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IMPACT OF LICHENS ON SOIL MICROBOCOENOSIS IN TUNDRA AND FOREST

Abstract. The impact of tundra and forest terricolous lichens on soil microbocoenoses was studied in field and laboratory experiments on the Taymyr Peninsula and in Estonia. It has been established that terricolous lichens generally stimulate the development of soil microorganisms enriching the ground with carbon, nitrogen, and some mineral nutrients and having physical influence on soil moisture conditions. Still, the leaching secondary lichen substances may have an antibiotic impact on individual components of microbocoenosis. The spore-forming bacteria are the most sensitive to the impact of lichen substances. The viable counts of micromycetes change under the cover of lichens to a smaller extent. The antibiotic influence of lichen substances on microflora is the highest in a thin soil layer in close contact with lichen thallus and practically non-existent already at the depth of 1—2 cm. The absence of lichens secondary compounds toxidity in deeper soil layers may be explained by low solubility of lichen substances in water, their ability to form chelates with metal ions, and transformation of these compounds by microflora. One and the same lichen species has the same impact on soil microbocoenoses in different soil-climatic conditions of tundra and forest.

Key words: lichens, soil microbocoenoses.

Introduction

Interaction between terricolous lichens and individual components of soil biota has not been studied thoroughly enough. Most of the studies on the interaction between lichens and microorganisms have been so far concentrated on the investigation of the impact of lichen substances on pathogenic microflora (Vartia, 1973; Lawrey, 1986). There exist only a few papers which deal with the impact of lichens on soil microflora (Harder, Uebelmesser, 1958; Malicki, 1965, 1970; Паринкина, 1989; Паринкина, Пийн, 1978, 1984, 1989; Пийн et al., 1984; Tearle, 1987; Толпышева, 1979). This problem is interesting both from the general ecological viewpoint and from the aspect of studying the effect of the metabolic products of lichens on microflora under natural conditions.

Our observations were carried out in tundra and polar desert zones of the Taymyr Peninsula (1976—1982) and in the forest zone in Estonia (1978—1985), as it was not possible to eliminate the probability of a different impact of one and the same lichen species on microflora under different soil-climatic conditions.

Objects and Methods

Five lichen species: *Cetraria cucullata* (Bellardi) Ach., *C. islandica* (L.) Ach., *C. nivalis* (L.) Ach., *Cladina arbuscula* (Wallr.) Hale et Culb., and *C. rangiferina* (L.) Nyl., were the same among the subject both in the forest zone of Estonia and in the tundras of Taymyr.

Other species studied were: *Alectoria ochroleuca* (Hoffm.) Massal, *Asahihea chrysantha* (Tuck.) Culb. et C. Culb., *Baeomyces carneus* Flörke, *B. roseus* Pers., *Bryoria nitidula* (Th. Fr.) Brodo et D. Hawksw., *Cetraria delisei* (Bory ex Schaerer) Nyl., *C. laevigata* Rass., *C. tilesii* Ach., *Cladina*

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mitis (Sandst.) Hustich, *C. stellaris* (Opiz) Brodo, *Cladonia symphycarpa* (Ach.) Fr., *Mycobilimbia hypnorum* (Lib.) Kalb et Hafellner, *Nephroma arcticum* (L.) Torss., *N. expallidum* (Nyl.) Nyl., *Pertusaria dactylina* (Ach.) Nyl., *Solorina crocea* (L.) Ach., *Stereocaulon alpinum* Laurer ex Funck, *S. rivulorum* Magnusson, and *S. vesuvianum* Pers.

In Taymyr the impact of terricolous lichens on soil microflora was studied in the polar desert zone (Cape Chelyuskin, 77°43′ N, 104°30′ E), and in the tundra zone — arctic tundras (the vicinities of M. Pronchishcheva Bay, 75°44′ N, 112°30′ E, and Dixon, 73°55′ N, 81°10° E), typical tundras (the region of the Ossipovka River, 73°43′ N, 81°8′ E), and southern tundras (in the vicinity of the Kresty meteorological station, 70°50′ N, 89°01′ E). On the territory of Estonia similar observations were carried out in juniper alvars of the West-Estonian Archipelago Biosphere Reserve (Vormsi Island, Rumpo, 58°40′ N, 23°30′ E) and in pine forests of Lahemaa National Park (Altja, 59°35′ N, 26°10′ E).

Except for the polar desert zone with heavy ground soils, the soils in the regions studied are sandy and loamy-sand ones.

The program of studies included determination of chemical properties of soil, investigation of microbial landscapes (Виноградский, 1952) under lichen cover using Perfilyev's capillary method (Аристовская, Паринкина, 1961), estimation of the viable counts of different groups of microflora and the effect of the antibiotic activity of lichens on test cultures by plate count method. The extent of the antibiotic activity was determined both on the basis of the sizes of sterile zones around lichen thallus pieces lying on agar media inoculated with colonies of microorganisms, and by making an analysis of the diversity of the species composition of bacteria by plate count method. To be able to determine the impact of lichens on microorganisms with the greatest possible accuracy, both the upper soil layer (0—1, 0—2 cm) and the close contact soil layer under lichen thalli were studied. The number of replicate soil samples analysed was three, each consisting of 10—12 samples from the subject plot. The results were processed statistically (arithmetic mean, error of mean, difference between two means, Fisher's index of species diversity).

