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# Diversity of lichens and allied fungi on Norway spruce (*Picea abies*) in the middle boreal forests of Republic of Karelia (Russia)

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**Abstract:** A detailed study of lichen diversity and estimation of epiphytic lichen cover characteristics on spruce as a key ecosystem component was performed in boreal forests of Karelia (NW Russia). The aims of the present paper are: (1) to study lichen diversity on Norway spruce in the middle boreal forests of southern Karelia (NW Russia), and (2) to estimate the main characteristics of epiphytic lichen cover on spruce trunks and branches. In total, 158 species of lichens and allied fungi were found on spruce, including 108 species on trunks, 78 on branches and 55 on snags. Seventeen species are listed in the Red Data Book of Republic of Karelia. Ten species are new for the biogeographical province *Karelia transonegensis* and two for the province *Karelia onegensis*. Twenty-two species are considered old-growth forest indicators. The total epiphytic lichen cover on spruce trees averaged 59% at the trunk base, 12% at a height of 1.3 m above ground level and 61% on branches. Predominantly, only 12 species contributed to the lichen cover of trunk and branches. Despite the predominance of crustose lichens colonising spruce trees, the main epiphytic lichen cover both on trunks and branches was provided largely by foliose species (57% of the total cover). Due to a variety of morphological features, spruce provides diverse microhabitats, which leads to high lichen species richness with different ecological requirements. Spruce trees play a significant role in maintaining the diversity and conservation of rare species.

**Keywords:** epiphytic lichens, epiphytic lichen cover, European boreal forests, middle boreal subzone, *Picea abies*

## INTRODUCTION

Protected old-growth forests (terminal stages of forest recovery after disturbance) in the boreal zone of Russia are represented mainly by spruce communities (Kazimirov, 1971; Dyrenkov, 1984). On the territory of Karelia, Norway spruce (*Picea abies* (L.) Karst., hereafter "spruce") dominated forests are located, mainly, in the south. In the absence of forest disturbance, pine (*Pinus sylvestris* L.), as well as deciduous tree species, are replaced by spruce in all middle boreal forest habitats except for bogs, drained sands and rocks (Gromtsev, 2008; Volkov, 2008). In Karelia, spruce forests occupy an area of 15810 km$^2$, representing 39% of the total territory covered by forests (Volkov, 2008).

Epiphytic lichens, as a species-rich group in boreal forests, play an important role for diversity and productivity of forest communities (Ellis, 2012). It is known that tree species is among the most important drivers of epiphytic community composition (Ódor et al., 2013). In the boreal zone, high lichen richness is mainly related to spruce forests (Pystina, 2003). In fact, spruce is the main stand-forming tree species and edificator of the forest physical environment. Under the spruce forest canopy, specific microclimatic conditions are created by the transformation of solar radiation, heat radiation, evaporation, precipitation capture, as well as its influence on turbulance (Protopopov, 1975). The strong environmental influence of spruce mainly relates to its crown features. Its dense, low-attached crown with descending branches contributes to a varied niche structure for epiphytes. Spruce crown has a maximum water holding capacity exceeding that of pine, cedar and fir (Gorbatenko, 1987). For 60 years old spruce, it was established that stemflow on trunk began after 2.4–5 mm rainfall and reached 2.3% on average (Kittredge, 1951). Moistening of trunk sites beneath the spruce crowns is also affected by precipitation force and volume. In the spruce forest, with precipitation up to 15 mm, the under-crown trunk sites receive from 4 to 6 times less moisture than within the inter-crown space. At the same time, in pine forests, the under-crown trunk sites of pine receive only 1.1–1.3 times less moisture than inter-crown spaces (Nikonov & Lukina, 2000). On spruce branches, light availability and humidity differ compared with the trunk under-crown sites. The level of branch position within the crown is the key variable determining niche variability and, consequently, species composition and epiphyte cover on spruce branches (Gorshkov et al., 2002). Furthermore, spruce stemflow is characterized by its higher acidity (pH ~3.8) as compared with the inter-crown space (pH ~5.0) (Nikonov et al., 2002). In natural conditions the pH of spruce bark is acidic, ranging from 2.8 to 4.5 (e.g. Barkman, 1958; Kuusinen, 1996a; Stepanova et al., 2001).

Lichen diversity on spruce has been intensively studied in spruce forests in different regions. The maximum number of lichen species (198) for spruce was recorded by A. Koskinen (1955) in Finland. However, this list included a large number of subspecific taxa, and a different taxonomic understanding of certain taxa. The majority of studies report fewer lichen species for spruce, generally ranging from 20 to 90. For example, 122 species were recorded for *Picea abies* in Norway (Holien, 1997), 83 in southern Finland (Kuusinen & Siitonen, 1998), 53 in Sweden (Bäcklund et al., 2016) and 86 in southern Estonia (Marmor et al., 2013). In the East of European Russia, in Komi Republic, 152 lichen species were recorded on *Picea* spp. (including *Picea abies* and *P. obovata*) (Pystina, 2003). Furthermore, several ecological studies emphasize factors controlling epiphytic lichen diversity and distribution on trunks and branches of spruce trees (e.g. Hilmo, 1994; Nascimbene et al., 2009, 2010; Bäcklund et al., 2016).

However, information on lichen species richness on spruce is still deficient for the territory of Karelia. So far, lichens on spruce have been studied only in the Kivach Strict Nature Reserve and Vodlozero National Park where 92 species were found (Stepanova, 2004). Over the period 2014–2017, an inventory of lichen diversity on spruce in these territories was continued and new study areas included: the Kizhi Sanctuary, Petrozavodsk City and the territory of Vodlinsky Forest.

Quantitative data of epiphytic lichen cover on spruce are very scattered, (Sõmermaa, 1972; Lõhmus & Lõhmus, 2001; Kuusinen, 1996b). Most often, the authors estimate only the frequency of lichen species occurrence (Kruys & Jonsson, 1997, Holien; 1998, Marmor et al., 2013). However, this variable could not provide an objective evaluation of epiphytic lichen cover, since the occurrence of lichen species can often be high while their coverage is low. Moreover, different scales are also used for lichen cover assessment (Halonen et al., 1991; Holien, 1997), instead of using a special framework that might significantly reduce subjectivity in the study.

Studies on patterns of spruce epiphytic lichen cover are sparse over the whole territory of Russia. Quantitative data on its main characteristics are still lacking. The aims of the present paper are: (1) to study lichen diversity of Norway spruce in the middle boreal forests of Republic of Karelia, and (2) to estimate the main characteristics of epiphytic lichen cover on trunks and branches of spruce.

## MATERIALS AND METHODS

### Study area

Field studies were carried out in pine, spruce, mixed aspen-spruce forest communities in the middle boreal subzone of Republic of Karelia (Northwest Russia). Sample plots were located in the Karelian part of the Vodlozero National Park (62°13'N, 36°46'E; 130,600 ha), Kivach Strict Nature Reserve (62°17'N, 34°00'E; 10,880 ha), Kizhi Sanctuary (62°06'N, 35°09'E; 50,000 ha) and Petrozavodsk City (61°50'N, 34°20'E; 13,500 ha). The location of these study areas was mapped and their climatic characteristics presented in a previous paper (Tarasova et al., 2017). Vodlinsky forest (62°06'N, 37°44'E; 142,630 ha) is located in the Pudozh district, bordering to the north and east with Arkhangelsk region, and to the west, with Vodlozero National Park. Forest management and clear-cutting have been applied within this territory since the 1950s, and at the present time forests are represented by recovering secondary deciduous and mixed deciduous-coniferous forests.

### Data collection

Sampling design was based on permanently established sample plots in the tree stands. A total of 68 sample plots of 25×30 m (40) and 100×100 m (28) were set up in different types of spruce and mixed (spruce-pine, aspen-spruce, birch-spruce) forests. A detailed geobotanical description of the studied community was performed for each sample plot including trees (height, age, basal area, crown density etc.) and the ground cover characteristics (shrub and herb cover, mosses and lichen cover) (Table 1) (Jarmishko & Ljanguzova, 2002). Time-since-disturbance of the studied forest communities was established as stages of succession ranging from 20 to 450 years in drained sites and 290–350 years for waterlogged sites.

Lichen diversity was described in each sample plot on 10–20 selected spruce trees. Measurements of the characteristics of epiphytic lichen cover on trunks were performed by using a frame measuring 10×20 cm positioned at the trunk base and breast height (1.3 m above ground level) on four sides (north, west, south, east).

