Folia Cryptog. Estonica, Fasc. 41: 45–54 (2005)

Influence of environmental factors on the local-scale distribution of cyanobacterial lichens: case study in the North Urals, Russia

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Abstract: Distribution and frequency of 11 cyanobacterial lichen species on *Populus tremula* trunks were studied in the mountain taiga of the North Urals. Within an area of 150×200 m, all aspen trunks were registered, and a range of environmental variables (including characteristics of tree stand, herbs, dwarf-shrubs and mosses; 30 variables in total) were noted within a circle of 6 m diameter around each tree. This study suggests the environmental variables to be of small importance for spatial distribution of the lichens on a local scale. However, the abundance of the species was shown to depend on size and vitality of their host trees, reaching maximal values in oldest damaged trees.

Kokkuvõte: Keskkonnategurite mõju tsüanobaktereid sisaldavate samblike levikule lokaalskaalas: piloot-projekt Põhja-Uuralitest, Venemaalt.

Põhja-Uuralite mägitaigas uuriti 11 tsüanobaktereid sisaldava samblikuliigi levikut ja sagedust haava (*Populus tremula*) tüvedel. 150×200 m alal registreeriti kõik haavatüved, ja 6 m läbimõõduga ringides ümber iga puu märgiti üles rida keskonna muutujaid (sealhulgas puistu karakteristikud, taimed, puhmad ja samblad; kokku 30 muutujat). Uurimusest tuleneb, et samblike ruumilise leviku jaoks lokaalskaalas on keskkonna muutujad vähese tähtsusega. Ometi sõltus liikide ohtrus peremeespuude suurusest ja elujõulisusest, saavutades suurima väärtuse vanimatel vigastatud puudel.

INTRODUCTION

Cyanobacterial lichens are a rather specific group of lichens from both physiological and ecological points of view. Many of them are highly sensitive to any kind of ecosystem disturbances and are suggested as being indicators of ecological continuity, or old-growth forest indicators (Gauslaa, 1994, Kuusinen, 1996, Sillett & McCune, 1998, etc.). Among cyanolichens, there is a range of rare and endangered species included to Red lists of many European countries. Use of cyanolichens as biological indicators as well as necessity of their conservation require better understanding of environmental factors influencing their distribution in different spatial scales, from a forest patch up to the species distribution area as a whole.

Factors determining distribution of lichen species at different spatial levels can be very different, for example, climate parameters, altitude, and regional air quality are responsible for the lichen distribution at regional scale, and forest vegetation parameters are of the highest importance at subregional spatial scale (Will-Wolf et al., 2004).

Our investigations were carried out in one of few old-growth forests left in the North Urals. Continental climate of the Ural Mountains together with high level of industrialization of the region does not advantage high diversity and abundance of epiphytic cyanolichens. Hot spots of cyanolichen diversity can be found in mountain taiga under conditions of higher humidity and low level of any kind of human activity though even these habitats are unfavorable for cyanolichens. Under these conditions, all relationships between lichens and environment are expected to be more pronounced. Our study was aimed to assess the importance of environmental factors for the distribution and frequency of cyanolichens on the local scale (few hectares within more or less homogeneous tree stand).

MATERIAL AND METHODS

The study was carried out in the mountain taiga of the North Ural near the village of Kytlym (Sverdlovsk region, 59°28'N, 59°14'E). The climate is moderately continental, with an annual aver-

age precipitation of 492 mm. The mean annual temperature is –0.2°C; mean January and July temperatures are –16.4°C and 13.9°C, respectively. The duration of the frost-free period is 96 days (Reference book..., 1965, 1968).

The area belongs to the middle taiga phytogeographical subzone (Kolesnikov et al., 1973). The sample plot was established in the lower part (460 m a.s.l.) of the western slope of Pervyi Bugor mountain (931 m a.s.l.). The tree stand was composed by *Picea obovata, Abies sibirica, Pinus sibirica, Populus tremula,* and *Betula pubescens* with an average age of 120 years. The soil was well-drained, deep and rocky, and was classified as brown forest mountain soil (Firsova, 1977). In the understorey vegetation, *Vaccinium myrtillus, Oxalis acetosella, Calamagrostis obtusata, Pleurozium schreberi,* and *Hylocomium splendens* dominated.