Results and Discussion

Growing on soil surface, lichens may affect soil microflora in different ways.

Determination of some chemical properties of soil showed that the pH of the soil under the lichen cover is lower than in bare ground. The content of total organic carbon was considerably higher, especially in alvar typical sod-calcareous soil which may be explained by greater biological activity of temperate climate soils. Under the lichen cover also a higher content of total nitrogen and soluble potassium (K_2O) was observed. The amount of mobile phosphorus (P_2O_5) fell under the representatives of the genera *Cladonia* and *Cladina*, but increased distinctly under *Cetraria* spp. (Table 1).

On soils poor in organic matter, mineral nutrients, and nitrogen, lichens stimulate the development of soil microorganisms in the initial soil formation stages due to the enrichment of soil with organic matter and a more stable moisture regime under lichen cover (Пийн et al., 1984). Similar results were obtained by P. V. Tearle (1987) while comparing the amounts of soluble sugars and polyols leached into fellfield soil fines from lichens with the composition and population size of the bacterial, yeast, fungal, and algal microflora.

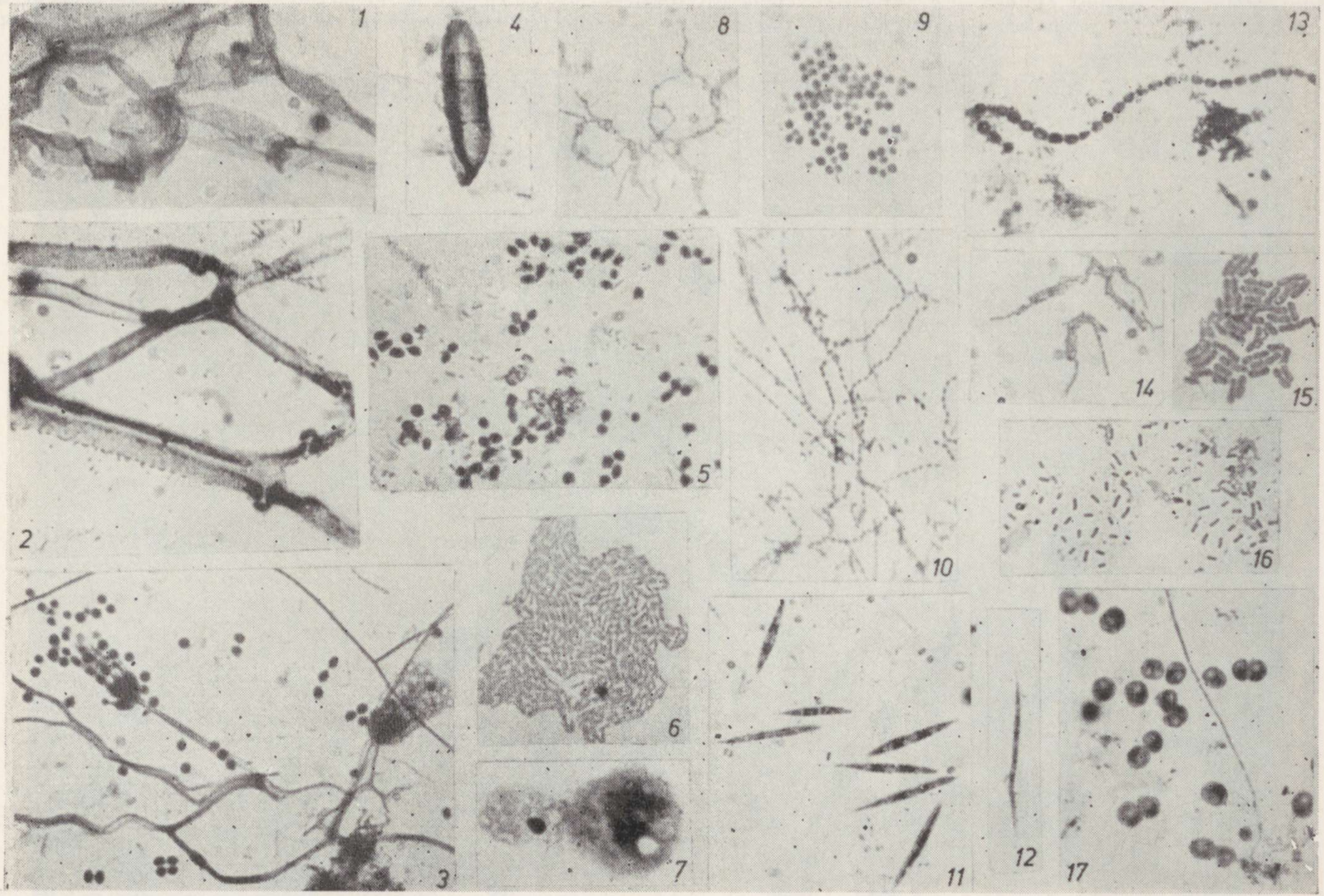

Fig. 1. The microbial landscape of soil under *Cetraria cucullata*, 0—1 cm. ×800. *1* — mycelium of moulds, *2* — mycelium of basidiomycetes, *3* — *Penicillium* sp., *4* — fungal spore, *5* — conidia of moulds, *6*, *15*, *16* — bacteria, *7* — soil amoeba, *8*, *14* — Nocardia spp., *9* — *Microcystis* sp., 10 — actinomycetes, *11*, *12*, *17* — soil algae, Chlorococcales, *13* — *Nostoc* sp.