Epiphytic lichen cover on spruce branches was studied in Vodlozero National Park within a windthrow area (~100 ha) in *Vaccinium myrtillus*-type spruce forest (175 years since-disturbance). Epiphytic lichen linear cover was recorded using a measuring tape (Bruteig, 1994) from the base to tip on 217 living branches of 20 fallen undamaged spruce trees aged from 120–260 years. In total, 30 branches with an average length 215 ± 20 cm and average age 80 ± 20 years, were selected from the total investigated in order to

**Table 1.** Main characteristics of studied forest communities in the middle taiga of the Republic of Karelia. Study areas: I – Vodlozero National Park, II – Kivach Strict Nature Reserve, III – Kizhi Sanctuary, IV – Petrozavodsk City, V – Vodlinsky Forest; type of forests: *Spr c m* – spruce forest *Calamagrostis arundinacea*–green mosses type, *Spr v m* – spruce forest *Vaccinium myrtillus*–green mosses type, *Spr v s* – spruce forest *Vaccinium myrtillus–Sphagnum* mosses type, *Spr e s* – spruce forest *Equisetum sylvaticum–Sphagnum* mosses type, *Spr herb* – spruce forest herb-rich type, *Asp c* – middle-aged aspen forest *Vaccinium myrtillus–Calamagrostis arundinacea* type, *Spr-Asp v m* – mixed aspen-spruce forest *Calamagrostis arundinacea–Vaccinium myrtillus* type, *Pn v m* – pine forest *Vaccinium myrtillus*–green mosses type; tree stand composition (% from basal area): S – spruce, P – pine, B – birch, As – aspen, Al – alder, Sr – rowan.

| Study area | Number of sample plots | Type of forest | | Time-since-disturbance, years | Basal area, $m^2ha^{-1}$ | Tree stand | Age of spruce trees, years |
|---|---|---|---|---|---|---|---|
| I | 10 | 1 | *Spr v m* | 175–450 | 19–29 | 82S10P4B4As | 24–270 |
| | 3 | 2 | *Spr v s* | 247–350 | 21–35 | 86S8P3As3B | 125–300 |
| | 4 | 3 | *Spr e s* | 250–380 | 21–25 | 81S16B2P1As1Sr | 109–301 |
| | 1 | 4 | *Spr herb* | 255 | 20 | 88S5P2B5As | 99–195 |
| | 2 | 6 | *Spr-Asp v m* | 160–180 | 27–31 | 59S19B18As2P2Sr | 28–143 |
| | 2 | 7 | *Asp c* | 80–100 | 29–30 | 46As30B18S3Sr2Al | 25–95 |
| II | 6 | 1 | *Spr v m* | 170–260 | 21–42 | 74S12B10As4P | 21–211 |
| | 1 | 2 | *Spr v s* | 256 | 37 | 72S4P24B | 125–206 |
| | 2 | 3 | *Spr e s* | 167–170 | 25–35 | 81S8As7B3P1Al | 82–157 |
| | 3 | 4 | *Spr herb* | 188–295 | 28–31 | 82S12B4P2As1Al | 85–245 |
| | 9 | 5 | *Spr c m* | 86–190 | 30–45 | 68S20B10As2P | 11–170 |
| | 5 | 6 | *Spr-Asp v m* | 160–190 | 34–37 | 49S31As12B8P | 28–143 |
| | 1 | 7 | *Asp c* | 80 | 39 | 68As30S1B1P | 31–72 |
| | 6 | 8 | *Pn v m* | 60–90 | 22–31 | 65P24S7As4B | 11–149 |
| III | 2 | 1 | *Spr v m* | 240–260 | 22–28 | 77S13As5B5P | 22–192 |
| | 2 | 6 | *Spr-Asp v m* | 150–160 | 31 | 47S32As13P8B | 42–126 |
| | 2 | 7 | *Asp c* | 85–100 | 19–24 | 64As15B11Sr5P3S2Al | 36–75 |
| IV | 1 | 1 | *Spr v m* | 210 | 28 | 59S22As9B9P1Sr | 84–168 |
| | 1 | 6 | *Spr-Asp v m* | 160 | 32 | 44S43As9B2P1Al1Sr | 38–150 |
| | 1 | 7 | *Asp c* | 110 | 25 | 38As32S16B10P1Sr | 19–78 |
| V | 4 | 7 | *Asp c* | 20–59 | 22–36 | 81As13B6S | 25–122 |

study epiphytic lichen cover of the main branch axis at different distances from the tree trunk. Each branch was divided into 10 cm long segments in which the average cover of each species was determined. The total amount of classes (segments) was 24. Lichen cover was recorded as a linear distance occupied by each thallus according to methods described by I. Bruteig (1993). The cm-measures were transformed to percentage cover for data analysis. The percentage cover of lichen taxon ($C_i$) on main branch axis was calculated as a proportion of lichen taxon length (in cm) to branch length:

$$C_i = 100\% \times \frac{\sum_{j=1}^{n} l_{ij}}{L}$$

where: $C_i$ – cover of *i* lichen taxon, %; $l_{ij}$ – length of *j* thallus of *i* lichen taxon on branch, cm; $L$ – length of branch, cm.

Total lichen cover ($C$) on a branch was defined as the sum of all species covers:

$$C = \sum_{i=1}^{n} C_i$$

where: $C$ – total lichen cover on the branch, %; $C_i$ – cover of *i* lichen taxon, %; $n$ – number of recorded lichen species.

The frequency ($F_i$) of lichen taxon was calculated according to following formula:

$$F_i = 100\% \times \frac{N_i}{N}$$

where: $F_i$ – frequency of *i* lichen taxon, %; $N_i$ – number of branches where the lichen has been recorded; $N$ – total (217) numbers of investigated branches.

Proportion in total cover of a lichen taxon ($R_i$) was defined as proportion of the lichen taxon cover to total lichen cover:

$$R_i = 100\% \times \frac{C_i}{C}$$

where $R_i$ – proportion in total lichen cover of *i* lichen taxon, %; $C_i$ – cover of *i* lichen taxon; $C$ – total lichen cover.

A total of 1995 collected lichen specimens were identified using standard microscopic techniques and spot tests. Sampled specimens belonging to the genus *Cladonia* and sterile crustose lichen species were identified by standard thin-layer chromatography (TLC) in the Laboratory of Experimental Botany of Petrozavodsk State University, Petrozavodsk, using solvent systems A, B, C and G (Orange et al., 2001). Specimens are deposited in the herbarium of Petrozavodsk State University (PZV).

**Data analyses**

Lichen cover on trunks of trees aged from 107–270 years (mean = 177 years) at different heights (n = 6700) was compared and statistically analyzed by an analysis of variance (one-way ANOVA, Microsoft Excel, 2007) and the *p*-value to evaluate the significance of observed differences (Ivanter & Korosov, 2010). Data on general characteristics of lichen cover on spruce trunks were presented for trees within the same age range (107–270 years). Data on studied forests with low time-since-disturbance (< 100 years) and trees with age < 100 years were only used for an assessment of total lichen diversity on spruce.

For lichen cover relevés (each measuring 10×20 cm) on studied trunk sites, the Shannon's information diversity index ($H$) was calculated according to the following equation:

$$H = -\sum_{i=1}^{N} S_i \times \ln S_i$$

where $S_i$ – share of *i*–species in percentage of total cover (relative cover); $N$ – total species number on analyzed area (0.02 $m^2$). Pielou's evenness index ($E$) (Pielu, 1969) is a measure of biodiversity which quantifies how equal the community is numerically and is calculated according to:

$$E = H / H_{max} = H / \ln N$$

where: $H$ – Shannon diversity index, $N$ – total species number on analyzed area (0.02 $m^2$) (Magurran, 1988). Its maximum value (1) is registered in cases where lichen cover in relevés on trunk sites have equal values and minimum (0) is observed when species have a significantly different cover.

Regression analysis (Microsoft Excel, 2007) was performed for lichen cover measurements at different distance from tree trunk, on main axis of 30 spruce branches from the lower part of the canopy. Some dependencies were described using one or two regression.

## LIST OF SPECIES

Taxa are arranged in alphabetical order; nomenclature of lichens, lichenicolous and non-lichenized fungi follows mainly Nordin et al.

(2011). For each species the substrates and locality numbers (see above) are listed.

Abbreviations and symbols: # – lichenicolous fungi; + – non-lichenized fungi; * – indicator species of old-growth forests; *Kol!* – new species for the biogeographical province *Karelia olonetsensis*, *Kon!* – new species for the biogeographical province *Karelia onegensis*, *Kton!* – new species for the biogeographical province *Karelia transonegensis*; KvR!, KzR!, VNP! VF! – new species for study areas: KvR – Kivach Strict Nature Reserve, KzR – Kizhi Sanctuary, Ptz – Petrozavodsk City, VNP – Vodlozero National Park, VF – Vodlinsky forest. Species included in the Red Data Book of the Republic of Karelia (2007) are marked as RK, and in the Red Data Book of the Russian Federation (2008) – RR. The types of forest communities are marked with the numbers 1–7 (see Table 1).

