Population characteristics of cephalolichen *Lobaria pulmonaria* (L.) Hoffm. at the northern limit of its range (Northwest Russia, Republic of Karelia)

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Abstract

The populations of *Lobaria pulmonaria* and their characteristics were studied at the northern limit of its range in the Republic of Karelia (Northwest Russia). The study was carried out in northernmost boreal zone on 8 permanent 100 × 100 m sample plots with last disturbance 180–270 years ago. It was found that in the north of the region, the number of substrate units on which lichen grows decreases with an increase of the time since last disturbance from 25 to 11 per ha. In the ontogenetic spectrum (excluding juvenile and immature thalli), virginal thalli prevailed. The proportion of generative thalli in forests in the mid-succession stages (mixed spruce-birch forests) was 2%, and they were absent at later stages (in preclimax spruce forests). In the studied forests, the main substrate of *Lobaria pulmonaria* was the trunks of living *Populus tremula* and *Salix caprea*. With an increase in the diameter and area of the trunk of *Populus tremula*, the number of thalli increased, and their average area decreased. An important role for *Lobaria pulmonaria* was played by the individual characteristics of the tree trunk, such as the height above ground, exposure, angle of inclination. The optimal conditions for the growth and development of this species were formed on the aspen trunks. Due to the collecting shape of crown and its wide radius, a large amount of precipitation flowed down the trunk during rain. Moreover, due to the wide and dense crown, the trunks were wet longer than other tree species. Comparison of the obtained data with similar studies done in the subzone of the middle taiga showed that at the limit of the range, the number of substrate units colonized by *Lobaria pulmonaria* and the number of thalli was smaller than in the south of Karelia. The share of generative thalli in the ontogenetic spectrum of species populations in forest communities of the north taiga subzone was 3 times smaller than in the middle taiga forests.

Key words: northern taiga ecosystems, time from last disturbance, population ecology, populations, populations at range limits

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Introduction

Epiphytic cephalolichen *Lobaria pulmonaria* (L.) Hoffm. is widespread in the boreal, temperate, montane and oceanic areas in the Northern Hemisphere and in cool tropical areas (Yoshimura 1998). It is believed that the species has a continuous range, however, at present, *L. pulmonaria* is found at different spots with different frequency. Over the past 60 years, the world population of *L. pulmonaria* has declined significantly, and the species is currently threatened with extinction in many countries of Western Europe due to the destruction of its habitat and atmospheric pollution (Clerc et al. 1992, Gauslaa 1995, Scheidegger et al. 1998, Zoller et al. 1999, Goward and Arsenault 2000, Gu et al. 2001, Richardson and Cameron 2004, Jüriado and Liira 2009, Scheidegger et al. 2012).

In the European part of Russia, *L. pulmonaria* is widely represented in the south of the Republic of Karelia (Kravchenko and Fadeeva 2008), in the north of Arkhangelsk region (Batalov et al. 2005) and in the Komi Republic (Pystina and Semenova 2009). In forest phytocoenoses in northern Russia (Murmansk Region, Nenets Autonomous Okrug) *L. pulmonaria* is rare [1, 2].

It is known that species populations at range limits are more vulnerable to adverse environmental factors (Sidorova and Churakova 2010, Markovskaya et al. 2018, Kadetov and Suslova 2019). According to the data of Kravchenko and Fadeeva (2008), at *L. pulmonaria* range limits in northwestern Russia there is no real threat to its existence. However, when conducting this study, only *L. pulmonaria* presence-absence data were taken into account.

At the same time, studies of the antioxidant enzyme activities (superoxide dismutase and catalase) in the *L. pulmonaria* thalli at different ontogenetic stages revealed significant differences between coenopopulations in forests in subzones of middle and northern taiga in northwestern Russia (Chirva et al. 2019). For example, a decrease in catalase activity in young thalli in the forest in the north taiga subzone may indicate their stress response to environmental conditions.

A study carried out in the forests in the middle taiga subzone showed that with an increase in the time since last disturbance from 80 to 450 years, the total number of *L. pulmonaria* thalli and the number of colonized substrate units increase as well, with no stabilization of these indices being observed in the series of communities studied (Ignatenko and Tarasova 2017, 2018). The restoration of the total area of thalli in phytocoenoses occurs after 200 years since severe disturbance. In old-growth forests (> 400 years old), *L. pulmonaria* colonize a broad spectrum of tree species in different life states, including lower branches of young spruce trees. At that, the share of regressive subpopulations decreases, while the share of colonizing subpopulations increases, which indicates successful reproduction of the species.

For a complex assessment of *L. pulmonaria* status at its range limits, it was necessary to study the size and ontogenetic structure of lichen populations in the communities, substrate preference, and the influence of habitat conditions (at the community, tree, and microenvironment level) on the qualitative and quantitative characteristics of the species.