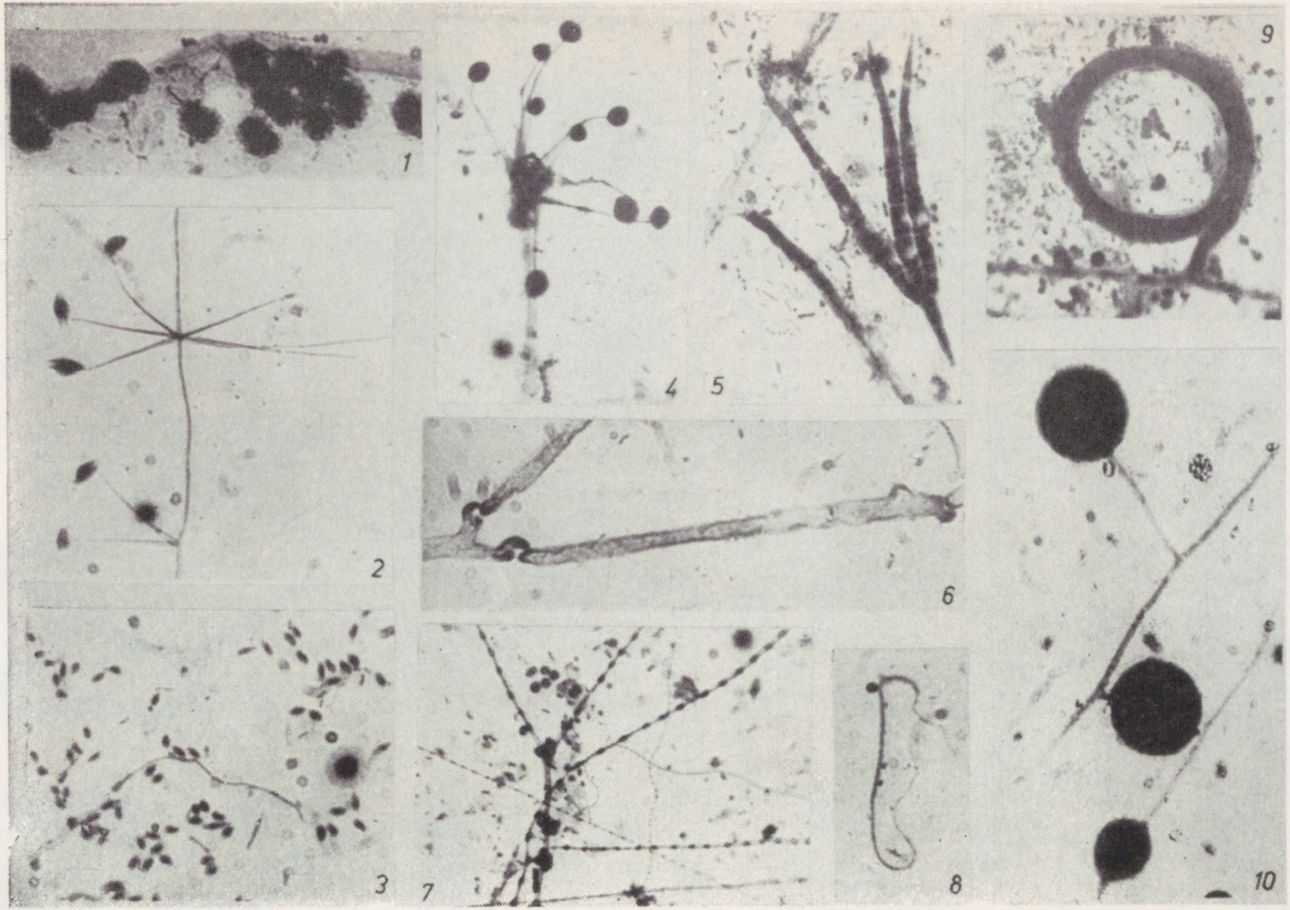

Fig. 2. The microbial landscape under *Cladina arbuscula* (mycelial forms), 0—1 cm ×800. *1* — spores of *Mucor*. sp., *2*, *3*, *4*, *5*, — conidia of micromycetes, *6* — mycelium of basidiomycetes, *7* — mycelium of moulds, *8* — unknown mycelial organism, *9* — capture rings of predacious fungi, *10* — chlamydospores of moulds.

