapid accumulation and turnover of soil carbon in a re-establishing forest, *Nature,* 1999, vol. 400, pp. 56–58. doi 10.1038/21867
12. Mukhin, V.A., Patova, E.N., Kiseleva, I.S., et al., Mycetobiont symbiotic algae of wood-decomposing fungi, *Russ. J. Ecol.,* 2016, vol. 47, no. 2, pp. 133–137.
13. Neustroeva, N.V., Mukhin, V.A., Novakovskaya, I.V., and Patova, E.N., Hostal variability of mycetobiont algae, *Vestn. Udmurt. Gos. Univ., Ser. Biol.,* 2017, vol. 27, no. 3, pp. 291–296.
14. Zavada, M.S., DiMichele, L., and Toth, C.R., The possible demi-lichenization of *Trametes versicolor* (L.: Fr.) Pilat (Polyporaceae): The transfer of fixed $^{14}CO_2$ from epiphytic algae to *T. versicolor, Northeast. Nat.,* 2004, vol. 11, no. 1, p. 33.
15. *Nordic Macromycetes,* vol. 3: *Heterobasidioid, Aphillophoroid and Gastmtcetoid Basidiomycetes,* Hansen, L. and Knudsen, H., eds., Copenhagen: Nordsvamp, 1997
16. Ryvarden, L. and Gilbertson, R.L., *European Polypores:* 2. *Meripilus–Tyromyces,* Oslo: Fungiflora, 1994.
17. Ryvarden, L. and Gilbertson, R.L., *European Polypores:* 1. *Abortiporus–Lindtneria,* Oslo: Fungiflora, 1993.
18. MycoBank DataBase. http://www.mycobank.org. Cited December 1, 2017.
19. AlgaeBase http://www.algaebase.org. Cited December 1, 2017.
20. Stewart, W.D., Fitgeral, G.P., and Burris, R.H., In situ studies on N_2 fixation using the acetylene reduction technique, *Proc. Natl. Acad. Sci. U. S. A.,* 1967, vol. 58, no. 5, pp. 1073–2078. . doi 10.1073/pnas.58.5.2071
21. Ettl, H. and Gärtner, G., *Syllabus der Boden-, Luft- und Flechtenalgen,* Stuttgart: Gustav Fischer, 2014. doi 10.1007/978-3-642-39462-1
22. Komárek, J., *Süßwasserflora von Mitteleuropa. Cyanoprokaryota III: Nostocales, Stigonematales,* Heidelberg: Springer Spektrum, 2013.
23. Andreeva, V.M., *Pochvennye i aerofil'nye zelenye vodorosli (Chlorophyta: Tetrasporales, Chlorococcales, Chlorosarcinales)* (Soil and Aerophilic Green Algae (Chlorophyta: Tetrasporales, Chlorococcales, Chlorosarcinales)), St. Petersburg: Nauka, 1998.
24. Novakovskii, A.B., Combination of Excel and R statistical package for data processing in ecology, *Vestn. Inst. Biol. Komi Nauch. Tsentra Ural. Otd. Ross. Akad. Nauk,* 2016, no. 3, pp. 26–33.
25. Voitsekhovich, A.A., Mikhailyuk, T.I., and Darienko, T.M., Photobionts of lichens. 2: Origin and correlation with mycobiont, *Algologiya,* 2011, vol. 21, no. 1, pp. 151–177.
26. Egorova, I.N., Dendrophilic algal synusiae in Khamar-Daban (Baikal region), *Bot. Zh.,* 2007, vol. 92, no. 4, pp. 477–489.
27. Egorov, V.I., The nitrogen regime and biological fixation of nitrogen in moss communities (the Khibiny Mountains), Euras. Soil Sci., 2007, vol. 40, no. 4, pp. 1134–467. doi 10.1134/S1064229307040138
28. Zackrisson, O., DeLuca, T.H., Gentili, F., et al., Nitrogen fixation in mixed *Hylocomium splendens* moss, Oecologia, 2009, vol. 160, pp. 1007–319. doi 10.1007/s00442-009-1299-8
29. Patova, E., Sivkov, M., and Patova, A., Nitrogen fixation activity in biological soil crusts dominated by cyanobacteria in the Subpolar Urals (European North-East Russia), *FEMS Microbiol. Ecol.,* 2016, vol. 92, no. 9, pp. 1–9. doi 10.1093/femsec/fiw131

Translated by D. Zabolotny