Populus tremula was selected as a phorophyte for studying cyanolichens because of high water capacity of its bark (Barkman, 1958) which is advantageous for cyanolichens. Within an area of 150×200 m, all aspen trees with diameter at breast height (DBH) of at least 30 cm were registered (182 trees). On all registered trunks, the frequencies of cyanolichens were recorded using a sample grid of 10 units adapted to fit half the circumference of each trunk (Herzig & Urech, 1991). The grid was placed sequentially on the basal (0–0.5 m above ground) halves of the trunks and on those at 1.0–1.5 m above ground. Thus, species frequency on the trunk ranged from 0 to 40. For species growing out of quadrates, only presence was recorded.

The following parameters were noted for each tree: DBH, class of vitality [1 – healthy, 2 – damaged (parasitic fungi or mechanical damages), 3 – dead], and inclination (measured with an inclinometer). Age of 45 healthy trees was determined with an increment borer. Obtaining of accurate age estimates for damaged aspens was problematic because of decaying of heartwood.

A range of environmental variables was registered within a circle of 6 m diameter around each tree: 1) tree stand characteristics (basal area of coniferous and deciduous trees, total basal area, and crown parameters); 2) density of young growth in three height classes: < 50 cm, 50–100 cm, and >100 cm; 3) density of shrubs and trees of undergrowth in three height classes: < 50 cm, 50–100 cm, and >100 cm; 4) characteristics of understorey vegetation [abundance and number of herb and dwarfshrub species, total cover of bryophytes, total cover of herbs and dwarf-shrubs, average height of lowest and tallest herb and dwarf-shrub layers, the share of three dominant species (*Calamagrostis obtusata, Oxalis acetosella,* and *Vaccinium myrtillus*)].

To estimate canopy cover above sample trees, 8 digital pictures of crowns were taken around each tree: at 4 cardinal points in circles of 0.5 m and 1 m radius around the tree (the camera was placed at the 1 m height from the ground). The percentage of open sky area (ratio of number of pixels that fall on the open sky to the total number of pixels) and the index of crown density (ratio of number of pixels that fall on the boundary sky/crown to the number of pixels that fall on the crown) were calculated in color images using SIAMS Photolab software (developed by SIAMS, Ekaterinburg, http://siams.com).

To determine ecological indices of the sites (indices of insolation, moistening, soil acidity, continentality, soil fertility, and thermal regime), Ellenberg's indicator values scale (Ellenberg et al., 1991) was used. Each species of the herb and dwarf-shrub layer was referred to one of ecological groups. Indices were calculated as weighted averages of Ellenberg's indicator values.

To determine bark acidity, samples of upper layer (1–2 mm) were collected from four cardinal points of 80 model aspen trees at 1–1.5 m height. Model trees were selected to allow for the balanced model of 2-way ANOVA (tree vitality and tree DBH as independent factors). In the laboratory, bark samples were cleaned from bryophytes and lichens under dissecting microscope and were ground with a laboratory mill. One gram of the powder was suspended in 25 ml of distillated water in stoppered vials, placed to a shaker for 30 min and then left for 30 min. After this, pH was measured with standard glass electrode without filtration.

RESULTS AND DISCUSSION

Sample tree and site characteristics

Sample aspens varied significantly in their size (Table 1). Age of model healthy trees ranged between 53 and 130 years. Pearson correlation coefficient between age and DBH was 0.66 at $p<0.05$; the mean DBH corresponds to the age of about 80 years. The age of largest damaged trees

Table 1. Some characteristics of the sample plot

Variables	Mean	SE	CV (%)	Min	Max
DBH of aspen trees (cm)	80.57	1.88	31.54	32.50	145.00
Total basal area of tree stand (m^2/ha)	41.42	1.47	48.07	0.00	108.61
% open sky: 0.5 m from the trunk	0.22	<0.01	26.33	0.07	0.48
% open sky: 1 m from the trunk	0.24	<0.01	25.34	0.10	0.47
Index of insolation	5.07	0.03	8.62	3.60	5.88
Index of moistening	5.60	0.01	3.53	5.03	6.05
Bryophyte cover (%)	55.57	1.68	40.99	10.00	95.00
Cover of herb and dwarf-shrub layer (%)	68.57	0.79	15.57	40.00	86.00
Average bark pH per trunk	6.10	0.05	7.62	4.40	6.77
Minimal pH value per trunk	5.69	0.07	11.49	4.19	6.64
Maximal pH value per trunk	6.49	0.04	5.79	4.82	7.09

can probably exceed 150 years. Healthy trees prevailed among aspens; 40.7% of aspens had different signs of damage (fruit bodies of fungi, mainly *Phellinus tremula,* mechanical injuries, frost splits, etc.), and only one tree was dead.