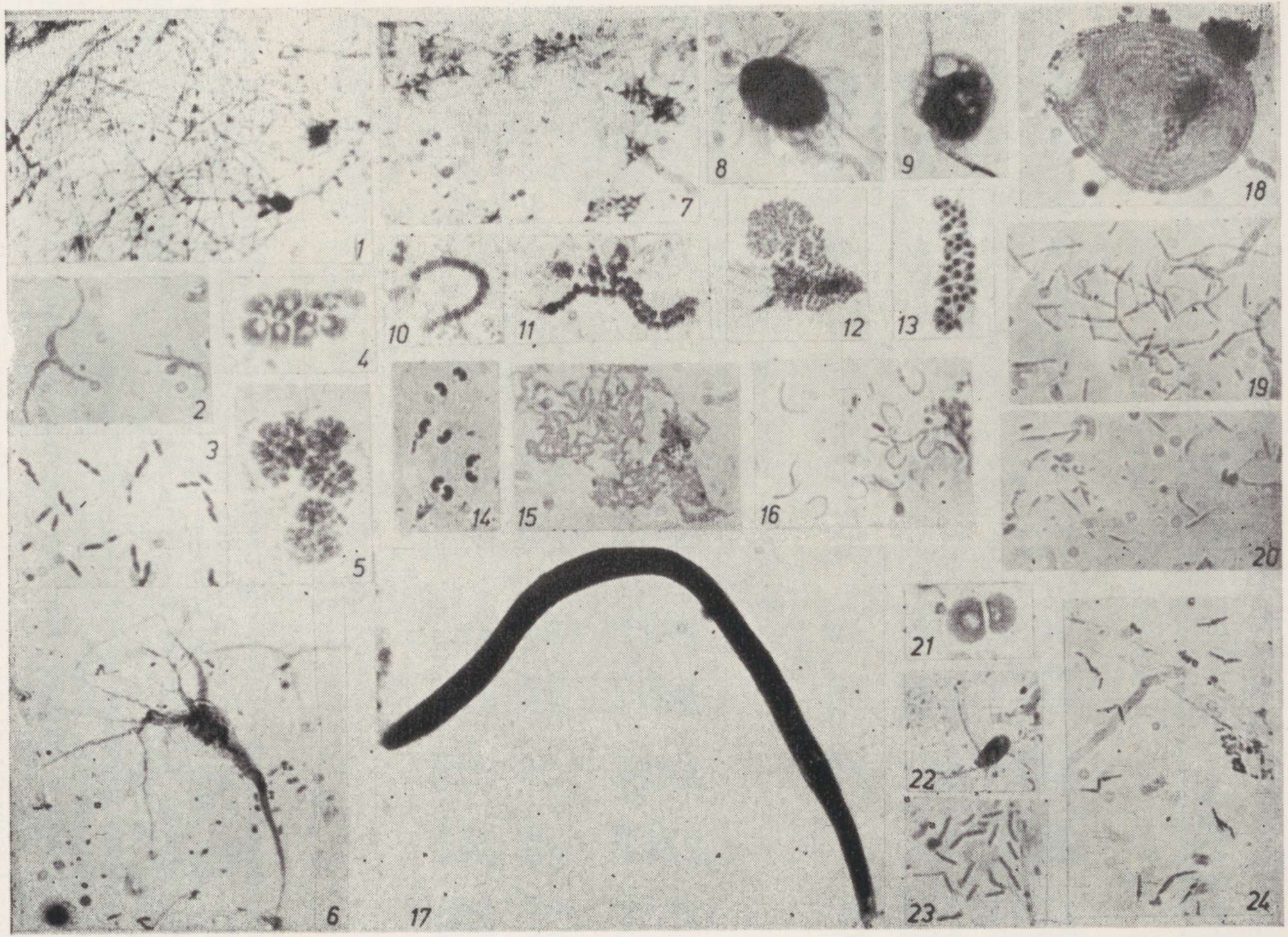

Fig. 3. The microbial landscape under *Cladina arbuscula* (nonmycelial forms), 0—1 cm. × 800. *1* — mycelium of actinomycetes, *2* — *Nocardia* sp., *3, 12, 15, 19, 20, 23, 24* — bacteria, *4, 7* — soil algae, Chlorococcales, *5, 21* — *Gloeocapsa* sp., *6* — *Reticulomyxa* sp., *8, 9, 18, 22* — protozoa, *10, 11* — *Nostoc* sp., *13* — soil algae, Chlorococcales, *14* — *Tetrarcus* sp., *16* — *Dactylococcopsis* sp., *17* — nematode.