*Acolium karelicum (Vain.) M. Prieto & Wedin – on trunks. VNP: 1. RK.

*Acolium inquinans (Sm.) A. Massal – on trunks, branches and snags. KvR: 3.

*Alectoria sarmentosa (Ach.) Ach. – on trunks and branches. KvR, KzR, Ptz, VNP: 1–5.

Anisomeridium polypori (Ellis & Everh.) M. E. Barr – on trunks. KvR, KzR: 2.

Arthonia mediella Nyl. – on trunks. VNP: 1.

Arthonia didyma Körb. – on trunks. Ptz: 1.

Arthonia spadicea Leight. – on young trunks. VF: 7. VF! *Kton*!

*Arthonia vinosa Leight. – on snags. VNP: 6. VNP! RK.

+Arthothelium scandinavicum Th. Fr. – on trunks and branches. KvR: 6, 8.

Bacidia arceutina (Ach.) Rehm & Arnold – on branches. KvR: 6.

Bacidia laurocerasi (Del. ex Duby) Vain. – on branches. KvR: 6.

Biatora albohyalina (Nyl.) Bagl. & Carestia – on trunks. VNP, VF: 7. VF!

Biatora efflorescens (Hedl.) Räsänen – on trunks and branches. KvR, VNP: 6, VF: 7. VF!

Biatora helvola Korb ex Hellb. – on trunks, branches and snags. KvR, Ptz: 6–7, VF: 7. VF!

Biatora globulosa (Flörke) Fr. – on snags. KvR: 6.

Biatora ocelliformis (Nyl.) Arnold – on trunks, branches and snags. KvR: 6, 8, VF: 7. VF!

Biatora vernalis (L.) Fr. – on mosses at trunk base. VNP: 1, 2.

Blastenia ferruginea (Huds.) A. Massal – on trunks. Ptz: 1.

Bryoria capillaris (Ach.) Brodo & D. Hawksw. – on trunks, branches and snags. KvR, KzR, Ptz, VNP, VF: 1–7. VF! Conf. L. Myllys.

*Bryoria fremontii (Tuck.) Brodo & D. Hawksw. – on branches. VNP, KvR: 6. RK, RR. Conf. L. Myllys.

Bryoria furcellata (Fr.) Brodo & D. Hawksw. – on trunks, branches and snags. KvR, VNP: 1–6, KzR: 1. Conf. L. Myllys.

Bryoria fuscescens (Gyeln.) Brodo & D. Hawksw. – on trunks, branches and snags. KvR: 1–6, KzR: 1, Ptz: 6, VNP: 1–4, 6. Conf. L. Myllys.

Bryoria nadvornikiana (Gyeln.) Brodo & D. Hawksw. – on trunks, branches and snags. KvR: 1, 2, 6, 7, KzR: 1, 6, Ptz: 6–7, VNP: 1, 6. RK. Conf. L. Myllys.

Bryoria vrangiana (Gyeln.) Brodo & D. Hawksw. – on snags. KvR: 1, 6, KzR: 1, 6, Ptz: 6–7, VNP: 1, 6–7, VF: 7. VF! Conf. L. Myllys.

Buellia arnoldii Servít – on branch. KvR: 6.

Buellia erubescens Arnold – on branch. KvR: 7.

Calicium glaucellum Ach. – on trunks, branches and snags. KvR: 2–3, 6, VNP: 1, 6.

Calicium parvum Tibell – on trunks. KvR: 1.

Calicium viride Pers. – on trunks. KvR: 1, KzR: 1, VNP: 1, 6–7.

Candelariella xanthostigma (Pers. ex Ach.) Lettau – on snags. KvR: 5.

Catillaria erysiboides (Nyl.) Th. Fr. – on trunks. VF: 7. VF! *Kton*!

Chaenotheca brunneola (Ach.) M ll. Agr. – on snags. KvR: 2–3, KzR: 1.

Chaenotheca chrysocephala (Turner ex Ach.) Th. Fr. – on trunks, branches and snags. KvR: 1–7, KzR: 1, Ptz: 6, VNP: 1–6, VF: 7. VF!

Chaenotheca ferruginea (Turner ex Sm.) Mig. – on trunks, branches and snags. KvR: 1–7, KzR: 1, 6, Ptz: 6–7, VNP: 6–7, 4.

Chaenotheca furfuracea (L.) Tibell – on upended roots. Ptz: 1.

Chaenotheca hispidula (Ach.) Zahlbr. – on trunk. KvR: 1.

*Chaenotheca laevigata Nádv. –on lignum. VNP: 1.

*Chaenotheca stemonea (Ach.) Müll. Arg. – on trunks. VNP: 2–3. RK.

*Chaenotheca subroscida (Eitner) Zahlbr. – on trunks, on lignum. KvR: 1–3, KzR: 1, VNP: 1, 6–7, VF: 7. RK.

Chaenotheca trichialis (Ach.) Th. Fr. – on trunks. KvR: 1, 6–7, KzR: 1, 6, VNP: 1, 6–7.

#Chaenothecopsis consociata (Nàdv.) A. F. W. Schmidt – on thalli of *Chaenotheca chrysocephala*. KvR: 1–5, KzR: 1, VNP: 1.

#Chaenothecopsis epithallina Tibell – on thalli of *Chaenotheca trichialis*. KvR: 1, VNP: 1.
+Chaenothecopsis nana Tibell – on trunk. KvR: 1.
*+Chaenothecopsis fennica (Laurila) Tibell – on trunks, on lignum. KzR: 5, VNP: 1, 3.
#Chaenothecopsis pusilla (A. Massal) A.F.W. Schmidt – on trunks. KvR: 1–3.
#Chaenothecopsis savonica (Räsänen) Tibell – on snags. VNP: 1–3.
*+Chaenothecopsis viridialba (Kremp.) A. F. W. Schmidt – on trunks. KvR: 2–3, VNP: 1. RK.
Chrysothrix candelaris (L.) J. R. Laundon – on branches and snags. KvR: 1.
Cladonia botrytes (K. G. Hagen) Willd. – at the trunk base. KvR: 1, VNP: 1.
Cladonia cenotea (Ach.) Schaer. – at the trunk base. KvR: 1–7, KzR: 1, 6, Ptz: 1, 6–7, VNP: 1–7.
Cladonia chlorophaea (Flörke ex Sommerf.) Spreng. – at the trunk base. KvR: 1, 5. The specimens contained fumarprotocetraric acid.
Cladonia coniocraea (Fl rke) Sperng. – at trunk base, on branches. KvR: 1–7, KzR: 1, 6, Ptz: 1, 6–7, VNP: 1–4, 6–7.
Cladonia cornuta (L.) Hoffm. – at trunk base, on branches. KvR: 1, 6, KzR: 1, 6, Ptz: 1, 6, VNP: 1, 4.
Cladonia crispata (Ach.) Flot. – at trunk base. KvR: 1, 5, VNP: 1.
Cladonia cyanipes (Sommerf.) Nyl. – at trunk base. KvR: 1. KvR! The specimen contained usnic, barbatic, 4–0 dimethylbarbatic acids.
Cladonia digitata (L.) Hoffm. – at trunk base. KvR: 1–7, KzR: 1, Ptz: 1, 6, VNP: 1–4.
Cladonia fimbriata (L.) Fr. – at trunk base. KvR: 1–7, Ptz: 1, VNP: 1 – 4, 6–7.
Cladonia gracilis subsp. turbinata (Ach.) Ahti – at trunk base. KvR: 1, VNP: 1.
Cladonia merochlorophaea Asahina – at trunk base. KvR: 4. The specimens contained merochlorophaeic, 4-0- methylcryptochlorophaeic and fumarprotocetraric acid.
Cladonia ochrochlora Flörke – at trunk base. KvR: 6.
*Cladonia parasitica (Hoffm.) Hoffm. – at trunk base. KvR: 2.
Cladonia rangiferina (L.) Weber ex F.H. Wigg – at trunk base, on low branches of young trees. KvR: 8, VNP: 1.
Cladonia squamosa (Scop.) Hoffm. – at trunk base. KvR: 1–5, VNP: 1–4.
Cliostomum leprosum (Räsänen) Holien & Tønsberg – on trunk. KzR: 1. KzR!
Coenogonium pineti (Ach.) Lücking & Lumbsch – on mosses at trunk base. KvR: 1, 6, VNP: 6.
*Evernia divaricata (L.) Ach. – on branches. KvR: 3, KzR: 1. RK.
Evernia mesomorpha Nyl. – on branches. KvR: 1–5, Ptz: 6, VNP: 1–4.
Evernia prunastri (L.) Ach. – on branches, rarely on trunks. KvR: 6, Ptz: 6, 7, VNP: 6.
Frutidella furfuracea (Anzi) M. Westb. & M. Svensson – on snags. VF: 7. VF!
Fuscidea pusilla Tønsberg – on branches. KvR: 1, 6, KzR: 1, 6, Ptz: 7, VNP: 6, VF: 7. VF! The specimen contains divaricatic acid.
Gyalecta truncigena (Ach.) Hepp – on trunks. KvR: 1.
Hypocenomyce scalaris (Ach. ex Lilj.) M. Choisy – on trunks. KvR: 1.
Hypogymnia physodes (L.) Nyl. – on trunks, branches and snags. KvR: 1–8, KzR: 1, 6 – 7, Ptz: 1, 6 – 7, VNP: 1–4, 6–7, VF: 7. VF!
Hypogymnia tubulosa (Shaer.) Hav. – on branches and snags. KvR: 1–8, KzR: 1, Ptz: 1, 6–7, VNP: 1–4, 6–7, VF: 7. VF!
*Hypogymnia vittata (Ach.) Parrique – on trunks, branches. KzR, VNP: 1.
Imshaugia aleurites (Ach.) S. L. F. Meyer – on trunks, branches. KvR: 1, 8, VNP: 1.
Japewia subaurifera Muhr & Tønsberg – on trunks, branches and snags. KvR: 1, 5, KzR: 4, VNP: 1. KzR!
Japewia tornoënsis (Nyl.) Tønsberg – on trunks, branch and snags. KvR: 6, KzR: 1, VNP: 4.
*Lecanactis abietina (Ehrh. ex Ach.) Körb. – on trunks. KvR: 1. RK.
Lecania cyrtella (Ach.) Th. Fr. – on resin. KvR: 7.
Lecania naegelii (Hepp) Diederich & van den Boom – on snags. VF: 7. VF!
Lecanora circumborealis Brodo & Vitik. – on trunks. VNP: 1.
Lecanora expallens Ach. – on trunks. KzR: 7, VNP: 1, 6. KzR! VNP! *Kton*! Specimens contained thiophanic, usnic acids, arthothelin and “expallens-unkown” substances.
Lecanora hypopta (Ach.) Vain. – on trunks. KzR, VNP: 1. KzR!
Lecanora phaeostigma (Körb.) Almb. – on trunks, branch and snags. KvR: 1–7, KzR: 1, VNP: 1–4, 6–7, VF: 7. KzR! VNP! VF! *Kton*!
Lecanora symmicta (Ach.) Ach. – on trunks, branches. KvR: 7–8, KzR: 6, Ptz: 6, VNP: 1, 6, VF: 7. VF!
Lecidea albofuscescens Nyl. – on trunks, snags. VNP: 2–3, VF: 7. VF! RK.