Materials and Methods

The studies were carried out in 2014–2016 in Northwest Russia, in the northern taiga forest communities of the Republic of Karelia. The relief of the territory is a hillyplain with prevailing heights from 5 to 250 m above sea level (Biske 1959). The climate is temperate, transitional from maritime to continental. The average annual air temperature varies from +3°C (in the south) to 0°C (in the north). The territory belongs to a zone with a high humidity with an average annual rainfall of 550–750 mm, which decreases from south to north (Romanov 1961). Most of the territory (54%) of the Republic of Karelia is covered by forests. Pine (*Pinus sylvestris* L.) phytocoenoses predominate, they account for 64% of the forested area, spruce (*Picea abies* (L.) H. Karst, *Picea obovata* Ledeb., *Picea* × *fennica* (Regel) Kom.) forests occupy 24%, birch (*Betula pendula* Roth, *Betula pubescens* Ehrh.) forests – 11%, aspen (*Populus tremula* L.) forests ~ 1%. Pine forests prevail in the north, while spruce and deciduous forests dominate in the south of the region (Volkov 2008). Major forest disturbance factors in Karelia are felling, fire and windfall (Gromtsev 2008). Over the past 100 years, most of Karelian forests were clear-cut. The current frequency of forest fires in Northwest Russia is 1–2 times a century (~ 60 years) for drained habitats and 1–2 times a millennium for waterlogged ones (Gorshkov 1998, 2001; Gromtsev 2007). However, in Karelia (the westernmost in the Eurasian taiga zone and the last in Fennoscandia), relatively large fragments of native forests are preserved. They account for ~ 9% of the region total area (Gromtsev 2003).

The work was carried out in two strictly protected areas – in Kostomuksha Nature Reserve and Paanajarvi National Park in two types of forest phytocoenoses: (1) grass-bilberry mixed spruce-birch communities (180–200 years since last disturbance) and (2) sub-climax bilberry feathermoss spruce forest (210–270 years since last disturbance).

Data collection was carried out on 8 permanent 100 × 100 m (1 ha) sample plots (SP) arranged according to the requirements adopted in geobotany. On each SP, geobotanical descriptions were performed, including the characteristics of forest communities (time since last disturbance, the share of particular tree species in the forest stand, the sum of cross-section areas of the trees, the crown density, soil cover characteristics) and individual trees (age, height, trunk diameter, substrate area from 0 to 2 m above ground, crown parameters) (Andreeva et al. 2002). To assess the time since last disturbance the method of studying tree (first of all, *Picea* spp.) population structure was used (Stavrova et al. 2016).

The thallus indices of *L. pulmonaria* were recorded by total counting on all substrates at a height of 0–2 m above ground. At the places of species growth, the characteristics of microconditions were recorded: trunk exposure, the height above ground, the angle of inclination of the trunk surface. For each thallus of *L. pulmonaria*, the total area and necrotic area (cm^2) were measured using the 25 × 25 cm frame. Also ontogenetic state was determined: virgin 1 (v1), virgin 2a (v2a), virgin 2b (v2b), virgin 2c (v2c), generative (g), sub-senile (ss), senile (s) (Mikhailova 2005, Ignatenko et al. 2020). Based on the spectrum of thalli of different ontogenetic states, the following types of subpopulations were distinguished: colonizing (col), extending (ext), stable (st), pseudo-extending (ps-ext), retrogressive (retr). All talli growing on the same tree were attributed to onesubpopulation.

Statistical data processing was based on regression analysis using the linear model: $y = aX + b$ (Andreeva et al. 2002, Ivanter and Korosov 2011). If there were relationships, the lines on the graphs were drawn in accordance with the regression model. In the absence of significant changes, a horizontal line at the average value was drown on the graph.

A total of 898 thalli of *L. pulmonaria* growing on 120 substrate units (standing or fallen living or dead trees and shrubs) were recorded.

Region	№ SP	GPS coordinates	Forest type	Time since last disturbance, years	The share of shrubs in the grass-shrub layer, %	The sum of basal areas, $m^2 ha^{-1}$			Tree composition, %	Tree species	Tree age, years
						live trees	standing dead trees	fallen dead trees			
1	1	64°30′ N 30°29′ E	s	250	69	29.7	3.4	6.3	74S12A11P3B	S	51-241
										A	151-163
	2	65°00′ N 30°19′ E	a-b	180	88	29.5	1.9	6	68S11B10P9A2W	S	53-171
										A	88-143
	3	65°01′ N 30°19′ E	a-b	200	88	27.2	3.8	10.9	78S10B7P4A1W	S	44-197
										A	93-154
	4	65°01′ N 30°19′ E	a-b	200	94	23.7	3.5	3.7	78S14P4B3W1A	S	47-197
										A	105-137
2	1	66°16′ N 30°26′ E	a-b	200	68	27.8	1.7	6.3	55S19A16B6P4W	S	76-189
										A	152
										W	71-96
	2	66°12′ N 30°35′ E	a-b	190	48	28.5	1.7	3.1	62S26B6P3A2W1R	S	57-183
										W	72-108
	3	66°18′ N 30°26′ E	s	270	80	22.4	1	4.2	85S10B3W2A	S	68-236
										A	126-154
	4	66°17′ N 30°27′ E	s	210	80	19.3	1	2.5	76E9B8A5W2P	S	53-196
										W	91-157