Table 1

Chemical properties of soil under lichen cover (0—2 cm)

Site	pH		C, %	Total N, %	C:N	Soluble nutrients, mg/100 g	
	H_2O	KCl				P_2O_5	K_2O
Southern tundra subzone, Taymyr Peninsula							
Ground in placor spotted tundra:							
spot, sandy-loam soil, bare ground	7.4	6.3	0.75	0.03	25.0	2.55	9.80
„ under *Cladonia symphycarpa*	6.3	5.5	1.99	0.07	28.0	1.25	16.70
spot, sandy soil, bare ground	6.4	5.2	1.27	0.07	18.0	2.53	26.20
„ under *Mycobilimbia hypnorum*	5.9	5.0	2.50	0.10	25.0	2.15	n. d.
Sandy banks of Dudypta River:							
bare ground	6.5	5.3	0.13	0.01	13.0	n.d.	10.30
under *Stereocaulon rivulorum*	5.2	4.1	0.41	0.03	13.6	„	19.50
„ *Baeomyces carneus*	5.5	4.4	0.37	0.03	12.3	„	30.40
Sandy ground in ravine:							
bare ground	6.9	5.3	0.16	0.01	16.0	„	15.00
under *Stereocaulon alpinum* var. *platycladum* Frey	5.4	4.1	0.56	0.03	18.6	„	21.90
Forest zone, juniper alvars in Estonia							
Typical sod-calcareous sandy-loam soil:							
bare ground	6.2	5.5	0.30	0.06	5.4	6.75	3.2
under *Cladina arbuscula*	3.6	3.2	0.9	0.67	8.7	3.60	13.70
„ *C. mitis*	3.9	3.2	6.70	0.47	9.6	2.20	13.10
„ *C. rangiferina*	4.8	3.9	7.90	0.44	8.5	2.00	18.90
Primitive leached sod-calcareous sandy soil:							
bare ground	6.5	5.3	0.90	0.16	1.3	7.50	2.10
under *Cetraria cucullata*	4.7	3.6	11.10	0.53	2.9	26.00	13.70
Primitive sandy soil, pebble rendzinas:							
bare ground	7.5	7.3	0.30	0.08	3.8	7.50	3.10
„ *Cetraria nivalis*	6.8	6.5	3.00	0.21	14.3	30.70	15.60
„ *C. islandica*	6.2	5.8	3.50	0.28	12.5	34.00	6.60

n. d. — not determined.

At the same time, strikingly expressed antibiotic characteristics of some secondary lichen substances may cause impoverishment in the composition of soil microbocoenoses. This phenomenon was first observed under natural conditions in the case of phycomycetes by R. Harder and E. Uebelmesser (1958) and in the case of bacteria by J. Malicki (1970).

It is very difficult to determine the extent of the antibiotic activity of a lichen under natural conditions by analysing the whole microbocoenosis. The more diverse the microbial coenosis, the more resistant it is to lichen substances. Still, in such coenoses which are exceptionally poor in the number of species, the antibiotic activity of lichens can be expressed more distinctly.

In that respect, the peculiarities of the microbial landscape in sandy soil under *Cetraria cucullata* may be of interest, as this species has compounds with considerable antibiotic properties (Vartia, 1973). Here the dominating components are moulds, basidiomycetes, and the representatives of Actinomycetales. The development of other microorganisms is depressed to a considerable extent (Fig. 1).

Table 2

Viable counts of soil fungi ($\times 10^3$/g air-dried soil, 0—1 cm or 0—2 cm) under lichen cover, Taymyr

Site	Numbers of fungi	t*
Polar desert, Cape Chelyuskin:		
bare ground	0.26±0.06	
under *Stereocaulon rivulorum*	0.27±0.04	0.14
„ *Cetraria tilesii*	0.25±0.07	0.11
„ *C. delisei*	0.28±0.07	0.22
Arctic tundra, M. Pronchishcheva Bay:		
bare ground	1.4±0.14	
under *Pertusaria dactylina*	1.8±0.70	0.56
Arctic tundra, Dixon:		
bare ground	0.6±0.07	
under *Bryoria nitidula*	11.0±3.0	3.0
„ *Cladina arbuscula*	80.0±20.0	3.9
„ *Stereocaulon vesuvianum*	150.0±10.0	14.9
„ *Cetraria islandica*	20.0±4.0	4.8
„ *C. delisei*	11.0±2.7	3.8
„ *Solorina crocea*	6.0±1.6	3.4
„ *Nephroma arcticum*	29.0±4.0	7.1
Typical tundra, Ossipovka River:		
bare ground	1.5±0.2	
under *Cladina arbuscula*	2.7±0.5	2.3
„ *Cetraria cucullata*	5.0±0.3	9.7
„ *C. nivalis*	49.0±5.0	9.5
„ *Stereocaulon rivulorum*	8±0.4	12.5
„ *S. alpinum*	10.9±1.1	8.5
Southern tundra, Kresty:		
bare ground	2.5±0.5	
under *Mycobilimbia hypnorum*	7.0±2.0	2.2
„ *Cladonia symphycarpa*	7.0±1.0	4.9
bare ground	undet.	
under *Stereocaulon rivulorum*	4.0±1.0	4.0
bare ground	1.7±0.4	
under *Stereocaulon rivulorum*	11.0±1.0	8.7
„ *Baeomyces carneus*	6.7±0.3	10.0

undet. — undetected by method used;
* probability of differences between the numbers of fungi in bare ground and under lichen cover (critical criterion = 2.7).

