Dynamics of Communities of Cryptogamic Organisms on Dead Wood after Reduction of the Emissions from a Copper Smelter

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Abstract—The dynamics of the species composition of mosses and lichens on the dead wood of fir and spruce in the southern taiga forests of the Middle Urals after the almost complete cessation of emissions from the Middle Urals copper smelter (Revda, Sverdlovsk region) was studied. Compared to the period of high emissions (1993–1994), the number of moss species in the immediate vicinity of the plant (1–2 km) increased from 1 to 27 by 2019, and the number of lichen species increased from 1 to 30. Nevertheless, the species richness of mosses and lichens remains reduced compared to that of the background territory, and the species composition differed significantly: many species typical for the background territory were absent, and species specific to the impaired territory were present. In polluted habitats, the proportion of species with predominantly sexual reproduction was higher.

INTRODUCTION

Assessment of the ability of natural ecosystems to recover after the reduction/cessation of external impact is one of the urgent problems of modern ecology. The processes of recolonization of degraded territories after the reduction of emissions from industrial enterprises differ significantly both between groups of organisms [1] and between species within a particular group due to differences in their ability to disperse [2, 3]. Cryptogamic organisms have a high colonizing ability due to the huge number of formed small diaspores and the wide range of their dispersal [4, 5]. However, the success of colonization depends not only on the characteristics of diaspores (size, dispersal distance) and distance from their source [6], but also on the width of the ecological niche of species [7] and reproductive strategy, e.g. the predominant dispersal using generative or vegetative diaspores, which differ significantly in terms of survival [8].

Dead wood (DW) plays an important role in maintaining the diversity of cryptogamic organisms in forest ecosystems: the number of species on it can be up to 84% of the total species richness [9, 10]. At the same time, no special studies have been conducted on the colonization of large wood residues after the reduction of emissions from metallurgical plants. A few studies on the restoration of cryptogamic organisms in contaminated areas were devoted to changes in diversity in the ground cover [11, 12], on the trunks of living trees [2], or did not consider the substrate confinement [13–15].

The main purpose of this study was to analyze the patterns of moss and lichen colonization of DW in spruce–fir forests after the almost complete cessation of emissions from a large copper smelter in the Middle Urals. The study area was convenient for the investigation of the recovery dynamics of the considered groups since data on the state of moss-lichen communities during the period of high emissions (1993–1994) were available. It has been reliably established that during this period, within a radius of 1–2 km from the plant, epixylic communities of cryptogamic organisms on fallen trunks were represented by only two species, moss *Pohlia nutans* (Hedw.) Lindb. [16] and lichen *Placynthiella uliginosa* (Schrader) Coppins & P. James [17]. Another two lichen species (*Scoliciosporum chlorococcum* (Graewe ex Stenh.) Vezda, *Trapeliopsis flexuosa* (Fr.) Coppins & P. James) were recorded on other types of DW: standing dead trees and stumps [17].

During the first decade after almost complete cessation of emissions in the zone of maximum pollution, extremely low species diversity of mosses was retained, although local areas with a large number of species were found [15]. The active colonization of living tree trunks by epiphytic lichens was also shown in the area of the former "lichen desert" near the plant [2]. Data on the recolonization of soil and living trees by mosses

Table 1. Sizes of the studied wood remains

Dimensional characteristics	Background zone		Impact zone	
	fir	spruce	fir	spruce
Log length, m				
mean ± SE	10.5 ± 1.0	20.6 ± 2.4	12.5 ± 0.9	13.4 ± 1.3
range	5.2–20.0	4.4–29.9	4.2–24.7	5.2–28.8
Log diameter, cm				
mean ± SE	14.4 ± 1.6	25.1 ± 3.8	16.9 ± 1.9	20.6 ± 2.4
range	5.3–29.0	7.0–56.1	7.0–44.6	7.2–55.4

and lichens, combined with data on a lower content of heavy metals in DW compared to forest litter [18], allowed a hypothesis to be developed about the probable rapid colonization of DW by mosses and lichens in the contaminated area, which was tested in this study.