Table 1. Characteristics of the studied spruce phytocoenoses on the territory of Karelia
Notes: 1 – Kostomuksha Nature Reserve, 2 – Paanajarvi National Park; № SP – sample plot number; types of forest (a-b – grass-bilberry mixed spruce-birch communities, s – bilberry feather-moss spruce forest); tree species (S – spruce, A – aspen, W – willow, B – birch, P – pine, R – rowan).

Results

It was found that in northern taiga mixed spruce-birch communities, the number of thalli varies from 63 to 232 pcs per ha, averaging at 125 pcs per ha, while in spruce forests the number of thalli varies from 73 to 123 pcs per ha and averages at 91 pcs per ha. Probably, a smaller number of thalli in spruce forests is related to a decreased ability of potential substrate for *L. pulmonaria*. Thus, the share of deciduous tree species (the main forophytes for *L. pulmonaria*) in the stand is higher in spruce-birch phytocoenoses than in subclimax spruce forests, and averages 23 and 18%, respectively. At the same time, an increase in the time since last disturbance from 180 to 270 years decreases by half the number of substrate units on which the lichen grows (from 25 to 11 pcs per ha (R^2= 0.62; p = 0.05)).

In the ontogenetic spectrum of populations of *L. pulmonaria* (excluding juvenile and immature thalli), in most cases (70%) virginal thalli dominate (Fig. 1.A), and the share of sub-senile and senile thalli is on average 9 and 13%, respectively. It is to be noted that in spruce forests there are no thalli with apothecia, and in mixed spruce-birch forests they account for only 2%.

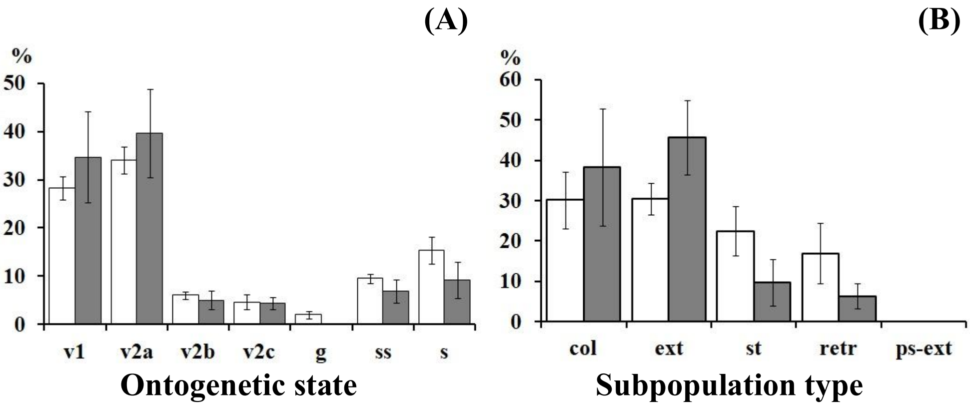

Fig. 1. (A) Age-related spectra of populations and (B) the share of various types of subpopulations of *Lobaria pulmonaria* in the phytocoenoses in the subzone of the northern taiga of Karelia. *Notes*: white – grass-bilberry mixed spruce-birch forests, gray – bilberry feather-moss spruce forests.

In the subpopulation spectrum (Fig. 1.B), in communities with the time since last disturbance of 180–200 years, colonizing and retrogressive subpopulations account for 30% each, and in phytocoenoses with the time since last disturbance of 210–270 years, 38 and 46%, respectively. It was found that in mixed spruce-birch communities, the share of stable and regressive subpopulations in the total spectrum is 2 times higher than in bilberry feather-moss spruce forest.

In the studied phytocoenoses, *L. pulmonaria* colonizes mainly deciduous trees – *Populus tremula* (45%), *Salix caprea* (43%), *Sorbus aucuparia* (5%), *Betula* spp. (4%) (Table 2, 3). Single thalli were found on the branches of *Picea* spp. (3%). At the same time, 74% of the substrate units of *L. pulmonaria* are represented by living trees, 18% are standing dead trees, and 8% are fallen dead trees. On the fallen dead trees, *L. pulmonaria* was most often found on *S. caprea* trunks (75%). It is important to note that in the bilberry feather-moss spruce forest, thalli of *L. pulmonaria* colonize a smaller variety of substrates (Table 3). Thus, in mixed spruce-birch communities, the species was recorded on fallen dead mountain ash and aspen, while it did not grow on these types of substrate in sub-climax spruce communities.