An example of a very diverse microbocoenosis could be the microbial landscape of typical sod-calcareous soil under *Cladina arbuscula* (Figs. 2, 3). This species, similarly to *Cetraria cucullata*, also contains usnic acid, but its antibiotic impact almost does not express itself due to a high resistance of the abundant and diverse microbial community, whose components differ in their nutrition needs. Fungi which gather often diverse bacterial and algal cells around their hypha dominate also here (Fig. 2). Blue-green algae of the genera *Gloeocapsa*, *Nostoc*, and *Tetrarcus* are abundant, also species of Chlorococcales are quite numerous. Bacterial flora is diverse, the occurrence of actinomycetes and microorganisms of the genus *Nocardia* is observed regularly, protozoa are well-developed, and nematodes are found quite frequently (Fig. 3).

It is easier to determine the antibiotic activity of lichen substances by the reactions of different microorganism groups and species belonging to them.

Table 3

Viable counts of soil fungi ($\times 10^3$/g oven-dried soil; 0—2 cm) under the lichen cover of juniper alvars, Vormsi Island, Estonia

Site	Numbers of fungi	t*
Typical sod-calcareous sandy-loam soil:		
bare ground	90±18	
soil under *Cladina arbuscula*	660±18	22.8
„ *C. mitis*	120±37	2.4
„ *C. rangiferina*	660±151	3.7
Primitive leached sod-calcareous sandy soil:		
bare ground	undet.	
soil under *Cetraria cucullata*	300±67	4.4
Primitive sandy soil, pebble rendzinas:		
bare ground	40±8	
soil under *Cetraria nivalis*	330±71	4.1
„ *C. islandica*	35±11**	0.4

undet. — undetected by method used;
* see Table 2;
** $p<0.95$.

Analyses have shown that the viable counts of moulds in all the subject soils under lichen cover either do not change considerably in comparison with the same data of bare ground, or exceed it to a great extent (Tables 2, 3). The observed phenomenon remains the same irrespective of the season and weather conditions (Паринкина, Пийн, 1984) and it is caused by the fact that the development of moulds depends on the presence of organic matter in the soil environment.

There also exist data about the impact of terricolous lichens on the species diversity of fungi. T. Y. Tolpysheva (Толпышева, 1979) has noted differentiation in micromycetes species under *Cladina stellaris* and *C. rangiferina* in the podzolic soils of the Kola Peninsula pine forests. In the case of equal counts of fungi, changes in the species composition of the section *Biverticillata-Symmetrica* of the genus *Penicillium* were observed. Some of these species were absent under lichen cover. The total number of the species of the genus *Penicillium* under lichens was 30% higher than in the plots without vegetation.

The analysis of the counts of ammonifying bacteria shows that also their numbers under lichen cover either do not differ much from those of bare ground, or exceed it (Table 4). However, the level of the species diversity of this group of bacteria changes noticeably under the impact of lichens and may serve as an indicator of the antibiotic effect of lichens. This has enabled us to draw up a row of lichen species corresponding to their inhibition intensity on microflora, which is quite similar to the row based on the results which were obtained by test culture microorganisms (Table 5).

The estimation of the antibiotic activity of lichens by means of test cultures showed that spore-forming bacteria were the most sensitive to lichen substances and that the development of these bacteria was the most strongly depressed by lichens containing usnic acid. Nonspore-forming bacteria, actinomycetes, and yeasts are less sensitive to the impact of that lichen compound. Observations of test-culture fungi exhibited no sensitiveness to usnic acid (Паринкина, Пийн, 1978, 1984).

Table 4

Viable counts of ammonifying bacteria ($\times 10^3$/g oven-dried soil, 0—2 cm) under the lichen cover of juniper alvars, Vormsi Island, Estonia

Site	Numbers of bacteria	t*
Typical sod-calcareous sandy-loam soil:		
bare ground	2460±310	
soil under *Cladina arbuscula*	960±200	4.0
„ *C. mitis*	810± 78	5.1
„ *C. rangiferina*	2960± 98	1.5
Primitive leached sod-calcareous sandy soil:		
bare ground	1520±191	
soil under *Cetraria cucullata*	1230±226	0.9
Primitive sandy soil, pebble rendzinas:		
bare ground	190± 21	
soil under *Cetraria nivalis*	2560±299	13.6
„ *C. islandica*	2780±190	3.1

* see Table 2.