MATERIALS AND METHODS

The study was carried out on a territory subjected to long-term (since 1940) atmospheric pollution by emissions from the Middle Ural copper smelter (MUCS), located near the town of Revda, Sverdlovsk oblast, in the spruce−fir forests of the southern taiga subzone. The main components of the emissions were sulfur oxides and dust particles with metals (Cu, Fe, Zn, Pb, Cd, etc.) and metalloids (As) adsorbed on them. In the late 1980s, emissions (sulphur dioxide and heavy metals) amounted to 140 000 tons/year, in 1995−1998 they were 71 000−96 000 t/year, and after the reconstruction of the enterprise in 2010 emissions were 3000−5000 t/year [19]. A detailed description of the study area, the degree of degradation, and recovery dynamics of several ecosystem components were published earlier [19−21].

In 2019, felled spruce trees (*Picea obovata* Ledeb.) and fir (*Abies sibirica* Ledeb.) of 2nd and 3rd stages of decomposition (according to P. V. Gordienko) were investigated on four plots. These stages are characterized by the following features: 2nd stage − the bark is mostly preserved, the wood is dense with the first signs of decomposition; 3rd stage − the bark fell off in places, the top layer of wood is soft, and there is the presence of pronounced decay. The nature and strength of the relationship between the diagnosed stage of deadwood decomposition and its density did not depend on the pollution zone, which allows us to use the decomposition stage scales not only for the background conditions, but also for technogenically transformed forests [22]. The choice of these stages was due to the fact that they were characterized by the largest number of epixylous species of mosses and lichens [23, 24]. A total of 95 DW fragments were examined: 56 in the impact zone (25 firs and 31 spruces) and 39 in the background zone (21 firs and 18 spruces).

Moss and lichen species were recorded on the trunk, branches, and stumps of a fallen tree, both on bark remnants and on bare wood. Samples not identifiable in the field were collected for species identification in the laboratory. For this, standard methods and identification keys were used [25−37].

The species of mosses and lichens were divided into two groups: those with a predominantly sexual type of reproduction and those with a predominantly vegetative type of reproduction. For mosses, the subdivision was made based on the frequency of sporophyte formation (species with frequent sporophyte formation were assigned to species with a predominantly sexual type of reproduction, species with rare sporophyte formation were assigned to species with predominantly vegetative reproduction) [27, 28, 38]. Lichen species forming soredia and/or isidia were assigned to species with predominantly vegetative reproduction, species without soredia and/or isidia, but forming apothecia, were assigned to species with predominantly sexual reproduction.

Statistical analysis was performed using the PAST 4.12 software. The Jaccard similarity index was used for the comparison of the species composition of communities. Similarity dendrograms were plotted using the UPGMA method.

RESULTS

Characteristics of the studied wood residues. The dimensional characteristics of the examined deadwood of fir and spruce are shown in Table 1. In the background zone, the average diameter of spruce logs significantly exceeded the diameter of fir logs (nonparametric t-test with permutations, 10 000 permutations, $P = 0.014$), but the distributions were similar (Kolmogorov−Smirnov test, $D = 0.37$; $R = 0.116$). The average length of spruce logs also exceeded the length of fir logs ($P = 0.014$), but the distributions did not differ significantly ($D = 0.38$; $R = 0.088$). In the impact zone, the average values and size distributions between fragments of different tree species did not differ significantly.

Number of species and species composition. In total, 50 moss species (Table 2) and 52 lichen species (Table 3) were found in the study area on the DW. In the background zone, 47 moss species and 42 lichen species were revealed, with 46% of all moss species and 42.3% of lichen species specific to the background zone.

Table 2. List of moss species on dead wood of fir (F) and spruce (S) at different distances from the MUCS