Interestingly, in the north-taiga communities, the average thallus area on the trunks of two main phorophytes (*P. tremula* and *S. caprea*) differs significantly (Table 3). Thus, in mixed spruce–birch communities, the average thallus area of *L. pulmonaria* on *S. caprea* is 507.7 ± 120.2 cm^2, and on *P. tremula* is 51.2 ± 14.1 cm^2 (U-test, p = 0.001). In bilberry feather-moss spruce forest, a similar trend is observed that on *S. caprea* the average area of thalli is 210.8 ± 98.4 cm^2, and on *P. tremula* – 35.7 ± 8.4 cm^2 (U-test, p = 0.05). Such differences are due to the fact that on the willow trunks in the subpopulation spectrum there are ~ 1.5 times fewer thalli with a small area of virginal 1, 2a, 2b states than on aspen trees. Also, on the trunks of *S. caprea*, the proportion of regressive subpopulations is 12 times higher than on the trunks of *P. tremula*.

Forest type	Substrate	N	*Age*	*H*	H_{cr}	L_{cr}	D_0	D_{130}	R_{cr}	*S*
a	*Picea* spp.	2	**92.5** ±0.5	**11.5** ±4.5	**6.3** ±3.8	**5.3** ±0.8	**15.1** ±6.5	**13.5** ±5.9	**1.0** ±0.2	**0.9** ±0.4
	Populus tremula	34	**117.1** ±3.9	**21.0** ±0.6	**13.2** ±0.7	**7.8** ±0.6	**36.4** ±1.9	**31.7** ±1.5	**2.5** ±0.1	**2.1** ±0.1
	Salix caprea	27	**87.6** ±4.5	**12.6** ±0.6	**6.3** ±0.5	**6.3** ±0.5	**31.1** ±2.3	**23.2** ±1.3	**1.6** ±0.1	**1.6** ±0.1
	Sorbus aucuparia	3	**78.5** ±5.5	**10.7** ±1.8	**6.3** ±1.2	**4.3** ±0.9	**13.5** ±0.4	**12.2** ±1.0	**1.3** ±0.1	**0.8** ±0.1
b	*Picea* spp.	2	**64.0** ±0.0	**2.5** ±4.8	**1.0** ±2.4	**1.6** ±4.1	**5.3** ±8.6	**4.1** ±8.1	**0.8** ±0.7	**0.3** ±0.02
	Populus tremula	13	**143.6** ±6.5	**25.5** ±1.9	**17.5** ±0.9	**8.0** ±1.6	**52.3** ±3.4	**43.2** ±3.2	**2.4** ±0.3	**3.0** ±0.2
	Salix caprea	6	**124.0** ±33.0	**13.2** ±0.9	**7.2** ±1.1	**6.0** ±1.1	**35.9** ±7.6	**28.6** ±6.4	**1.5** ±0.2	**2.0** ±0.4

Table 2. Taxation parameters of the main substrates of *Lobaria pulmonaria* in forest communities of Karelia in the north taiga subzone. *Notes*: Forest type: a – grass-bilberry mixed spruce-birch communities, b – sub-climax bilberry feather-moss spruce forest. N – The number of substrate units. Taxation parameters of trees are indicated as: Age – tree age, years; H – tree height, m; D_0 – trunk diameter at the base of the tree, cm; D_{130} – trunk diameter at a height of 1.3 m; H_{cr} – height of the lower boundary of the crown, m; L_{cr} – the length of the crown, m; R_{cr} – the radius of the crown, m; S – substrate area, m^2. M±m: M – average value, m – standard error.

It was found that with increasing age of the main substrate of *L. pulmonaria* living *P. tremula* trees from 90 to 160 years, the following taxation parameters of the tree increase: trunk diameter (at a height of 1.3 m) – from 30 to 48 cm (R^2 = 0.74; p = 0.001), the crown radius – from 2.3 to 3.2 m (R^2 = 0.65; p = 0.05), the height – from 20 to 27 m (R^2 = 0.60; p = 0.05), the substrate area – from 1.9 to 3.2 m^2 (R^2 = 0.75; p = 0.05). With the tree growth, the physical and chemical properties of the substrate, the moisture and light conditions change, and the time required for the colonization, growth and development of lichens increases.