Bark pH was found to vary in great extent both between and within sample trees. Range within the same trunk sometimes reached 2.2 units, so we had to treat minimal, maximal and average pH values for each trunk as separate variables (Table 1). Two-way ANOVA (SS III, DBH and vitality as fixed factors) revealed significant contribution of DBH to the variability of maximal pH values (F = 5.5, df=4, 63, p<0.01); bark pH smoothly rose with the increase of tree size (Fig. 1). Bark of damaged trees tended to be slightly more acid (difference was not significant, F = 2.57, df=1, 63, p=0.11). For the variability of minimal pH values, DBH was not found to be an important factor; tree vitality, on the contrary, contributed significantly (F = 4.4, df=1, 63, p<0.05). Acidification of the bark of damaged trees might probably be explained by activity of parasitic fungi secreting acidic substances though this question needs special investigations. High variability of pH values within the same trunk is most probably due to "dripzone effect" (Goward & Arsenault, 2000). For example, acid leachates from neighbouring coniferous trees can cause acidification of aspen bark

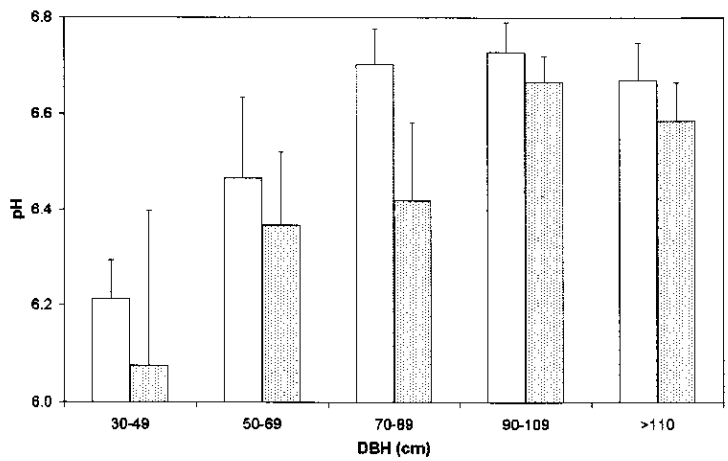

Fig. 1. Maximal values of bark pH (from 4 measurements) *vs* aspen DBH (means ± SE). White bars – healthy trees, dotted bars – damaged trees.

which in turn leads to the inoculation of aspens by acidophytic lichens that are generally not typical for this phorophyte, such as *Hypogymnia physodes* and *Vulpicida pinastri*. Generally, the range of pH values at the sample plot (4.19–7.09) corresponds to values found for aspen trunks in middle and southern boreal forests of Finland (Kuusinen, 1994).

Mean values of the total basal area and crown cover indicate rather close tree stand. Basal area was the most variable among environmental parameters registered; crown characteristics were more stable (Table 1). Cover of bryophytes also varied in a great extent indicating differences in soil moistening. Though variation coefficients of ecological indices were low, actual range of ecological factors can be rather high: for example, minimal found value of insolation index (3.6) corresponds to shadowed habitats while maximal value (5.88) falls between half-shadowed and half-opened habitats (Ellenberg et al., 1991). Thus, within the more or less homogeneous local tree stand, some heterogeneity of environmental factors exists which can be of importance for distribution and abundance of epiphytic lichens.

Table 2. List of species under study and their frequencies

Species	No of findings	% of *P. tremula* trunks colonized
Collema subflaccidum Degel.	5	2.74
Leptogium intermedium (Arnold) Arnold	1	0.55
L. saturninum (Dicks.) Nyl.	12	6.59
Lobaria pulmonaria (L.) Hoffm.	17	9.34
Nephroma parile (Ach.) Ach.	18	9.89
N. resupinatum (L.) Ach.	16	8.79
Pannaria pezizoides (Weber) Trevis.	10	5.49
Peltigera aphthosa (L.) Willd.	6	3.30
P. canina (L.) Willd.	24	13.19
P. polydactylon (Neck.) Hoffm.	6	3.30
P. praetextata (Sommerf.) Zopf	5	2.76