Table 5

Decrease of the level of antibiotic activity of the lichen species studied

Level of the antibiotic activity of lichens, determined by:		
Analysis of bacterial species diversity (plate count method, Fisher's index)		Testcultures
Species	Fisher's index	
Cetraria nivalis	— 0.79001	*Cetraria nivalis*
C. cucullata	— 0.92649	*C. cucullata*
Cladina mitis	— 0.92741	*Cladina mitis*
Baeomyces carneus	— 0.96054	*C. arbuscula*
Alectoria ochroleuca	— 1.01010	*Nephroma arcticum*
Cladina arbuscula	— 1.02040	*Alectoria ochroleuca*
Nephroma arcticum	— 1.03928	*Bryoria nitidula*
Stereocaulon alpinum var. *platycladum* Frey	— 1.09351	*Baeomyces carneus*
Bryoria nitidula	— 1.10922	*Asahinea chrysantha*
Solorina crocea	— 1.19917	*Stereocaulon alpinum* var *platycladum*
Cetraria laevigata	— 1.23203	*S. alpinum* var. *alpinum*
Cladonia symphycarpa	— 1.24758	*Baeomyces roseus*
Mycobilimbia hypnorum	— 1.31371	*Cladonia symphycarpa*
Nephroma expallidum	— 1.38998	*Solorina crocea*
Cetraria delisei	— 1.39290	*Cetraria delisei*
Stereocaulon rivulorum	— 1.50159	*Nephroma expallidum*
Asahinea chrysantha	— 1.50599	*Cetraria islandica*
Stereocaulon alpinum var. *alpinum*	— 1.56606	*Stereocaulon rivulorum*
Cetraria islandica	— 1.66593	*Cetraria laevigata*
Baeomyces roseus	— 1.66606	*Mycobilimbia hypnorum*

Inhibition of spore-forming bacteria by secondary lichen substances, which may be accurately and easily carried out in laboratories, is difficult to observe under natural conditions. The probability of determining the antibiotic impact of lichens is higher in the soil particles which are in close contact with lichen thalli (Table 6).

Table 6

Viable counts of microorganisms ($\times 10^3$/g oven-dried soil) and usnic acid (%/g dried matter) in the soil layer in close contact with lichen thalli and at the depth of 0—1 cm and 0—2 cm

Site	Fungi	t*	Ammonifying bacteria	t	Spore-forming bacteria	t	Usnic acid	
							soil	lichen
Juniper alvar, Estonia, Vormsi Island								
Cladina arbuscula:								
close contact layer	560±101	1.2	63±14	3.2	7±0.09	3.57	0.14	1.6
depth 0—1 cm	430±43		138±19		12±1.4		undet.	
C. mitis:								
close contact layer	1400±115	7.0	457±160**	1.9	6±1.5**	4.0	0.09	1.72
depth 0—1 cm	350±96**		153±10		16±2		undet.	
Cetraria cucullata:								
close contact layer	530±58	1.3	234±28	2.3	8±2**	23.3	0.42	0.70
depth 0—1 cm	390±95		710±200**		57±0.7		undet.	
C. nivalis:								
close contact layer	360±46		2850±150	1.4	61±10	8.2	0.51	n.d.
depth 0—1 cm	n.d.		2450±250		283±25		undet.	
Typical tundra, Taymyr, Ossipovka River								
C. nivalis:								
close contact layer	58±7	1.04	907±40	18.3	undet.	3.7	n.d.	n.d.
depth 0—1 cm	49±5		113±17		2.6±0.7		n.d.	
Pine forest, Estonia, Altja								
Cladina stellaris:								
close contact layer	1027±59	6.6	1575±219	7.3	2.3±0.6	10.7	n.d.	n.d.
depth 0—2 cm	1680±79		4317±300		11.3±0.6		n.d.	
C. arbuscula:								
close contact layer	690±25	1.1	20980±966	11.1	2.9±0.12	4.6	n.d.	n.d.
depth 0—2 cm	797±91		10130±1480		7.5±1.0		n.d.	

n.d. — not determined;
undet. — undetected by method used;
* see Table 2;
** $p<0.95$.

Table 7

Viable counts of microorganisms ($\times 10^3$/g oven-dried soil, 0—1 cm under the cover of *Stereocaulon* spp., Taymyr Peninsula

Site	Fungi	t*	Ammonifying bacteria	t	Spore-forming bacteria	t
Stereocaulon rivulorum						
close contact layer	14±1.5 8±4.4	4.0	44±11** 3.2±0.4	3.5	0.16±0.04** 0.90±0.02	18.5
S. alpinum						
close contact layer	9.7±0.3 10.9±1.1	1.05	243±2 159±6	13.3	1.4±1.0** 7.2±1.8**	3.0

* see Table 2;
** $p<0.95$.

The absence of the inhibition of lichen substances on spore-forming bacteria already at the depth of 2 cm indicates that leached metabolic products of lichens do not penetrate to deep soil layers even in mechanically light soils and remain mainly in the soil layer which is in close contact with lichen thalli. The absence of the toxidity of lichen substances in deeper soil layers may be explained by poor solubility of lichen substances in water, their ability to form chelates with metal ions (Schatz, 1963; Iskandar, Syers, 1971), and the decomposition of these compounds by soil microflora (Bandoni, Towers, 1967; Паринкина, Пийн, 1989). Therefore, it is difficult to explain the results obtained by J. Malicki (1965) according to which usnic acid could be found at the depth of 70 cm.