Forest type	Substrate	The number of substrate units	The share of the substrate (%)	The number of thalli	Average thalli area (cm^2)
grass-bilberry mixed spruce-birch communities	*Picea* spp. (live)	2	2	4	**21.7** ± 15.8
	Populus tremula (live)	34	36	293	**51.2** ± 14.1
	Populus tremula (fallen dead)	2	2	28	**218.0** ± 94.4
	Salix caprea (live)	27	28	168	**507.7** ± 120.2
	Salix caprea (fallen dead)	6	6	33	**447.5** ± 186.5
	Salix caprea (standing dead)	15	16	94	**517.7** ± 197.0
	Sorbus aucuparia (live)	3	3	5	**539.6** ± 138.8
	Sorbus aucuparia (standing dead)	3	3	10	**208.2** ± 103.1
	Others	3	3	7	**57.4** ± 35.6
sub-climax bilberry feather-moss spruce forest	*Picea* spp. (live)	2	7	16	**9.2** ± 3.0
	Populus tremula (live)	13	48	178	**35.7** ± 8.4
	Salix caprea (live)	6	22	42	**210.8** ± 98.4
	Salix caprea (standing dead)	2	7	18	**114.8** ±75.8
	Others	4	15	19	**114.2** ± 39.4

Table 3. Substrate types of *Lobaria pulmonaria* in forest communities of the north taiga subzone of Karelia. *Notes*: M±m: M – average value, m – standard error.

Therefore, the number of thalli increased (Fig. 2.A), and the average area decreased with an increase in the diameter and area of the trunk (Fig. 2.B).

The angle of inclination of the trunk surface is one of the most significant characteristics of the habitat of epiphytic lichens. Positively inclined trunks receive 2–3 times more moisture from the atmosphere than negatively inclined ones. They are better lit and contribute to better fixation of lichen diasporas (Barkman 1958, Gorshkov 1986, Tarasova et al. 2012).

Therefore, with an increase in the angle of inclination of the tree in a positive direction, the coverage and species diversity of epiphytic lichens increase (Gorshkov 1986, Tarasova 2000, Stepanova 2004, Zhuravleva 2007).

In the studied communities, *L. pulmonaria* occupies tree trunks with the inclination varying from -36 to 81°, with the average inclination of +16°. On aspen, the most of thalli (53%) grows on the trunks with inclination varying between 2 and 12°.

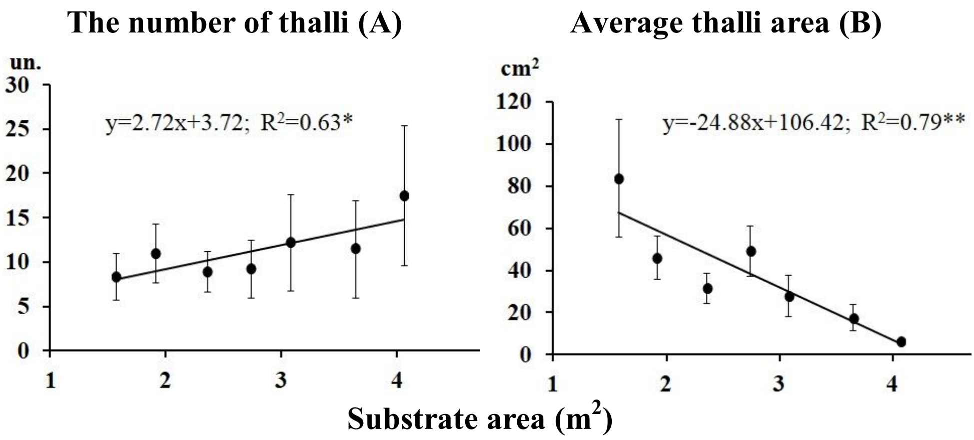

Fig. 2. Quantitative indicators of *Lobaria pulmonaria* on *Populus tremula* trees with different trunk lateral surface area in spruce phytocoenoses in the north taiga subzone. *Notes*: The lines are drawn in accordance with linear regression equations. Error bars indicate standard error of the mean (* – $p < 0.05$, ** – $p < 0.01$). R^2 is the coefficient of determination.

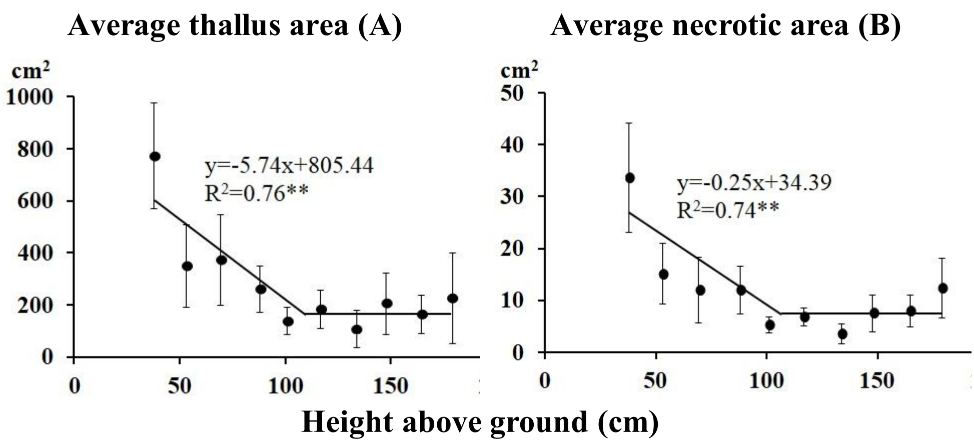

Fig. 3. Quantitative indicators of *Lobaria pulmonaria* on trunks of live *Salix caprea* trees at different heights above ground in spruce phytocoenoses in the north taiga subzone. *Notes*: The lines are drawn in accordance with linear regression equations. Error bars indicate standard error of the mean (** – $p < 0.01$). R^2 is the coefficient of determination.