Species	Reproduction type	Distance from plant and substrate							
		1 km		2 km		30 km		31 km	
		F	S	F	S	F	S	F	S
Amblystegium serpens (Hedw.) Bruch, Schimp. et W. Gümbel	1	–	–	+	+	–	–	+	–
Atrichum undulatum (Hedw.) P. Beauv.	1	–	–	–	–	–	–	–	+
Aulacomnium palustre (Hedw.) Schwägr.	2	–	–	–	–	+	–	–	–
Brachytheciastrum velutinum (Hedw.) Ignatov et Huttunen	1	–	–	+	+	+	+	+	+
Brachythecium salebrosum (Hoffm. ex F. Weber et D. Mohr) Bruch, Schimp. et W. Gümbel	1	–	–	+	+	+	+	+	+
Bryum caespiticium Hedw.	1	–	–	–	–	+	–	–	–
B. pallescens Schleich. ex Schwägr.	1	–	–	+	+	–	–	–	–
B. rubens Mitt.	2	–	–	–	–	–	+	–	–
Callicladium haldanianum (Grev.) H.A. Crum	1	–	–	–	+	+	+	+	+
Calliergon cordifolium (Hedw.) Kindb.	2	–	–	–	–	–	–	–	+
Campylophyllopsis sommerfeltii (Myrin) Ochyra	1	–	–	–	+	+	–	–	–
Ceratodon purpureus (Hedw.) Brid.	1	–	–	–	+	–	+	–	–
Cirriphyllum piliferum (Hedw.) Grout	2	–	–	–	–	+	–	+	+
Climacium dendroides (Hedw.) F. Weber et D. Mohr	2	–	–	–	–	+	–	+	+
Dicranum fuscescens Turner	2	–	–	–	–	+	+	+	+
D. majus Turner	2	–	–	–	–	–	–	+	–
D. montanum Hedw.	2	–	–	–	+	+	+	+	+
D. polysetum Sw.	2	–	–	–	–	+	+	+	+
D. scoparium Hedw.	1	–	–	–	+	+	+	+	+
Drepanocladus polygamus (Bruch, Schimp. et W. Gümbel) Hedenäs	2	–	–	–	–	–	–	+	–
Herzogiella turfacea (Lindb.) Z. Iwats.	1	–	–	+	–	–	+	–	–
Hylocomiadelphus triquetrus (Hedw.) Ochyra et Stebel	2	–	–	–	+	+	+	+	+
Hylocomium splendens (Hedw.) Bruch, Schimp. et W. Gümbel	2	–	–	–	+	+	+	+	+
Jochenia pallescens (Hedw.) Hedenäs	1	–	–	–	–	+	+	+	+
Oncophorus wahlenbergii Brid.	1	–	–	–	+	+	+	+	+
Physcomitrella patens (Hedw.) Bruch, Schimp. et W. Gümbel	1	–	–	+	–	–	–	–	–
Plagiomnium cuspidatum (Hedw.) T.J. Kop.	1	–	–	–	+	+	+	+	+
P. drummondii (Bruch et Schimp.) T.J. Kop.	1	–	–	–	–	+	+	+	+
P. elatum (Bruch et Schimp.) T.J. Kop.	2	–	–	–	–	+	–	+	+
P. ellipticum (Brid.) T.J. Kop.	2	–	–	–	–	–	–	+	+
P. medium (Bruch et Schimp.) T.J. Kop.	1	–	–	–	–	+	+	+	–
Plagiothecium denticulatum (Hedw.) Bruch, Schimp. et W. Gümbel	2	–	–	+	+	+	+	+	+
P. laetum Bruch, Schimp. et W. Gümbel	2	–	–	+	+	+	+	+	+
P. latebricola Bruch, Schimp. et W. Gümbel	2	–	–	–	–	–	–	+	–
Pleurozium schreberi (Brid.) Mitt.	2	+	–	–	+	+	+	+	+
Pohlia nutans (Hedw.) Lindb.	1	+	+	+	+	+	+	+	+

Table 2. (Contd.)