Cyanolichen species composition

A total of 11 cyanolichen species were found on the 182 aspens sampled (Table 2). Most of them, especially *Nephroma* species and red-listed species *Lobaria pulmonaria*, have been often mentioned as indicators of old-growth forests in Eurasia and North America (Rose, 1976, Kuusinen, 1996, Kondratyuk et al., 1998, Sillett & McCune, 1998, etc.). At 60.18% of investigated aspen trunks, at least one cyanolichen species was found. However, the share of trunks inoculated by individual species proved to be very low and in most cases did not exceed 10%. *Leptogium intermedium*, which was found on a single aspen tree, was excluded from the further analysis.

Frequency of cyanolichens *vs* site characteristics

Factor analysis was applied to reduce the total variation of measured environmental variables to three independent factors that were interpreted respectively as site insolation, soil fertility and canopy openness (Table 3). Interpretation of factor 1 and factor 3 looks at the first glance very similar: both of them reflect light conditions. The difference seems to be in the following: factor 1 includes parameters of grass and dwarf-shrub layer thus reflecting light regime over the 6 m diameter sample plot while factor 3 includes mainly the crown parameters which were registered within 1 m from the trunk and hence reflects insolation of the sample trunk. Factor loadings of parameters of the host trees, undergrowth trees and young growth were negligible. Three extracted factors explained 45% of the total variance.

At the next step of analysis, Spearman rank order correlation coefficients were calculated between lichen frequencies and the factors extracted (Table 4). *Peltigera* species and *Collema subflaccidum* did not show any dependency from the factors extracted; for the rest of species, significant correlation with at least one factor was revealed. Frequency of four cyanolichen species negatively correlated with site insolation (though correlation was extremely weak). The most probable, this is not the low site insolation which favors development of cyanolichens, but accompanying higher ambient humidity. Besides,

Table 3. Factor loadings of site and phorophyte variables (marked with * loadings are >0.5)

Variables	Factor 1 Site insolation	Factor 2 Soil fertility	Factor 3 Canopy openness
Phorophyte data			
DBH	-0.24	0.00	-0.33
Vitality	-0.23	-0.06	-0.06
Inclination	-0.31	-0.02	-0.03
Tree stand characteristics			
Basal area of coniferous trees	-0.29	0.11	-0.40
Basal area of decidious trees	0.35	0.03	-0.41
Total basal area	0.02	0.11	-0.62*
% open sky:			
0.5 m from the trunk	0.17	0.04	0.81*
1 m from the trunk	0.10	0.05	0.80*
Crown density:			
0.5 m from the trunk	-0.04	-0.23	-0.68*
1 m from the trunk	-0.04	-0.26	-0.68*
Density of young growth			
height < 50 cm	-0.13	0.35	-0.10
height 50–100 cm	-0.28	0.13	0.11
height >100 cm	-0.46	0.02	0.30
Density of shrubs and trees of undergrowth			
height < 50 cm	0.19	-0.22	-0.15
height 50–100 cm	0.19	0.00	0.28
height >100 cm	-0.16	-0.03	0.17
Understorey vegetation			
Abundance of herb and dwarf-shrub species	0.30	0.64*	0.31
Number of herb and dwarf-shrub species	0.24	0.77*	0.25
Cover of bryophytes	-0.07	-0.58*	0.33
Cover of herb and dwarf-shrub layer	0.67*	0.14	0.32
Mean height of the lowest herb layer	0.69*	-0.02	0.15
Mean height of the tallest herb layer	0.72*	0.34	0.11
The share of:			
Calamagrostis obtusata	0.66*	-0.12	-0.07
Oxalis acetosella	-0.69*	0.52*	-0.17
Vaccinium myrtillus	-0.07	-0.89*	-0.12
Site indices (based on Ellenberg's indicator values scale)			
Index of insolation	0.82*	-0.40	0.07
Index of moistening	0.73*	0.09	0.30
Index of soil acidity	0.61*	0.66*	0.05
Index of continentality	0.28	-0.76*	0.01
Index of soil fertility	0.01	0.90*	0.14
Index of thermal regime	0.06	-0.15	-0.20
% of variation explained	16	16	13

Table 4. Spearman rank order correlation coefficients for correlation between lichen frequencies and environmental data (* – p<0.05, ** – p<0.01, *** – p<0.001)