LECIDEA ERYTHROPHAEA Flörke ex Sommerf. – on branches. KvR: 6.

LECIDEA LEPRARIOIDES Tønsberg – on trunks, branches. KvR: 1.

LECIDEA NYLANDERI (Anzi) Th. Fr. – on trunks, branch and snags. KvR: 1, 5–7, KzR: 1, 6, VNP, VF: 7. VF!

LECIDEA TURGIDULA Fr. – on trunks, branches and snags. KvR: 5–8, KzR, VNP: 1, 6, VF: 7. VNP! VF! *Kton*!

LEPRARIA ELOBATA Tønsberg – at trunk base. KzR: 6. KzR! The specimen contained atranorin, zeorin and stictic acid complex.

LEPRARIA INCANA (L.) Ach. – at trunk base. KvR: 1, KzR: 1, Ptz: 6, VNP: 1. KzR! The specimens contained divaricatic acid, atranorin and zeorin.

LEPRARIA JACKII Tønsberg – at trunk base. KvR: 1–7, KzR: 1, Ptz: 1, 6, VNP: 1–3, 7, VF: 7. VF! The specimens contained atranorin, roccellic/angardianic, jackinic/rangiformic and norjackinic/norrangiformic acid.

*LEPTOGIUM SATURNINUM (Dicks.) Nyl. – on branches. KvR: 6.

*LOBARIA PULMONARIA (L.) Hoffm. – on lower branches of young trees growing near large aspens with *L. pulmonaria*. KvR: 1, 6, VNP: 1. RK, RR.

LOXOSPORA ELATINA (Ach.) A. Massal – on trunks, branches. KvR: 1–7, KzR: 1, 6, VNP: 1–3, 6.

MELANELIXIA SUBAURIFERA (Nyl.) O. Blanco et al. – on branches and snags. KvR, VNP: 6. VNP! RK.

MELANOHALEA EXASPERATULA (Nyl.) O. Blanco et al. – on snags. VNP: 6.

MELANOHALEA OLIVACEA (L.) O. Blanco et al. – on branches and snags. KvR: 5–7, VNP: 7.

MICAREA MELAENA (Nyl.) Hedl. – at trunk base. KvR: 1.

MICAREA DENIGRATA (Fr.) Hedl. – on branches and snags. KvR, KzR: 1, 6.

MICAREA MISELLA (Nyl.) Hedl. – on branches and snags. KzR: 1, Ptz: 6.

MICROCALICIUM AHLNERI Tibell – on trunk. VNP: 1.

*MICROCALICIUM DISSEMINATUM (Ach.) Vain. – on trunks. KvR: 1–7, KzR: 1, VNP: 1–4, 6.

MYCOBLASTUS AFFINIS (Shaer.) T.Shauer – on branches and snags. VNP: 1–3.

MYCOBLASTUS SANGUINARIUS (L.) Norman – on trunks, branches and snags. KvR: 1–8, KzR: 1, VNP: 1–4, 5–7, VF: 7. VF!

+MYCOCALICIUM SUBTILE (Pers.) Szatala – on lignum. KzR: 1, 6, VNP: 1.

*NEPHROMA BELLUM (Spreng.) Tuck. – on mosses at trunk base. KvR: 6. RK.

*NEPHROMA PARILE (Ach.) Ach. – on mosses at trunk base. KvR: 3–4.

*NEPHROMA RESUPINATUM (L.) Ach. – on mosses at trunk base. KvR: 3–4, 6.

OCHROLECHIA ALBOFLAVESCENS (Wulfen) Zahlbr. – on trunks and snags. KvR: 1–4, KzR, VNP: 1. The specimens contain variolaric, lichesterinic and protolichesterinic acids.

OCHROLECHIA ARBOREA (Kreyer) Almb. – on trunks. Ptz: 1. The specimens contain lichexanthone, gyrophoric and lecanoric acids.

OCHROLECHIA BAHUSIENSIS H. Magn. – on trunks and snags. KvR, KzR: 1, VNP: 1, 5–6. The specimens contained gyrophoric, lecanoric acids and murolic acid complex.

OCHROLECHIA MAHLUENSIS Räsänen – on branches. KvR: 1, 6, KzR: 1, VNP: 3–4. The specimens contained gyrophoric and lecanoric acids.

OCHROLECHIA MICROSTICTOIDES Räsänen – on trunks and snags. KvR: 1, 7, Ptz: 6, KzR: 1, VNP: 1–3, VF: 7. VF! The specimens contain variolaric and lichesterinic acids.

OCHROLECHIA PALLESCENS (L.) A. Massal. – on trunks. VNP: 1.

OPEGRAPHA NIVEOATRA (Borrer) J. R. Laundon – on trunks. KzR: 6.

OPEGRAPHA VULGATA (Ach.) Ach. – on trunks. VNP: 1, 6. VNP! *Kton*!

PARMELIA SULCATA Taylor – on trunks, on branches and snags. KvR: 1–8, KzR, Ptz: 1, 6–7, VNP: 1–4, 5–7, VF: 7. VF!

PARMELIOPSIS AMBIGUA (Wulfen) Nyl. – on trunks, on branches and snags. KvR: 1–8, KzR, Ptz: 1, 6–7, VNP: 1–4, 5–7, VF: 7. VF!

PARMELIOPSIS HYPEROPTA (Ach.) Vain. – on trunks, on branches and snags. KvR: 1–8, KzR, Ptz: 1, 6–7, VNP: 1–4, 5–7, VF: 7. VF!