Species	Reproduction type	Distance from plant and substrate							
		1 km		2 km		30 km		31 km	
		F	S	F	S	F	S	F	S
Polytrichum longisetum Sw. ex Brid.	2	−	−	−	−	+	−	−	−
Ptilium crista−castrensis (Hedw.) De Not.	2	−	−	−	+	+	+	+	+
Pylaisia polyantha (Hedw.) Bruch, Schimp. et W. Gümbel	1	−	−	−	−	−	−	+	−
Rhizomnium punctatum (Hedw.) T.J. Kop.	1	−	−	−	−	−	−	+	+
Rhodobryum roseum (Hedw.) Limpr.	2	−	−	−	−	+	+	−	−
Rhytidiadelphus subpinnatus (Lindb.) T.J. Kop.	2	−	−	−	−	+	+	−	+
Sanionia uncinata (Hedw.) Loeske	1	+	−	+	+	+	+	+	+
Sciuro−hypnum oedipodium (Mitt.) Ignatov et Huttunen	1	−	−	+	+	+	+	+	+
S. populeum (Hedw.) Ignatov et Huttunen	1	−	−	−	+	+	−	+	+
S. reflexum (Starke) Ignatov et Huttunen	1	−	−	+	+	+	+	+	+
S. starkei (Brid.) Ignatov et Huttunen	1	−	−	−	+	+	+	+	+
Sphagnum squarrosum Crome	1	−	−	−	−	−	+	−	−
Tayloria tenuis (Dicks. ex With.) Schimp.	1	−	−	−	+	−	−	−	−
Tetraphis pellucida Hedw.	2	+	−	+	+	+	+	+	+
Number of species		4	1	13	25	34	30	35	32

Here and in Table 3 types of reproduction: 1—predominantly sexual, 2—predominantly vegetative.

In the background zone, the composition of moss communities somewhat differed between DW of different tree species (similarity coefficient was 0.68), although the number of species was similar (41 and 38 on fir and spruce DW, respectively). Nine species specific to fir (*Pylaisia polyantha*, *Plagiothecium latebricola* etc.) and six species specific for spruce (*Bryum rubens*, *Calliergon cordifolium* etc.) were revealed.

In the background zone, the number of lichen species on spruce (33) was higher than on fir DW (26, similarity coefficient was 0.41), which was largely determined by the high diversity of epiphytes remaining on the branches after the fall of the tree: 16 species were specific for spruce DW in the background area, out of which 7 were found on the branches (*Bryoria nadvornikiana*, *Evernia mesomorpha*, *Hypocenomyce leucococca*, *Hypogymnia tubulosa*, *Lecanora pulicaris*, *Mycoblastus fucatus*, *Tuckermanopsis chlorophylla*).

In the impact zone, 27 moss species and 30 lichen species were identified. The number of lichen species at distances of 1 and 2 km did not differ (23 species at each site), while the species richness of mosses at a distance of 1 km was significantly lower than at a distance of 2 km (4 and 27 species, respectively, see Table 2). The similarity coefficients of the background and impact zones were 0.48 (mosses) and 0.39 (lichens).

A number of epixilic mosses typical of the background territory were absent near the plant (*Dicranum fuscescens*, *Rhizomnium punctatum*, *Jochenia pallescens*, etc.). Interestingly only two moss species, rare for the Urals, were noted in the impact zone. These species under normal conditions grow either only on damp soil (*Physcomitrella patens*), or on soil and excrement (*Tayloria tenuis*), also *Bryum pallescens*, the species typical for the Southern Urals, but rare for the Middle Urals was detected [39]. In contrast to the background territory, in the impact zone, the number of moss species on the spruce DW (25) was significantly higher than on the fir DW (14); the similarity coefficient was 0.44.

In the impact zone, epiphytic lichens, very sensitive to pollution, were not found, but these lichens remained in the background area on the branches of fallen trees (*B. nadvornikiana*, *E. mesomorpha*, *Fuscidea arboricola*, *H. tubulosa*) and the remains of the bark (*Lepraria* spp.). The epibryophyte lichens of the genus *Peltigera* were also not revealed in the impact zone. At the same time higher species diversity of the genus *Cladonia*, many of which are known to be epigeic, typical of dry habitats (*C. crispata*, *C. furcata*, *C. gracilis*, *C. ochrochlora*, *C. rei*) was detected in the impact zone [32]. These species included *C. rei*, the species that prefers anthropogenic habitats [32]. A highly toler-

Table 3 List of lichen species on dead wood of fir (F) and spruce (S) at different distances from the MUCS