Species	Factor 1 Site insolation	Factor 2 Soil fertility	Factor 3 Canopy openness
Collema subflaccidum	0.04	0.09	-0.11
Leptogium saturninum	-0.23 **	0.04	-0.16 *
Lobaria pulmonaria	-0.19 **	0.12	-0.10
Nephroma parile	-0.16 *	0.10	-0.06
N.resupinatum	-0.28 ***	0.06	-0.09
Pannaria pezizoides	-0.04	0.15 *	-0.10
Peltigera aphthosa	0.106	-0.003	0.074
P. canina	-0.111	0.062	-0.002
P. polydactylon	0.013	0.026	0.008
P. praetextata	-0.021	0.075	-0.090

site insolation has been reflecting history of the plot: for instance, high insolation means previously happened tree-fall which was followed by rapid development of light-demanding forbs and deciduous young growth. Epiphytic lichens inoculated the sample trunk at least tens of years ago, so looks probable that lichen occurrence correlates not with present-day but with previous-day environment.

Rather unexpected was the absence of correlation of lichen frequency with canopy openness (excluding for *Leptogium saturninum),* i.e. with light regime of the microhabitat. As in the case of site insolation, the effect of trunk insolation hardly can be separated from that of other factors, especially, from water relations. Crown parameters significantly affect amount of water passing down as stemflow. Epiphytic gelatinous cyanolichens often grow in rain-tracks; however, presence and pattern of rain-tracks can not be predicted from our data on crown cover and density.

Multiple linear stepwise regression analysis (ridge regression) showed that environmental variables accounted for a very low (<20%) part of variability of cyanolichen species frequency (Table 5). For different species, from 6 to 15 site variables were included to the model; so extracting of one or two major factors was not possible. Integral parameters (number of cyanolichen species per trunk and total frequency of cyanolichens) were found to be "more predictable" on the base of collected site characteristics.

Discriminant analysis was applied to data on presence/absence of lichen species (without quantitative information on frequency). The results confirmed the conclusion of the multiple regression analysis: frequency of correct predictions of presence/absence of lichen species was extremely low and ranged from 16 to 66%.

Table 5. Results of ridge step-wise regression analysis (*df1* is a number of variables included to the model, *df2* is *df* Error)

	Adjusted *R2*	*df1*	*df2*	*F*	*p*
Collema subflaccidum	0.036	7	179	1.99	0.059
Leptogium saturninum	0.140	12	174	3.52	<0.001
Lobaria pulmonaria	0.151	11	175	4.01	<0.001
Nephroma parile	0.052	6	180	2.71	0.015
N. resupinatum	0.180	12	174	4.40	<0.001
Pannaria pezizoides	0.119	9	177	3.79	0.001
Peltigera aphthosa	0.046	6	174	2.45	0.027
P. canina	0.139	9	171	4.24	<0.001
P. polydactylon	0.033	7	173	1.89	0.074
P. praetextata	0.063	7	173	2.72	0.010
Peltigera spp. (total frequency)	0.097	7	173	3.77	<0.001
Total frequency of cyanolichens	0.214	15	171	4.38	<0.001
No of cyanolichen species	0.345	13	173	8.52	<0.001

Thus, predictive power of collected environmental data is very low. This means that at the few hectares spatial scale heterogeneity of site characteristics seems not to influence significantly the occurrence of cyanolichens.

Relationship between phorophyte parameters and frequency of cyanolichen species

The dependency of lichen community composition on such trunk parameters as size (i.e. tree age), inclination and vitality is of wide knowledge (Barkman, 1958; Kalgutkar & Bird, 1968; Bates, 1992, etc.). However, as indicated above, phorophyte parameters showed very weak correlation with factors extracted, and their influence on lichen occurrence was not adequately analysed. Because of this, two-way ANOVA was used to estimate contribution of tree DBH and vitality to the overall variability of lichen frequency [5 groups of DBH × 2 vitality classes (healthy and damaged)]. To assess influence of tree inclination, one-way ANOVA was used (number of observations did not allow three-way ANOVA).

For *Lobaria pulmonaria*, *Nephroma resupinatum* and *Peltigera aphthosa* DBH was found to contribute significantly to the variability of frequencies (Table 6). Frequency of *L. pulmonaria* and *N. resupinatum* was higher on larger trunks (Fig. 2). Tree vitality was also of high importance for these species, especially for *N. resupinatum*, which was found on damaged trees only. Combination of the factors (DBH + vitality) was highly significant for three species mentioned above, and also for *Nephroma parile* and for the total frequency of *Peltigera* species.