PELTIGERA POLYDACTYLON (Neck.) Hoffm. – on mosses at trunk base. VNP: 1.

PERTUSARIA ALBESCENS (Huds.) M. Choisy & Werner – on trunks and branches. KzR: 1, VNP: 1–3. The specimens contain fatty acids.

PERTUSARIA AMARA (Ach.) Nyl. – on trunks, on branches and snags. KvR, VNP: 1–3, 6, VF: 7. VF!

PERTUSARIA BOREALIS Erichsen – on trunks. KvR: 5, 7, VNP: 6. Specimens contain the fumarprotocetraric acid complex. KvR! *Kon*!

*PERTUSARIA COCCODES (Ach.) Nyl. – on branches and snags. KzR: 6, VNP: 2.

PERTUSARIA PUPILLARIS (Nyl.) Th. Fr. – on branches and snags. KvR: 1, VNP: 2.

PHLYCTIS ARGENA (Ach.) Flot. – on trunks and branches. KvR, VNP: 6, VF: 7. VF!

PHYSCIA ALNOPHILA (Vain.) Loht. et al. – on branches. KvR: 6–7.

PHYSCIA STELLARIS (L.) Nyl. – on branches. VNP: 7. VNP!

PLACYNTHIELLA ICMALEA (Ach.) Coppins & P. James – on trunks and branches. KzR: 1.

PLATISMATIA GLAUCA (L.) W. L. Culb & C. F. Culb. – on trunks, on branches and snags. KvR: 1–8, KzR, Ptz: 1, 6–7, VNP: 1–4, 5–7, VF: 7. VF!

PSEUDEVERNIA FURFRURACEA (L.) Zopf. – on trunks, on branches and snags. KvR: 1, 6, Ptz: 6, VNP: 1–2.

RAMALINA DILACERATA (Hoffm.) Hoffm. – on branches. KvR: 6. RK.

RAMALINA FARINACEA (L.) Ach. – on trunks and branches. KvR: 6, VNP: 1, 6.

*RAMALINA THRAUSTA (Ach.) Nyl. – on branches. KvR, VNP: 1, 6. RK.

ROPALOSPORA VIRIDIS (Tønsberg) Tønsberg – on trunks and branches. KvR: 1, 6. VF: 6. VF! The specimens contained perlatolic acid.

ROSTANIA OCCULTATA (Bagl.) Otálora, P.M. Jørg. & Wedin – on branch. KvR: 6. RK.

+SAREA DIFFORMIS (Fr.) Fr. – on resin. KvR: 6, KzR: 1, VNP: 1, 6, Ptz: 6. KvR! KzR! VNP! *Kon*! *Kton*!

+SAREA RESINAE (Fr.: Fr.) Kuntze – on resin. KvR, KzR: 1, VNP: 1, 6. KvR! KzR! VNP! *Kton*!

SCOLICIOSPORUM CHLOROCOCCUM (Graewe ex Stenh.) Vězda – on trunks and branches. KvR: 1, 5, KzR: 1, 6, VNP; 1, VF: 7. VF!

STRANGOSPORA MORIFORMIS (Ach.) Stein – on trunks. VF: 7. VF!

TOENSBERGIA LEUCOCOCCA (R. Sant.) Bendiksby & Timdal – on branches. Ptz: 6–7.

TRAPELIOPSIS FLEXUOSA (Fr.) Coppins & P. James – at trunk base and snags. KzR, VNP: 1.

TUCKERMANOPSIS CHLOROPHYLLA (Willd.) Hale – on trunks, on branches and snags. KvR: 1–8, KzR, Ptz: 1, 6–7, VNP: 1–4, 5–7, VF: 7. VF!

USNEA BARBATA (L.) Weber ex F. H. Wigg. – on branches. KvR: 6, KzR: 1. KvR! RK.

USNEA DASOPOGA (Ach.) Nyl. – on trunks, on branches and snags. KvR: 1–8, KzR, Ptz: 1, 6–7, VNP: 1–4, 5–7, VF: 7. VF!

USNEA GLABRESCENS (Nyl. ex Vain.) Vain. ex Räsänen – on trunks, on branches and snags. KvR: 2, 6, KzR: 6, VNP: 1–3, 6.

USNEA HIRTA (L.) Weber ex F.R. Wigg. – on branches and snags. KvR: 1.

USNEA LAPPONICA Vain. – on branches and snags. KvR: 1, 6.

USNEA SUBFLORIDANA Stirt. – on trunks, on branches and snags. KvR: 1–8, KzR, Ptz: 1, 6–7, VNP: 1–4, 5–7, VF: 7. VF!

VIOLELLA FUCATA (Stirt.) T. Sprib. – on trunks. KvR: 6, VNP: 1, 6, KzR: 1, VF: 7. The specimens contain atranorin and fumarprotocetraric acid. KzR! VNP! VF! *Kton*!

VULPICIDA PINASTRI (Scop.) J.-E. Mattsson & M. J. Lai – on trunks, on branches and snags. KvR: 1–8, KzR, Ptz: 1, 6–7, VNP: 1–4, 5–7, VF: 7. VF!

XYLOGRAPHA PALLENS (Nyl.) Malmgren – on lignum and trunks. VNP: 6. VNP! *Kton*!

XYLOGRAPHA VITILIGO (Ach.) J. R. Laundon – on lignum and trunks. KvR: 6. The specimen contain stictic acid complex.

XYLOPSORA CARADOCENSIS (Leight. ex Nyl.) Bendiksby & Timdal – on snags. KzR: 1. KzR!

XYLOPSORA FRIESII (Ach.) Bendiksby & Timdal – on trunks. KvR: 1, 6, KzR: 1, VNP: 1, 4.

## RESULTS AND DISCUSSION

### Lichen diversity

Lichen diversity was analyzed on 980 spruce trees within 68 sample plots in 31 ha total study area. Recorded lichen diversity on spruce in southern Karelia is represented by 158 species (147 lichen species, 4 lichenicolous and 7 non-lichenized saprotrophic fungi). Crustose lichens (90 species, 61%) contributed mainly to species richness. Fruticose and foliose species were represented in lower proportions, 23% (34 species) and 16% (23 species), respectively.

Amongst recorded lichens on spruce, *Lobaria pulmonaria* and *Bryoria fremontii* are included in the Red Data Book of Russian Federation (Red..., 2008). Seventeen species are regionally protected in Republic of Karelia (Red..., 2007): *Acolium karelicum*, *Arthonia vinosa*, *Bryoria fremontii*, *Bryoria nadvornikiana*, *Chaenotheca stemonea*, *Chaenotheca subroscida*, *Chaenothecopsis viridialba*, *Evernia divaricata*, *Lecanactis abietina*, *Lecidea albofuscescens*, *Lobaria pulmonaria*, *Melanelixia subaurifera*, *Nephroma bellum*, *Ramalina dilacerata*, *Ramalina thrausta*, *Rostania occultata*, *Usnea barbata*. Two species are new for the biogeographical province *Karelia onegensis* and 10 – for *Karelia transonegensis*. Some lichen species were found in the studied areas for the first time: in total 4 – in the Kivach Strict Nature Reserve, 11 – in the Kizhi Sanctuary and for the entire Zaonezhsky peninsula, 10 – in the Vodlozero National Park, 36 – in the Vodlinsky forestry.

The maximum number of lichen species (110) was found in spruce forests of the *Vaccinium myrtillus*–green mosses type, the minimum (17) in the pine forest, *Vaccinium myrtillus*–green mosses type with young spruce trees. However, in this study, it is difficult to compare meaningfully the lichen species composition in these different forest and community types because of the different size and number of the study areas. Lichen species diversity is closely associated with such parameters as the size and number of the study area and tree number. Our data include 158 lichens and allied fungi recorded on about 1000 spruce trees within an area of 0.31 $km^2$. Similar number of species (152) was recorded in the entire Komi Republic territory, 172,200 $km^2$ in extent (Pystina, 2003). Holien (1997) found 122 lichens on 400 spruce trees within 1.62 $km^2$ in Norway. The 242 lichens were recorded on spruce in the whole Leningrad region (84,500 $km^2$) during over more than 200 years of studies (data by D. Himelbrant, E. Kuznetsova & I. Stepanchikova; Stepanchikova: personal communication, 2017). Thus, it could be inferred that the regional species pool of lichens on spruce in Karelia lying within the middle boreal subzone amounts to about 200 species.