Species	Reproduction type	Distance from plant and substrate							
		1 km		2 km		1 km		31 km	
		F	S	F	S	F	S	F	S
Absconditella lignicola Vězda & Pišút	1	+	–	–	+	+	+	+	+
Amandinea punctata (Hoffm.) Coppins & Scheid.	1	–	–	–	+	–	–	–	–
Bacidina phacodes (Körb.) Vězda	1	–	+	–	–	–	–	–	–
Bryoria nadvornikiana (Gyeln.) Brodo et D. Hawksw.	2	–	–	–	–	–	–	–	+
Catinaria atropurpurea (Schaer.) Vezda & Poelt	1	–	–	–	+	+	–	+	–
Chaenotheca ferruginea (Turner ex Sm.) Mig.	1	–	–	+	–	–	+	–	+
Cladonia botrytes (Hag.) Willd.	1	+	+	–	–	–	–	+	–
C. cenotea (Ach.) Schaerer	2	–	–	–	–	–	+	+	+
C. chlorophaea (Flörke ex Sommerf.) Spreng.	2	+	+	+	+	–	–	+	–
C. coniocraea (Flörke) Spreng.	2	+	+	+	+	+	+	+	+
C. crispata (Ach.) Flot.	1	–	+	–	–	–	–	–	–
C. fimbriata (L.) Fr.	2	+	+	+	+	+	+	+	+
C. furcata (Huds.) Schrad.	1	–	+	–	–	–	–	–	–
C. gracilis (L.) Willd.	1	+	+	–	–	–	–	–	–
C. ochrochlora Flk.	2	+	–	+	+	–	–	–	–
C. rei Schaer.	2	+	+	+	+	–	+	+	–
Dimerella pineti (Ach.) Vězda	1	–	–	+	–	–	–	–	–
Evernia mesomorpha Nyl.	2	–	–	–	–	–	+	–	+
Fuscidea arboricola Coppins & Tønsberg	2	–	–	–	–	+	+	+	+
F. pusilla Tønsberg	2	–	–	–	–	–	+	+	+
Hypocenomyce caradocensis (Leight. ex Nyl.) P. James & Gotth. Schneid.	1	+	+	+	+	+	–	–	–
H. leucococca R. Sant.	2	–	–	–	–	–	+	–	–
Hypogymnia physodes (L.) Nyl.	2	+	+	+	+	+	+	+	+
H. tubulosa (Schaer.) Hav.	2	–	–	–	–	–	–	–	+
Lecanora pulicaris (Pers.) Ach.	1	–	–	–	–	–	+	–	+
Lepraria elobata Tønsberg	2	–	–	–	–	–	+	–	+
L. incana (L.) Ach.	2	–	–	–	–	–	–	–	+
Lepraria sp.	2	–	–	–	–	–	–	+	+
Micarea denigrata (Fr.) Hedl.	1	–	–	–	–	–	–	+	–
M. myriocarpa V. Wirth and Vězda ex Coppins	1	–	–	–	–	–	–	+	–
M. prasina s.l.	1	+	+	+	+	+	+	+	+
Mycobilimbia carneoalbida (Müll. Arg.) S. Ekman et Printzen	1	–	–	+	–	–	–	–	–
Mycoblastus alpinus (Fr.) Hellb.	2	–	–	–	–	–	–	+	–

Table 3 (Contd.)

Species	Reproduction type	1 km		2 km		1 km		31 km	
		F	S	F	S	F	S	F	S
M. fucatus (Stirt.) Zahlbr.	2	–	–	–	–	–	+	–	–
Parmelia sulcata Tayl.	2	–	–	+	+	–	+	+	+
Parmeliopsis ambigua (Wulfen) Nyl.	2	–	–	–	–	–	+	+	–
P. hyperopta (Ach.) Vain.	2	–	–	–	–	–	+	–	–
Peltigera canina (L.) Willd.	1	–	–	–	–	–	–	+	–
P. polydactylon (Neck.) Hoffm.	1	–	–	–	–	+	+	+	+
P. praetextata (Flörke ex Sommerf.) Zopf.	2	–	–	–	–	+	+	–	+
Pycnora sorophora (Vain.) Hafellner	2	–	–	–	–	–	+	–	–
Placynthiella dasaea (Stirton) Tønsberg	2	–	+	–	–	–	+	–	–
P. icmalea (Ach.) Coppins & P. James	1	+	+	+	+	–	–	–	+
P. uliginosa (Schrader) Coppins& P. James	1	+	+	+	+	–	–	–	–
Rinodina degeliana Coppins	2	–	–	+	–	–	+	+	+
Ropalospora viridis (Tønsberg) Tønsberg	2	+	–	–	+	–	+	–	–
Scoliciosporum chlorococcum (Graewe ex Stenh.) Vězda	1	+	+	+	+	–	+	+	–
Trapeliopsis flexuosa (Fr.) Coppins & P. James	2	+	+	+	+	–	–	+	–
T. granulosa (Hoffm.) Lumbsch	2	+	+	–	+	–	–	–	+
Tuckermanopsis chlorophylla (Willd.) Hale	2	–	–	–	–	–	–	–	+
T. sepincola (Ehrh.) Hale	1	+	+	–	–	–	–	–	–
Vulpicida pinastri (Scop.) J.–E. Mattsson & M.J. Lai	2	+	+	–	+	–	+	+	+
Number of species		19	20	17	19	10	26	24	24