The largest number of *L. pulmonaria* thalli both on live (62%) and dead-standing (55%) willows was recorded on moderately (5–26°) inclined trunks.

The lichen thalli were recorded on trunks at a height of 6 to 192 cm. On aspen, most thalli (76%) grow at a height of 60 to 160 cm, whileon willow 65% of thalli were found at a height of 60-140 cm above ground. In single cases, there were specimens growing at a height of more than 2 m above ground (not counted).

It was found that on willow trunks, the areas of *L. pulmonaria* thalli and necrotic areas decrease from 770 to 180 cm^2 and from 30 to 10 cm^2, respectively, with an increase in the height from the ground up to 110 cm. With a further increase in the height from the ground these indices do not change (Fig. 3.A, 3.B). This is probably due to the fact that large, older thalli are located in the lower part of the trunk. As a rule, they are virgin 2c – senile thalli that account for 63–89% of the total number of thalli are located at a height of up to 1 m above ground.

Under conditions of the north taiga subzone area in Karelia, the thalli of *L. pulmonaria* on the trunks of live aspen were most often found on south-east and west-sides of trees; they account for 17 and 16% of the thalli number, respectively (Fig. 4.A). The smallest number of thalli was recorded on north-east (7%) and east (7%) sides of trees. The average thallus area on the north, north-east and east sides is 2 times higher than on other sides of the trunk (Fig. 4.B).

On goat willow, 52% of thalli were found on north and north-west sides of trees (Fig. 5.A). The largest average area was recorded for thalli located on north, north-east, and north-west sides (Fig. 5.B). It was revealed that the contribution of necrosis to the total thalli area was greatest in thalli on south sides of willow trunks (Fig. 6.A), and north-east and westsides of aspen trunks (Fig. 6.B). However, the share of necrotic areas on north sides of aspen trees did not exceed 9%, whereas on south sides of willow trees it reaches 20%. This was probably due to longer stay of thalli in a dry state on south sides of *S. caprea* trunks as they were more likely to be exposed to direct sunlight than thalli at the same sides on *P. tremula* trunks. This was evidenced by a significant difference between the length and radius of the crown (U-test, $p = 0.05$) of *S. caprea* and *P. tremula* (Table 2). Due to the high values of tree height, radius and length of crown, stemflow on aspen can reach 9.4% of the total rainfall in the community (Molchanov 1961). Owing to the wide and dense crown, aspen trunks were in a wet state longer than those of willows.

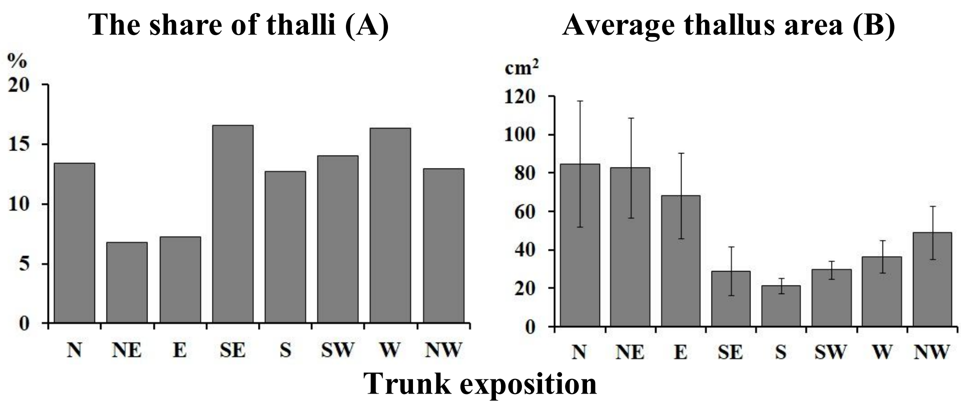

Fig. 4. Quantitative indicators of *Lobaria pulmonaria* at various *Populus tremula* trunk expositions in spruce phytocoenoses in the north taiga subzone. *Notes*: Error bars indicate standard error of the mean.