Most cyanolichen species had a similar pattern of response to phorophyte parameters: their frequency increased with an increase of tree size and with lowering of its vitality thus reaching maximal values on the largest damaged trunks. The only exception was *Peltigera* species (Fig. 2) that showed maximal frequency on small-sized

Table 6. Results of ANOVA (*SS* III) for the lichen frequencies (*df* Error= 170 in all cases)

Species	Sources of variation			
	DBH	Tree vitality	DBH + vitality	Tree inclination
	df=4	*df*=1	*df*=4	*df*=2
	F	*F*	*F*	*F*
	p	*p*	*p*	*p*
Collema subflaccidum	1.59	1.91	0.12	1.56
	0.179	0.169	0.883	0.186
Lobaria pulmonaria	5.68	7.63	4.22	5.65
	<0.001	0.006	0.016	<0.001
Leptogium saturninum	1.30	3.86	1.80	1.01
	0.271	0.051	0.169	0.406
Nephroma parile	1.86	2.69	1.46	2.47
	0.120	0.103	0.235	0.046
N. resupinatum	3.72	8.46	7.57	3.79
	0.006	0.004	0.001	0.006
Pannaria pezizoides	1.29	1.59	1.08	1.34
	0.275	0.210	0.343	0.258
Peltigera aphthosa	2.57	1.35	6.52	3.80
	0.040	0.246	0.002	0.005
P. canina	1.53	0.99	0.67	2.01
	0.197	0.322	0.511	0.095
P. polydactylon	0.52	0.61	2.05	1.45
	0.719	0.436	0.131	0.219
P. praetextata	0.44	0.82	0.97	0.44
	0.782	0.366	0.380	0.782
Peltigera spp. (total frequency)	0.65	0.06	1.10	2.96
	0.626	0.806	0.334	0.021