ant species *P. uliginosa* passing to DW from dead moss was found only in the impact area, as well as explerent *Tuckermanopsis sepincola*, characteristic of open habitats and actively colonizing living trunks in former contaminated areas [2]. In the impact zone the DW of spruce and fir were almost the same in terms of the number of species (26 and 24 species, respectively).

The described patterns are well reflected in similarity dendrograms (Fig. 1). For both mosses and lichens, a cluster of the background territory is distinguished. A significant proportion of lichen species specific to the impact area determined the formation of the impact zone cluster; e.g., the similarity within the pollution zones was higher than the similarity on the DW of the same tree species in different zones. The species composition of mosses on DW of spruce in the impact zone was closer to the background zone, while the least species-rich communities of DW of fir in the impact zone were isolated. For mosses, the similarity between DW of different tree species was higher in the background area, and for lichens, in the impact area.

Contribution of species with different reproductive strategies. In the background zone, mosses with different types of reproduction were represented by almost the same number of species: the first group (mainly sexual reproduction) − 24 species, the second group (mainly vegetative reproduction) − 23. The ratio of groups did not depend on the species of DW (Fig. 2a). The impact zone was dominated by species of the 1st group (19 species), while only 8 species of the 2nd group were noted. The proportion of species of the first group in the impact zone on the DW of fir was 71.4%, and on the DW of spruce it was 68%. All moss species specific to the impact zone belong to the first group.
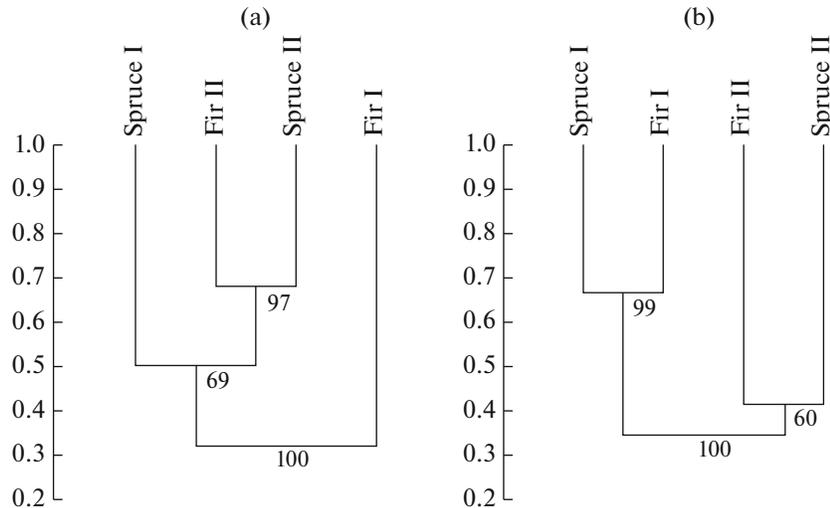
Fig. 1. Dendrograms of the similarity of the species composition of mosses (a) and lichens (b) on dead wood of spruce and fir in different load zones (I, impact, II, background). The Jaccard coefficient and the UPGMA method were used. The bootstrap support numbers are shown in the bases of the clusters (% of 1000 replicates).
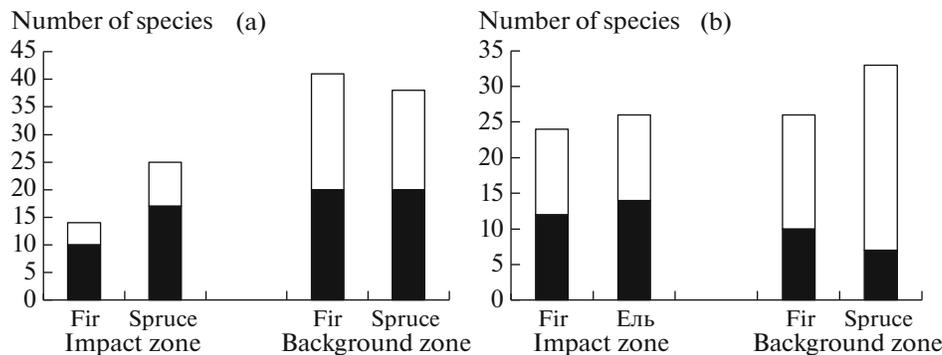