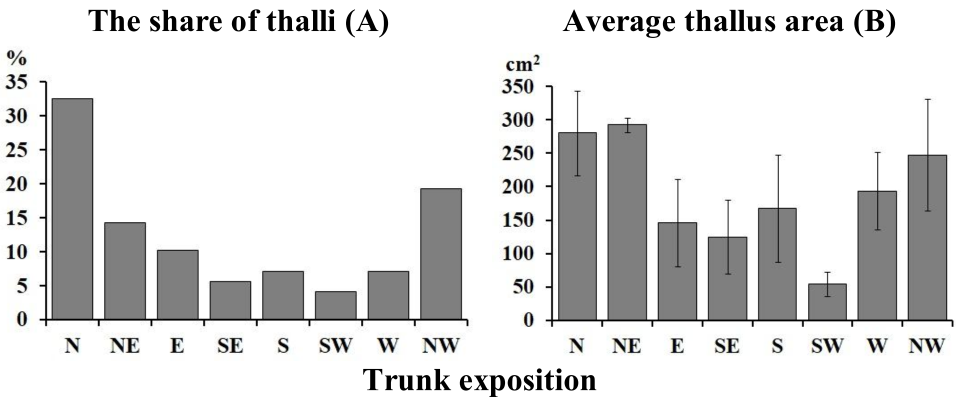

Fig. 5. Quantitative indicators of *Lobaria pulmonaria* at various *Salix caprea* trunk expositions in spruce phytocoenoses in the north taiga subzone. *Notes*: Error bars indicate standard error of the mean.

In forest phytocoenoses in the north taiga subzone the projective cover of bryophytes on the main substrates of *L. pulmonaria* (live willow and aspen trees) varied from 5 to 40% and from 5 to 30%, respectively. It was revealed that on willow trees most of the thalli (73%) are found on trunks with bryophyte cover of 10–20%, while on aspen trees 53% of the studied thalli grow on trunks with similar bryophyte covering. Interestingly, 23% of *L. pulmonaria* thalli are found on aspen trees with an abundance of bryophytes up to 5%. This probably also indicates that *P. tremula* trunks remain moist for a longer time than trunks of *S. caprea*.

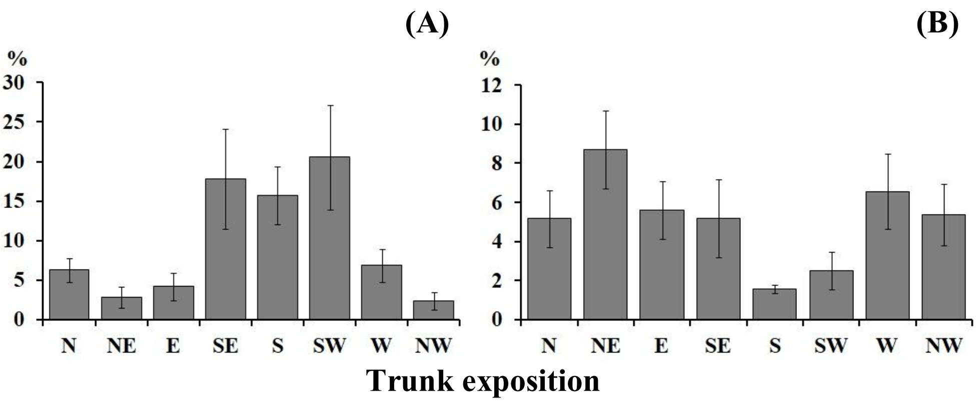

Fig. 6. The average share of necrotic area in the total thallus area of *Lobaria pulmonaria* at different trunk expositions of *Salix caprea* (A) and *Populus tremula* (B) in spruce phytocoenoses in the north taiga subzone. *Notes*: Error bars indicate standard error of the mean.

Discussion

At the total length of reconnaissance routes of ~ 110 km, only a few habitats of *L. pulmonaria* were found in forest communities in the north taiga subzone. In the studied territory, *L. pulmonaria* was found in spruce phytocoenoses with a time since last disturbance of 180 years or more. In the middle taiga subzone, the species was recorded in middle-aged aspen forests as soon as 80 years after the disturbance (Ignatenko and Tarasova 2018).

One of the main reasons of rare findings of *L. pulmonaria* in the north of the region was the absence of its main substrate, which is *P. tremula* for taiga (Istomina 1996, Kravchenko and Fadeeva 2008, Pystina and Semenova 2009, Mikryukov 2011, Ignatenko and Tarasova 2015, 2017, 2018; Ignatenko 2018). Pure aspen forests in northwest Russia are found only in the middle taiga subzone (Volkov 2008). In northern taiga forests, aspen was found only as a small admixture in birch forests and mixed spruce-birch communities. Due to this, on the northern limits of the range, the species is often found also on *S. caprea* since the bark of this tree is similar in structure (cracked), mineral content and pH to *P. tremula* (Gauslaa 1995). However, *S. caprea* is significantly inferior to *P. tremula* in its taxation parameters, which affects the qualitative and quantitative characteristics of *L. pulmonaria* subpopulations. Thus, the tree age and trunk area of *S. caprea* are lower than that of *P. tremula*, which means that the potential space and time for the growth and development of lichen thalli is smaller on this substrate.