Moreover, the number of lichen species is affected not only by the size of study area and microhabitat diversity, but also by the time-since-disturbance of forest communities. The relatively high lichen species diversity recorded on spruce in this study might be explained by the heterogeneity of conditions revealed by sampling from different forest types with different time-since-disturbance, from spruce trees with different ages as well as due to investigating various microhabitats within individual trees. Various studies have reported increasing lichen diversity on spruce with increasing time-since-disturbance (e.g. Hilmo, 1994; Nascimbene et al., 2009, 2010; Marmor et al., 2011). In forest communities, within a single tree species, such as spruce, the number of microhabitats available for epiphytic lichen colonization increases with increasing time-since-disturbance. These microhabitats comprise, for example, spruce trees of different ages, including old, aged over 200 years, extended trunk base located near the soil, dead lower branches of large diameter, lignum in some sites of the trunk and branches, barkless branches (snags), stable bark, trunk sites with different angle of inclination of the surface, numerous microcracks, old resin, etc. (e.g. Holien, 1997, 1998; Hilmo et al., 2009).

In fact, spruce forests at the final stage of development play a key role in the conservation of many rare species including protected lichens, many of which occur only in such forests and could be “indicators of habitat continuity”. Twenty two indicator species of old-growth boreal forests were recorded (Andersson et al., 2009) – *Acolium karelicum*, *A. inquinans*, *Alectoria sarmentosa*, *Arthonia vinosa*, *Bryoria fremontii*, *Chaenotheca laevigata*, *C. stemonea*, *C. subroscida*, *Chaenothecopsis fennica*, *Chaenothecopsis viridialba*, *Cladonia parasitica*, *Evernia divaricata*, *Hypogymnia vittata*, *Lecanactis abietina*, *Leptogium saturninum*, *Lobaria pulmonaria*, *Microcalicium disseminatum*, *Nephroma bellum*, *N. parile*, *N. resupinatum*, *Pertusaria coccodes* and *Ramalina thrausta*.

Development of a complex of different microhabitats within a single tree determining species diversity is a particular characteristic of spruce. The species composition of lichens occurring in the lower part of the trunk and on branches varied significantly: 108 species were recorded on trunks, 78 on branches and 55 on snags. Analysis of substrate specificity of lichens within spruce trees established that 52% of species were associated only with trunks, 27% with branches and 18% with snags (Table 2). Thus, the proportion of specific species was higher on trunks, while for 71 (45%) lichens, no strong substrate preferences within spruce trees were registered.

Many studies have demonstrated a higher number of lichen species on spruce in boreal forests compared with other tree species (e.g. Koskinen, 1955; Sõmermaa, 1972; Holien, 1997). However, for biodiversity of boreal forest, aspen is supposed to be a hotspot in both Eurasia and North America (Lundström et al., 2013). In our previous lichen inventory of forest communities in middle boreal subzone of Karelia (Tarasova et al., 2017), 178 species were found on aspen trees. The 83 lichens were common on both as-

**Table 2.** Substrate preferences of lichens and allied fungi within spruce trees

| | | Habitats | | |
|---|---|---|---|---|
| | | Lower part of trunks (0–2 m) | Branches | Snags |
| Total number of species | Number of species | 108 | 78 | 55 |
| | Proportion in total species number, % | 68 | 49 | 35 |
| Specific species | Number of species | 56 | 21 | 10 |
| | Proportion in total species number in this habitat, % | 52 | 27 | 18 |

pen and spruce according to a comprehensive analysis of species composition on both trees. These results support the importance of spruce and aspen in maintaining boreal forest biodiversity (e.g. Koskinen, 1955; Pystina, 2003; Pykälä et al., 2006).

Species composition specificity on spruce has been documented by several researchers. For example, 26 species were found only on spruce in the old-growth forests of the Komi Republic (Pystina, 2003). Several studies have emphasized the characteristics of spruce lichen diversity, such as predominance of crustose species (e.g. Hyvärinen et al., 1992; Tønsberg, 1992) as well as the high diversity of species belonging to *Caliciales* (e.g Holien, 1996; Kruys & Jonsson, 1997; Lõhmus & Lõhmus, 2001), and the characteristically low diversity of *Cladonia* species (Pystina, 2003).

## Characteristics of epiphytic lichen cover on trunks

Assessment of epiphytic lichen cover characteristics was carried out on 700 trunks within 40 sample plots. Total epiphytic lichen cover on spruce trees averaged 59% at the trunk base (0–20 cm) and 12% at a height of 130–150 cm above ground level (Table 3). Lichen cover percentage differed significantly between the trunk base and trunk sites at a height of 130–150 cm ($p = 0.001$). These differences are also reflected in the frequency values of occurrence of relevés with lichens at the two studied heights (Fig. 1). A greater number of relevés with a higher lichen cover was recorded at the trunk base whilst at a height of 130–150 cm above ground level there were more relevés without lichens.

The mean number of species per analyzed area (0.02 $m^2$) was 1.9, the minimum was 0 and maximum was 6. The mean number of species differed significantly at the two studied height levels ($p = 0.001$) reaching 3 at the trunk base and 1.4 at a height of 1.3 m above ground level. The occurrence of trunk sites without lichens at the base of the trunk was 2%, 30% at 1.3 m above ground level (Table 3). A 2-fold lower species diversity of lichens at 1.3 m in comparison with the trunk base is reflected in the values of the Shannon's information diversity index, 0.37 and 0.57, respectively. Values of Pielou's evenness index also differed significantly at different heights on the trunk: an average of 0.58 at the trunk base, 0.68 at a height of 1.3 m above ground level ($p = 0.001$). Thus, epiphytic lichen cover at 1.3 m above ground level is more uniform than at the base of the trunk, where the dominance of particular species was more clearly observed.

The majority of total epiphytic lichen cover on spruce trunks was accounted for by 12 species exceeding 1% in cover (Table 3). Both at the trunk base and at 1.3 m above ground level, the proportion of these species accounted for 95%

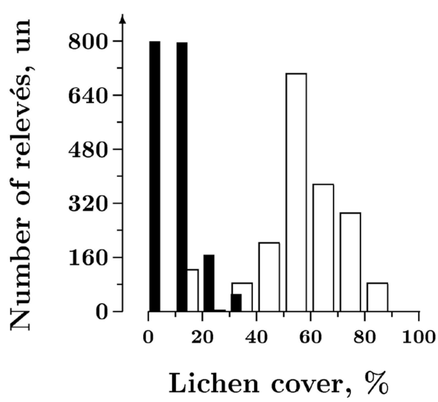


**Fig. 1.** Number of relevés with different values of lichen percentage cover at trunk base (white column) and at height of 130–150 cm above the ground level (bold column).

**Table 3.** The main characteristics of epiphytic lichen cover on trunks of *Picea abies* in forest communities of southern Karelia

| | Height above the ground level, cm | | | | | |
|---|---|---|---|---|---|---|
| | 0-20 | 130-150 | 0-20 | 130-150 | 0-20 | 130-150 |
| Taxa | Average cover, % | | Frequency of occurrence, % | | Proportion of total cover, % | |
| *Calicium viride* | 0.02 | 0.3 | 0.2 | 3.1 | <0.1 | 3.2 |
| *Chaenotheca chrysocephala* | 0.1 | 2.1 | 1.9 | 16.8 | 0.4 | 15.7 |
| *Chaenotheca ferruginea* | 0.3 | 0.7 | 1.5 | 2.2 | 0.5 | 2.7 |
| *Chaenotheca trichialis* | 0.16 | 0.1 | 0.8 | 1.8 | 0.3 | 1.1 |
| *Cladonia cenotea* | 0.5 | – | 1.3 | – | 0.8 | – |
| *Cladonia coniocraea* | 0.3 | – | 0.9 | – | 0.5 | – |
| *Cladonia digitata* | 0.07 | – | 0.3 | – | <0.1 | – |
| *Cladonia fimbriata* | 0.02 | – | 0.23 | – | <0.1 | – |
| *Cladonia* spp.* | 26.3 | 0.2 | 62.0 | 0.8 | 39.2 | 0.7 |
| *Cladonia squamosa* | 0.04 | – | 0.4 | – | 0.1 | – |
| *Evernia mesomorpha* | <0.01 | – | 0.06 | – | <0.1 | – |
| *Hypogymnia physodes* | 3.4 | 3.3 | 41.1 | 41.2 | 6.3 | 31.6 |
| *Lepraria* spp. | 19.7 | 0.3 | 63.6 | 3.7 | 34.5 | 1.8 |
| *Loxospora elatina* | 0.9 | 0.6 | 5.3 | 6.4 | 2.4 | 3.4 |
| *Microcalicium disseminatum* | 0.2 | 1.1 | 1.1 | 5.9 | 0.4 | 6.2 |
| *Mycoblastus sanguinarius* | 0.02 | 0.02 | 0.7 | 0.6 | <0.1 | 0.1 |
| *Ochrolechia androgyna* | 0.05 | <0.01 | 2.2 | 0.4 | 0.1 | 0.1 |
| *Parmelia sulcata* | <0.01 | <0.01 | 0.1 | 0.1 | <0.1 | <0.1 |
| *Parmeliopsis ambigua* | 3.2 | 2.2 | 54.4 | 39.0 | 7.4 | 25.9 |
| *Parmeliopsis hyperopta* | 1.8 | 0.01 | 36.4 | 0.2 | 4.0 | 0.1 |
| *Platismatia glauca* | 0.06 | 0.4 | 2.2 | 6.2 | 0.1 | 2.3 |
| *Vulpicida pinastri* | 0.02 | – | 1.4 | 0.1 | <0.1 | <0.1 |
| Sum of *Cladonia* spp. | 27.2 | 0.2 | 64.6 | 0.8 | 40.8 | 0.7 |
| Sum of *Caliciales* spp. | 0.8 | 4.9 | 6.2 | 30.2 | 1.8 | 33.2 |
| Sum of *Pertusaria* spp. | <0.01 | <0.01 | 0.1 | 0.2 | <0.1 | <0.1 |
| Sum of *Usnea* spp. | <0.01 | <0.01 | 0.1 | 0.2 | <0.1 | <0.1 |
| Sum of *Bryoria* spp. | – | <0.01 | – | 0.2 | – | 0.1 |
| Foliose species | 35.4 | 6.1 | 84.5 | 52.2 | 58.0 | 60.7 |
| Crustose species | 21.8 | 5.8 | 70.9 | 39.1 | 39.3 | 38.8 |
| Fruticose species | 0.4 | 0.01 | 3.1 | 0.3 | 0.7 | 0.2 |
| Total | 58.9 | 11.9 | 97.9 | 69.4 | 100 | 100 |