Fig. 2. Number of moss (a) and lichen (b) species on dead spruce and fir wood in different load zones. Black shading is the number of species with a predominantly sexual type of reproduction, without shading is the number of species with a predominantly vegetative type of reproduction.

The lichen communities of the background area were dominated by species of the second group (69%) (see Fig. 1b). However, in the contaminated area, the ratio was reversed: the proportion of species of the first group was 57%. At the same time, in the impact zone, the proportion of reproduction types was approximately the same on the DW of both tree species, while in the background zone on the DW of spruce, a higher proportion of vegetatively propagating species was noted (see Fig. 2b). This was due to the presence of epiphytes on branches, which we mentioned above, a majority of epiphytes were soredia-forming species (*B. nadvornikiana, E. mesomorpha, F. arboricola, H. tubulosa*), and species of the genus *Lepraria*. Out of the ten species specific to the impact zone, nine belong to the first group.

DISCUSSION

In the background zone, the species richness of mosses (42 species) and lichens (47) was similar. Although a detailed analysis of the interactions between mosses and lichens was not included in our tasks, it is necessary to note their different directions. On the one hand, relatively fast-growing mosses forming a high biomass were obviously also stronger competitors for the substrate compared to lichens. On the other hand, mosses can be a substrate for epibryophyte lichen species [40]. In our study, these were lichens of the genus *Peltigera,* which were noted on the DW only in the background habitats.

The influence of the tree species on the composition of epixylic communities within the same biotope is

understudied. The differences between substrates described in the literature [10, 23] were associated not so much with the tree species, but with a complex of habitat factors (type of plant community, altitude, duration of the decomposition stage, etc.). Our data indicate a greater substrate differentiation of lichens compared to mosses in the background area. Fir and spruce belong to the same group, coniferous trees with acidic bark; therefore, the lichen biota of living trees of these phorophyte species is similar [41, 42]. Substrate differences found by us in the species composition of lichens were mainly due to the higher number of branches on the fallen spruce compared to fir. The rate of biological decomposition of branches is low compared to stem wood, which is due to the location of the substrate relative to the ground [43]. Therefore, after the fall of the tree, the epiphytic communities formed during the life of the tree last longer on the branches. In addition, the greater species richness of lichens on DW of spruce may be due to the larger size of fragments compared to fir.

The key result of the study is the finding that after the reduction and then almost complete cessation of plant emissions, there was a rapid increase in the species richness of epixylous communities of cryptogamic organisms. Compared to the period of high emissions (1993−1994), by 2019 the number of moss species increased from 1 to 27, and the number of lichen species increased from 1 to 30. Such a high rate of recovery contrasts with the consistently low species diversity of the herb-dwarf shrub layer in the contaminated area, despite the reduction in emissions [19]. Probably, in polluted habitats, DW is a more "attractive" substrate for cryptogamic organisms due to lower metal concentrations and a higher water content in woody residues compared to forest litter [18]. The presence of rare moss species in the impact zone may be due to the low moss coverage on logs; e.g., the lack of interspecific competition.

The number of lichen species on the DW in the impact zone (30 species) was higher than on living trees: on fir trunks at distances of 1 and 2 km in 2018, 8 and 13 species of epiphytic lichens were recorded, respectively [2]. All these epiphytic species were also noted on the DW, with the exception of a very sensitive *E. mesomorpha*.