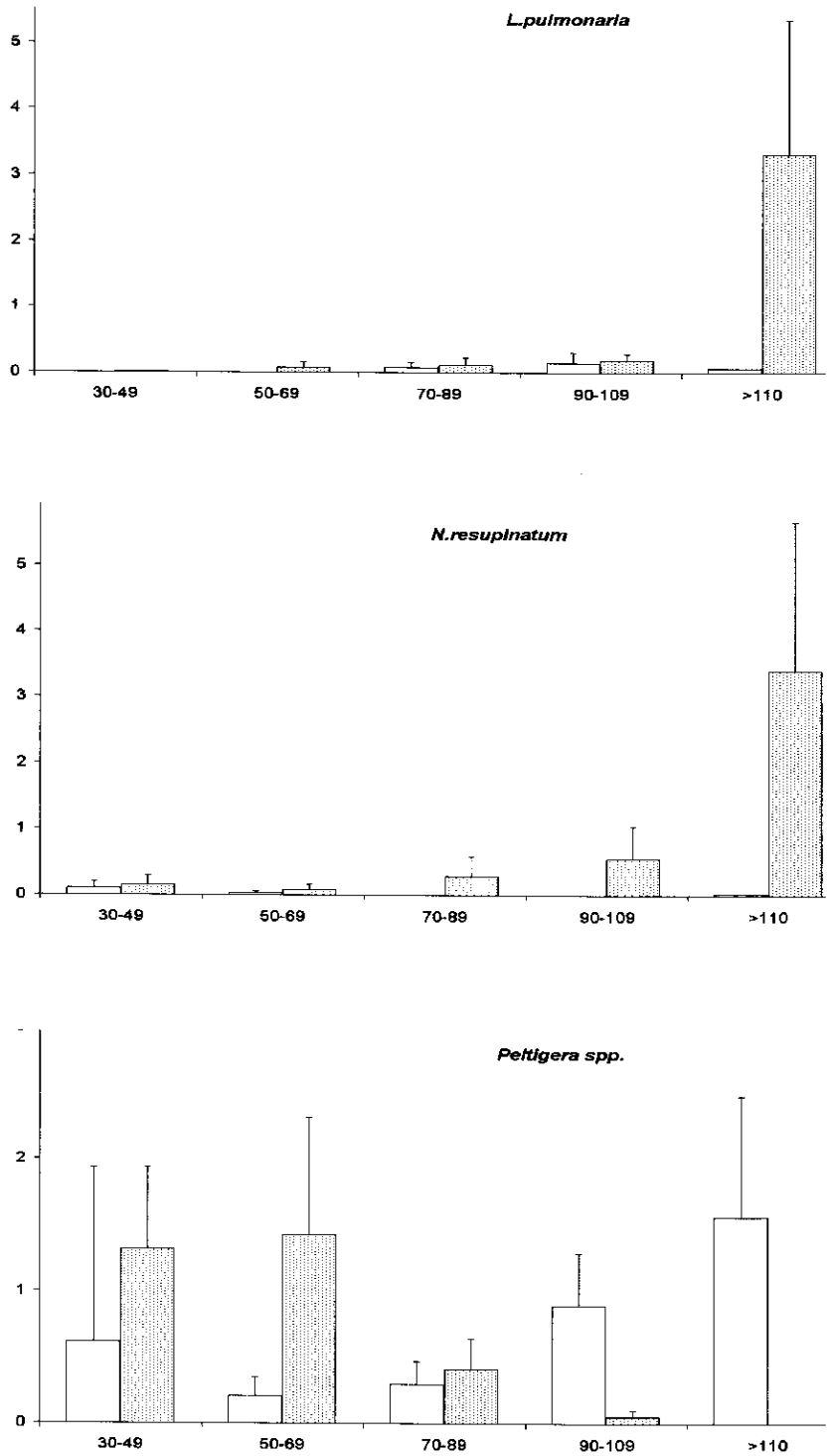

Fig. 2. Frequencies of cyanolichens *vs* DBH of host trees (means ± SE). Axes: X – DBH (cm), Y – lichen frequency. White bars – healthy trees, dotted bars – damaged trees.

damaged trunks. Making comparisons with successional stages, we may suggest different patterns of epiphytic successions on bases of healthy and damaged trunks. We suppose that reason for this difference can be in relationships between *Peltigera* species and characteristics of successively changing epiphytic bryophyte communities. This relationship can include, first, direct moss-lichen competition and, second, indirect influence of bryophytes on *Peltigera* species through changes in the water regime of microhabitat.

Frequencies of three species (*Lobaria pulmonaria, Nephroma resupinatum,* and *Peltigera aphthosa)* were influenced by inclination of trunks: the highest frequency was found on trunks with inclination more than 15°.

Thus, preferred habitats for the majority of studied cyanolichens are large trees that were shown to have highest values of bark pH. However, we failed to reveal statistically significant correlation between frequency of cyanolichens and bark pH. The only exception was *Nephroma resupinatum* which showed significant correlation with minimal pH value per trunk (Spearman rank order correlation coefficient –0.26, $p < 0.05$). Thus, pH values, at least in the range found in this study, hardly can be regarded as an important factor for the growth of cyanolichens.

CONCLUSIONS

This study suggests low probability to predict both presence and frequency of cyanolichens from the data on the range of environmental variables within small (few hectares) relatively homogeneous tree stand. This is in contrast to results on larger scales where authors usually manage to reveal major factors influencing lichen species distribution (forest type, macroclimate, air pollution, etc.). Spatial scale of our study causes relatively low range of variability of environmental factors, and within this range the factors seem not to be limiting for cyanolichens (except for the size of host tree). Impossibility to extract major factors that are responsible for the lichen distribution causes low predictive power of collected variables. Besides, low frequency of studied cyanolichen species makes the obtaining of statistically significant results very difficult.

Another reason of failure to find clear dependency between lichen distribution and site characteristics is in not taking in the account reproductive potential of lichens studied (number of propagules produced, distance of propagule dispersion, success of survival, etc.). However, biological features like limited dispersion ability, which was mentioned for most of lichen species studied (Scheidegger, 1995; Zoller et al., 2000), can be of high importance in defining patterns of lichen distribution within a small area and can mask significance of ecological factors. Simply stated, lack of propagules can cause absence of lichens even in the most favorable environment.

ACKNOWLEDGMENTS

We are grateful to Yu. Paivina, A. Kharin, and I. Sharounova for their help in the field works, O. Mezhevikina for the measuring of bark pH, and A. Ermakov for the analysis of digital images of canopy cover. The study was funded by Swiss National Science Foundation (Project 7SUPJ62353)

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