Note. Rare taxa with a frequency of occurrence less than 1% are not included in the Table.

of the total lichen cover in total. Thus, lichen cover on spruce is mainly due to only 8% of the total listed species which play an important role in ecosystems as well as in maintenance of the general lichens biomass in the spruce forests of the middle boreal subzone.

The spruce trunk base was dominated by species belonging to the genera *Cladonia* and *Lepraria* which together accounted for about 75% of the total cover. The percentage cover of the species *Hypogymnia physodes*, *Parmeliopsis ambigua* and *P. hyperopta* at the trunk base was significantly lower, but their occurrence was sufficiently high and comparable to the dominant species (Table 3).

At height of 1.3 m above the ground level, the dominant species were *H. physodes, P. ambigua* and *Chaenotheca chrysocephala* (Table 3). The cover percentage of these dominant species reached 73% of the total lichen cover on spruce trunk at breast height. Cover and frequency of occurrence of other lichens were much lower.

Thus, according to the results of this study, foliose species play the main role in epiphytic lichen cover of spruce trunks at the two studied height levels. Moreover, despite the predominance of crustose lichens in the list of species, foliose species play the main role in the formation of epiphytic lichen cover (57% of total cover) on spruce.

The trunk base of spruce and at 1.3 m above ground level represent different habitats for lichens due to significant differences of humidity and light availability. The trunk base is characterized by more favorable habitat conditions for lichens resulting in high lichen cover values. However, a limitation in species lichen diversity relates to the competitive ability of *Cladonia* species which strongly restrict colonization of other species at the trunk base. At 1.3 m above ground level on spruce trunks less favorable conditions for lichens result in both lower species diversity, as well as a lower level of competition between species in this habitat.

Some studies demonstrated differences between the values of the cover and number of lichen species on spruce trees at different heights from the ground as higher values of lichen cover on the trunk base compared with breast height have been reported. In a study by Sõmermaa (1972) in Estonian forests, lichen cover at spruce trunk bases and at 1.3 m about ground level ranged from 21–64.5% and 9–52 %, respectively. Other studies reported 58% average lichen cover at a trunk height of 0.8 m on spruce in Estonia (Lõhmus & Lõhmus, 2001) and 21% in Finland (Kuusinen, 1996b). For *Picea obovata* in forests of the Middle Urals, the following values of lichen cover at trunk base and breast height were obtained, 18–38% and 0–10% respectively (Mikhailova, 1996). The composition of dominant lichen species in the middle boreal forests of Karelia corresponds to known data on boreal forests of other European territories.

### Characteristics of epiphytic lichen cover on branches

In total, 75 lichen species were found on *Picea abies* branches. However, only 15 species form the main part of lichen cover on spruce branches (Table 4). The total percentage of lichen cover on branches ranged from 0 to 100% with a mean value of 61%.

**Table 4.** Epiphytic lichen cover on main axis of *Picea abies* branches

| Taxa | Average cover, % | Frequency of occurrence, % | Proportion of total cover, % |
|---|---|---|---|
| *Hypogymnia physodes* | 46 | 96 | 75 |
| *Platismatia glauca* | 9 | 76 | 14 |
| *Parmeliopsis ambigua* | 4 | 48 | 7 |
| *Mycoblastus sanguinarius* | 1 | 25 | 2 |
| *Pertusaria* spp. | 0.6 | 19 | 0.9 |
| *Ochrolechia* spp. | 0.4 | 11 | 0.6 |
| *Parmelia sulcata* | 0.2 | 10 | 0.3 |
| *Tuckermanopsis chlorophylla* | 0.2 | 20 | 0.3 |
| *Hypogymnia tubulosa* | 0.1 | 8 | 0.2 |
| *Bryoria* spp. | 0.1 | 7 | 0.1 |
| *Bryoria capillaris* | <0.1 | 3 | 0.1 |
| *Usnea* spp. | 0.1 | 13 | 0.1 |
| *Alectoria sarmentosa* | 0.1 | 4 | 0.1 |
| *Vulpicida pinastri* | 0.1 | 5 | 0.1 |
| *Imshaugia aleurites* | 0.1 | 5 | 0.1 |
| Foliose species | 59 | 96 | 96 |
| Crustose species | 2 | 29 | 3 |
| Fruticose species | 0.2 | 20 | 0.3 |
| Total | 61 | 96 | 100 |

Note. Rare taxa with a frequency of occurrence less than 1% are not included in the Table.

Foliose lichens were more abundant on spruce branches than fruticose and crustose species. Their occurrence and proportion in total lichen cover accounted for 96% (Table 4). Crustose and fruticose species on analysed branches had a lower frequency of occurrence (29%, 30%) and cover (3%, 0.3%, respectively) values (Table 4).

*H. physodes* was the dominant species on analysed branches, contributing to 75% of total lichen cover. All other species were represented by significantly lower cover values, e.g. *P. glauca* 14%, *P. ambigua* 7% and other species < 2% (Table 4).

The low cover of pendulous lichens *Usnea*, *Bryoria* and *Alectoria* can be explained by their vertical growth and small area of attachment point to branches. Therefore, cover of these species on main axis tended to be low. The number of lichen species per branch varied from 0 to 10 with an average number of 3.5 species.

A high diversity of lichens on branches is characteristic of spruce species richness. More than half of the total species recorded was found on branches, including 21 which occur only here. Ecological studies of lichens on spruce branches, with an emphasis on lichen distribution and succession in relation to measurable environmental variables using quantitative methods, have only been carried out by Bruteig (1994) and Hilmo (1994). Differences in lichen distribution on trunk and branches of trees have mostly been interpreted to be a result of different microclimatic conditions and substrate properties.

Distribution of lichen species along 10 cm long segments of main branch axis of spruce from tree trunk to top was studied. The average number of species per branch 10 cm long segment decreased rapidly from 2.6 to 1.7 along the distance from the tree trunk to the branch tip (Fig. 2, Table 5). Total lichen cover remained relatively stable with value 65% along the inner 170 cm on branches, followed by a rapid decrease to 0% near the branch tip.

There were significant differences in the coverage of some lichen species and in the localization of thalli along branches. For most species on branches, a decrease in cover with increasing distance from the trunk was recorded (*P. ambigua*, total cover of crustose species) (Fig. 2d, 2f). However, cover of *P. glauca* started to decrease at a greater distance from the tree trunk (Fig. 2e). No changes of the *P. glauca* cover, from 0–130 cm from tree trunk, and only then it decreases. Moreover, cover of *H. physodes*, had maximum cover closer to the branch tips (Fig. 2e). Thus, according to the obtained results, there is clear differentiation of microhabitats within the spruce branches, which is reflected in the distribution patterns of lichen species cover along the branch.