Table 7 shows a decrease in the numbers of spore-forming bacteria in tundra soil under the cover of representatives of the genus *Stereocaulon* which contains no usnic acid and has no (or a weak) antibiotic activity with respect to the test cultures of spore-forming bacteria. In our previous investigations (Паринкина, Пийн, 1978) it was shown that the development of microflora is inhibited under *Stereocaulon rivulorum* in sandy soils which have a low content of mineral nutrients. Therefore, it is obvious that atranorin and lobaric acid, lichen substances with weak antibiotic activity (Vartia, 1973), may noticeably inhibit microorganisms in poor soils which contain few microorganisms in number and species.

Hence, the peculiarities of the development of microbocoenoses under the cover of terricolous lichens depend on several factors. On the one hand, the level of the metabolic activity of lichens and the composition of their metabolites can be mentioned. On the other hand, characteristics of soil cover and, related to it, abundance of soil microflora, are of importance. In mixed populations, inhibitory metabolic products of some species may be the source of nutrition for others (Freitas, Frederickson, 1978). Therefore, in diverse microbocoenoses the antibiotic activity of lichens is less strongly expressed due to the lower sensitivity of coenosis. In poor coenoses the antibiotic impact of lichens is more distinct.

In general, the lichen cover stimulates the development of microflora due to a more stable moisture regime and a higher content of mineral nutrients and organic matter for the microorganisms in the place where lichen is attached to the soil. In this region natural decomposition of terricolous fruticose lichens takes place. Further study of this process is needed.

The observations carried out in tundra and forest zones showed that one and the same lichen species had the same stimulating and inhibiting impact on soil microbocoenoses both in tundra and in the forest.

REFERENCES

Bandoni, R. J., Towers, G. H. N. 1967. Degradation of usnic acid by microorganisms. — Canad. J. Biochem. **45**, 7, 1197—1201.

Freitas, N., Frederickson, A. G. 1978. Inhibition as a factor in the maintenance of the diversity of microbial ecosystems. — J. Gen. Microbiol., **106**, 2, 307—320.

Harder, R., Uebelmesser, E. 1958. Über dia Beeinflussung niederer Erdphycomyceten durch Flechten. — Arch. Mikrobiol., **31**, 1, 82—86.

Iskandar, J. K., Syers, J. K. 1971. Metal-complex formation by lichen compounds. — J. Soil. Sci., **23**, 3—7.

Lawrey, J. D. 1986. Biological role of lichen substances. — The Bryologist, **89**, 2, 111—122.

Malicki, J. 1965, Wpływ kwasów porostowych na mikroorganizmy glebowe. I. Wypłukiwanie kwasów do gleby. — Ann. Univ. M. Curie-Sklodowska, C, **20**, 16, 239—248.

Malicki, J. 1970. Wpływ kwasów porostowych na mikroorganizmy glebowe. III. Wpływ gatunków z rodzaju *Cladonia* na stosunki bakteryjne w glebie zespołu *Peucedano-Pinetum cladonietosum.* — Ann. Univ. M. Curie-Sklodowska, C, **25**, 11, 75—80.

Schatz, A. 1963. Soil microorganisms and soil chelation. The pedogenic action of lichen and lichen acids. — J. Agr. and Food Chem., **11**, 2, 112—118.

Tearle, P. V. 1987. Cryptogamic carbohydrate release and microbial response during spring freeze-thaw cycles in Antarctic fellfield fines. — Soil Biol. and Biochem., **19**, 4, 381—390.

Vartia, K. O. 1973. Antibiotics in lichens. In: The Lichens. V. Ahmadjian, M. E. Hale, eds. Academic Press, New-York; London, 547—561.

Аристовская Т. В., Паринкина О. М. 1961. Новые методические приемы изучения почвенных микроорганизмов. — Почвоведение, 1961, 1, 20—28.

Виноградский С. Н. 1952. Микробиология почвы. Проблемы и методы. АН СССР, Москва.

Паринкина О. М. 1989. Микрофлора тундровых почв. Эколого-географические особенности и продуктивность. Наука, Лен. отд., Ленинград.

Паринкина О. М., Пийн Т. 1978. Почвенный микробоценоз как индикатор условий среды под покровом напочвенных лишайников. In: Лихеноиндикация состояния окружающей среды. АН Эстонской ССР, Таллинн, 107—113.

Паринкина О. М., Пийн Т. Х. 1984. Особенности микробоценозов под покровом напочвенных лишайников. In: Флора и группировки низших растений в природных и антропогенных экстремальных условиях среды. АН Эстонской ССР. Таллинн, 51—69.

Паринкина О. М., Пийн Т. Х. 1989. Разложение напочвенных кустистых лишайников в условиях бореальной зоны. — Экология, 1989, 3, 31—39.

Пийн Т. Х., Сдобникова Н. В., Паринкина О. М. 1984. Начальные стадии зарастания пятен голого грунта в южных тундрах Таймыра. In: Флора и группировки низших растений в природных и антропогенных экстремальных условиях среды. АН Эстонской ССР, Таллинн, 20—50.

Толпышева Т. Ю. 1979. Влияние лишайников на заселение почв микроскопическими грибами. — Микология и фитопатология, **13**, 3, 194—199.

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