The difference in the rate of recolonization of DW by mosses and lichens in the most polluted area (1 km from the plant) is of interest. The number of moss species at a distance of 1 km was significantly inferior to that at a distance of 2 km, while the number of lichen species at these distances was similar. It is possible that a higher level of toxicants in the substrate and a higher distance to the nearest sources of diaspores play a certain role in slowing down colonization. However, the leading role probably belongs to microclimate. At a distance of 1 km, the destruction of the tree and grass-shrub layers was much more pronounced [19]. It was

shown [44] that at this distance some aridization of the microclimate occurs: the average daily temperature measured at a height of 2 m was 0.7−1.0°C higher than the background values. In the herbaceous layer, this effect was even more pronounced: the maximum daily temperature was 3°C, and the daily temperature range was 4.3°C higher than the corresponding indicators for the background area [45]. This led to a decrease in the water content in the DW in the impact area compared to the background area, which was shown for woody residues of the 4th stage of decomposition [18]. Probably, the moisture deficiency limits the development of mosses. Lichen communities respond to aridization by increasing the proportion of xerophytes (for example, many species of the genus *Cladonia,* as well as *T. sepincola*, the species often found on treated wood in open habitats). Despite the fact that both mosses and lichens are poikilohydric, the differences in the degree of their tolerance to desiccation is high [46]. The analysis of moisture gradients at different scales (from the level of the trunk to altitudinal gradients) showed the predominance of mosses in the most humid habitats, which was replaced by the dominance of lichens in drier habitats [40, 47].

The substrate differentiation of mosses and lichens in the impact zone was multidirectional: the epixylous lichen communities on different types of substrates were characterized by a close number of species and a more similar species composition than in the background zone, while the differentiation of moss communities on different types of substrates in this zone, on the contrary, was pronounced. Since, as we already mentioned, the differences in the species composition of lichens on DW of spruce and fir in the background zone were primarily determined by the presence of epiphytes on spruce branches, most of which are very sensitive to pollution, their absence in the impact zone automatically led to an increase in similarity between the DW of different tree species.

It can be assumed, that reasons for the higher species richness of mosses on DW of spruce were associated with the features of the bark: a significant proportion of mosses prefer rough bark with a high water content [8]. Under the increasingly arid conditions of degraded territories, differences in moisture capacity between the rough spruce bark and the smooth fir bark can increase, which affects the formation of moss communities.

The role of the reproductive strategy of species in the success of recolonization of degraded territories is ambiguous. On the one hand, spores of sexual reproduction are smaller and, accordingly, have a greater dispersion range; on the other hand, their survival rate is lower than that of vegetative propagules [8]. Lichen spores, in addition, require the presence of a compatible photobiont for the development of the thallus. According to our data, in the impact area, epixylic communities of both mosses and lichens are charac-

terized by a higher proportion of species with predominantly sexual reproduction, while most of the species specific to the impact zone had predominantly sexual reproduction. At first sight, this contradicts the data obtained for the vicinity of the zinc smelter in Palmerton, the United States: after the cessation of emissions, the colonization of heavily polluted areas occurred mainly with vegetatively propagating lichen species (58% of the total number of species) [13]. However, epiphytic, epigeic, and epilithic lichens were considered in the Palmerton area, and no epixylic species were found. At the same time, for epixylic lichens in general, the prevalence of species with sexual reproduction is typical, especially expressed for obligate epixylic species, in which the proportion of such species reaches 75% [48]. The analysis of the advantages of different reproductive strategies during the recolonization of degraded territories requires more data and further accumulation of information.

CONCLUSIONS

The tested hypothesis was fully confirmed: the reduction of emissions in the polluted area initiated a significant increase in the species richness of epixylous mosses (from 1 to 27) and lichens (from 1 to 30). However, despite the positive changes, the number of species on the DW in the impact zone remained reduced compared to the background zone, and the species composition of the communities differed significantly from the background one due to the absence of many species typical of the background habitats and the presence of species specific to the impact areas.

This study should be considered only as the first stage in studying the patterns of DW recolonization by cryptogamic organisms. Further analysis requires a detailed assessment of the effect of physicochemical factors of DW (including the content of toxicants) on the qualitative and quantitative characteristics of epixylic communities, as well as comprehensive studies considering the restoration of the habitat as a whole.

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