On the peripheral sections of large branches located in the middle and lower parts of the tree crowns, the habitat conditions for epiphytic lichens are similar to those on the young branches in the upper crown. They are characterized by high precipitation availability, similar characteristics of the substrate, due to the young age of shoots and the presence of needles. In addition, the edges of large branches, as well as the upper branches, are affected by intense mechanical vibrations under the influence of wind (Alekseev, 1975; Protopopov, 1975; Galenko, 1983). Top branches also had the lowest lichens diversity with an average number of only 2 species. These branches were dominated by *H. physodes*, a species with high growth rate and ability to successfully colonize sites between needles (e.g. McCune, 1990, 1993; Hilmo, 1994; Esseen et al., 1996; Hyvärinen et al., 1999). Base of branches represents a habitat with reduced light intensity and humidity, rough bark and absence of needles. From branch tip to base light intensity falls 3 times, from 14–20% to 5–7% (compared with an open situation) and precipitation decreases from 100% to 17–40% (Protopopov, 1975). In habitat conditions, typical for the segments of large branches located inside the crown (lower light availability and humidity, greater thickness and fracture of the bark, lack of needles), the growth rate and competitive ability of *H. physodes* decreased and other lichen species (*P. glauca*, *P. ambigua*, *Mycoblastus sanguinarius*, *Pertusaria* spp., *Ochrolechia* spp.) with different environmental characteristics colonized these branch sites. The maximum number of taxa per one branch was recorded at their base and in the middle part of older than100-year-old trees.

Thus, the trunks and branches of spruce trees are significantly different habitats of epiphytic lichens, and this is related to the development of the substrate, such the tree bark, its texture, chemical and physical properties (Hilmo, 1994;

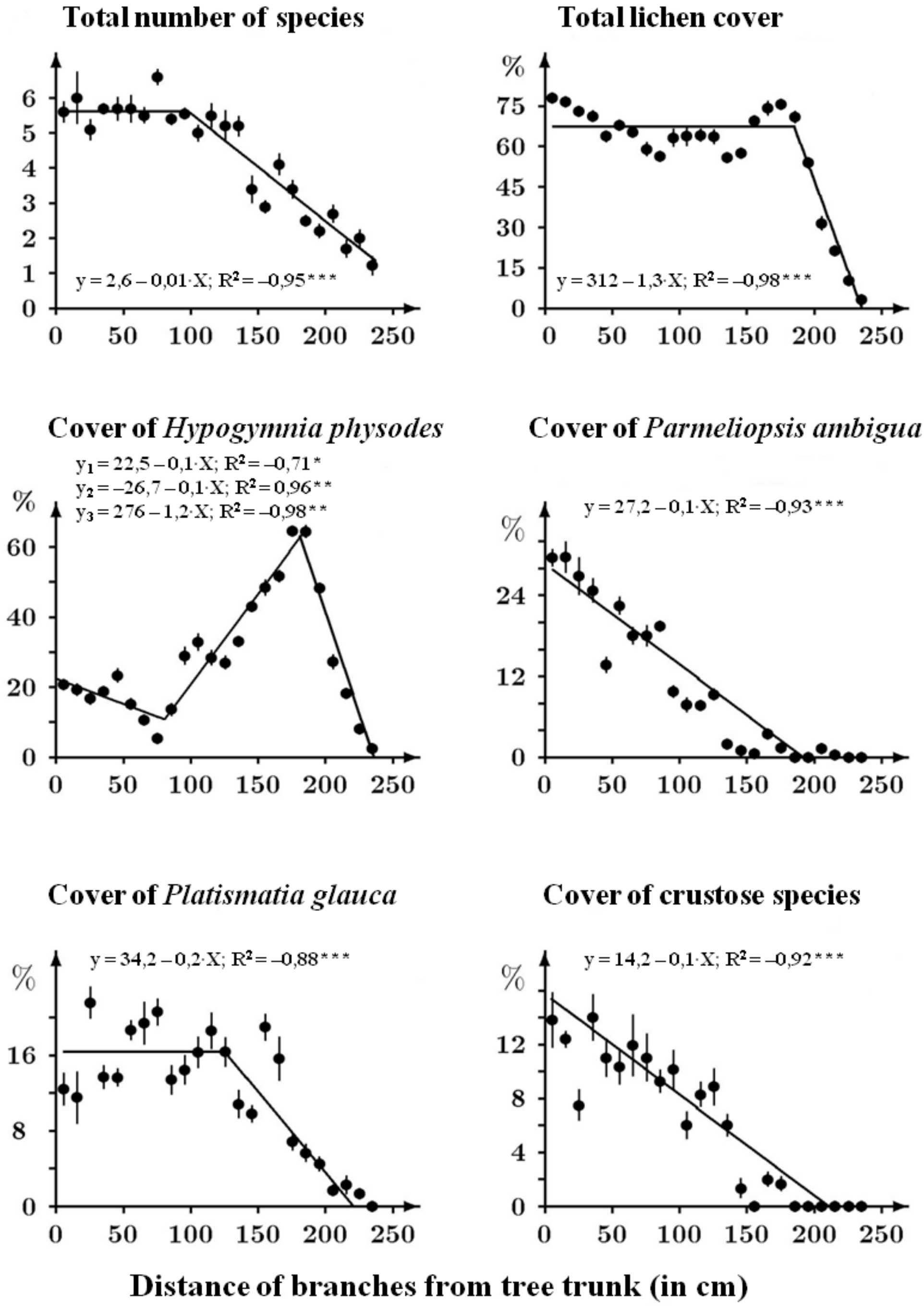


**Fig. 2.** Average total number of species, average total lichen cover, cover of different species and the group of crustose lichens on 10 cm-long segments of spruce branches at different distances (in cm) from tree trunk. Vertical lines represent standard error of mean values. Regression lines are drawn according to regression equations (Table 5).

**Table 5.** Results of linear regression analysis for dependencies between mean values of epiphytic lichen cover characteristics on main axis of spruce branches at different distance from the tree trunk. Abbreviations: r – correlation coefficient; n – sample size (number of classes); I – regression coefficients of equation; M – mean values of equations coefficients; Se – standard error of regression coefficient; t – Student coefficient; *,**,*** – significance level correspondingly to a values 0.05, 0.01, 0.001; significance level was determined for degrees of freedom n-1 – n-3 depending on number of estimated regression parameters.

| Characteristics of epiphytic lichen cover | Distance from tree trunk, cm | Statistical estimates | | | | | | Significance level |
|---|---|---|---|---|---|---|---|---|
| | | r | n | I | M | Se | t | |
| Total number of species | 1–140 | –0.95 | 24 | a | $-8.2\times10^{-3}$ | $0.5\times10^{-3}$ | –14.2 | *** |
| | | | | b | 2.62 | 0.08 | 32.5 | *** |
| Total lichen cover | 1–190 | –0.19 | 19 | a | –0.02 | 0.03 | –0.7 | – |
| | | | | b | 69.2 | 3.2 | 22.0 | *** |
| | 171–240 | –0.98 | 7 | a | –1.33 | 0.09 | –15.0 | *** |
| | | | | b | 312.0 | 20.0 | 16.0 | *** |
| Cover of *Hypogymnia physodes* | 1–90 | –0.71 | 9 | a | –0.14 | 0.05 | –2.7 | * |
| | | | | b | 22.5 | 2.8 | 8.1 | *** |
| | 81–190 | 0.96 | 11 | a | 0.48 | 0.046 | 11.0 | *** |
| | | | | b | –26.7 | 6.2 | –4.3 | ** |
| | 171–240 | –0.98 | 7 | a | –1.2 | 0.1 | –11.4 | *** |
| | | | | b | 276.0 | 21.3 | 13.0 | *** |
| Cover of *Parmeliopsis ambigua* | 1–240 | –0.93 | 24 | a | –0.14 | 0.01 | –12.0 | *** |
| | | | | b | 27.2 | 1.6 | 17.0 | *** |
| Cover of *Platismatia glauca* | 1–130 | 0.27 | 13 | a | 0.02 | 0.02 | 1.0 | – |
| | | | | b | 14.7 | 1.8 | 8.0 | *** |
| | 111–240 | –0.88 | 13 | a | –0.15 | 0.02 | –6.3 | *** |
| | | | | b | 34.2 | 4.5 | 8.1 | *** |
| Cover of crustose species | 1–240 | –0.92 | 24 | a | –0.07 | 0.006 | –11.0 | *** |
| | | | | b | 14.2 | 0.8 | 17.0 | *** |

Holien, 1997; Hilmo et al., 2009). It has been shown, for example, that trunks and branches with a smooth surface were unfavorable substrate for colonization by lichens (Romagni & Gries, 2000).

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