It is important to note that in the subzone of the middle taiga, *L. pulmonaria* grows in bilberry feather-moss spruce forest quite often. The species has established in the ecosystem since last disturbance of 410–450 years (likely due to the felling or forest fires) (Ignatenko and Tarasova 2017, 2018). This is probably due to the renewal of aspen in such communities in the windows after windthrow. The fact that *L. pulmonaria* massively populates the lower branches of young spruce trees also contributes to maintaining a high number of thalli in these forests. In old-growth northern taiga spruce forest with the time since last disturbance of more than 400 years (Paanajarvi National Park), there is no suitable substrate for the colonization of *L. pulmonaria*. Therefore, the species is not found in these phytocoenoses. In Kostomuksha Nature Reserve, as in the whole in the subzone of northern taiga, pine phytocoenoses predominate (85%), spruce communities account for only 14.5%, which are confined to the foot of the slopes and valleys of rivers and streams (Gromtsev 2009). Pine forests are potentially unsuitable for the distribution of the species, and fragments of spruce phytocoenoses can act as a kind of passages for the settlement of *L. pulmonaria*.

It has been found that at the limits of the range, the number of substrate units colonized by *L. pulmonaria* and the number of thalli is smaller than in the southern Karelia in similar types of forests with the same time since last disturbance (Ignatenko and Tarasova 2017, 2018; Ignatenko 2018). The share of generative thalli in the ontogenetic spectrum of species populationsin forest communities of the north taiga subzone is 3 times less than in mid-taiga communities. This is probably due to the high degree of fragmentation of this territory by pine phytocoenoses and the lack of suitable substrate, *i.e*. aspen and willow trees. In this regard, the frequency of occurrence of *L. pulmonaria* in the communities of the north taiga subzone decreases and leads to a decrease in the probability of fruiting bodies forming on the thalli, since thalli with a different genotype are required for sexual reproduction (Zoller et al. 1999). It is believed that the presence of sexual reproduction is characteristic of populations with high density (Scheidegger et al. 1995).

Colonizing and stable subpopulations predominate in the subpopulation spectrum in mid-taiga forests (Ignatenko and Tarasova 2018), while colonizing and extending subpopulations predominate in northern taiga. The data obtained indicate the relative biological youth of the studied subpopulations (Mikhailova 2005). A low proportion of regressive subpopulations indicates that in the vast majority of cases, reproduction in subpopulations after colonization of the substrate proceeds normally.

The results have shown that the diameter and area of the tree significantly affect the characteristics of *L. pulmonaria* – with an increase in these parameters of the trunk, the number of thalli increases and the average area decreases. Such changes in subpopulations may indicate the appearance of new thalli generations arising from maternal ones on large old trees (Ignatenko 2018, Ignatenko and Tarasova 2019). With the growth of a tree, a large number of different microbiotopes are formed on the aspen and willow bark (crevices, pores, roughness), and the substrate area increases, which has a positive effect on the growth and development of *L. pulmonaria* thalli (Gustafsson et al. 1992, Mikhailova et al. 2005, Öckinger et al. 2005, Ranius et al. 2008, Belinchón et al. 2009). The time factor is also important. Large, older trees are available for colonization over a longer period of time (Gu et al. 2001, Belinchón et al. 2009, Fritz et al. 2009, Brunialti et al. 2015). Similar data were obtained when populations of *L. pulmonaria* were studied in the mid-taiga forest of Karelia (Ignatenko 2018, Ignatenko and Tarasova 2019).

For epiphytic lichens, an important role is played by the individual characteristics of every trunk. *L. pulmonaria* grows in most cases on positively inclined surfaces of trees in northern taiga spruce forests, exposed to the north and west, at the height of more than 60 cm above ground. This is probably due to the requirement of a long stay of the thallus in a wet state for the successful growth of *L. pulmonaria*, as well as the absence of direct sunlight. Light plays an important role in the life of the lichen, however, direct sunlight can cause serious damage to the thallus and lead to its death (Gauslaa and Solhaug 2001). The damaging effect of strong solar insolation is probably indicated by the fact that the proportion of necrotic areason the thalli of *L. pulmonaria* growing on *S. caprea* was higher on the trunks with south exposure.

In phytocoenoses of the mid-taiga subzone, *L. pulmonaria* was recorded on the trunk with similar characteristics (Ignatenko 2018). At the same time, as well as on *S. caprea* trunks in the north taiga subzone, the average area of thallus necrosis on *P. tremula* decreases with increasing height above ground up to 1 m, and on the branches of *Picea* spp. up to 0.8 m, then this parameter stabilizes. This is probably due to less favorable conditions for the growth and development of *L. pulmonaria* thallion the lower part of the trunk: snow cover, competition with bryophytes, *etc*.

Epiphytic bryophytes play an important role in the microenvironment in lichen habitats. The developed moss cover on trees helps to maintain an appropriate level of moisture, which in turn has a beneficial effect on the growth and development of cyanolichens, compared to habitats where bryophytes are absent (Tarasova 2017, Tarasova et al. 2017). Thus, in forest phytocoenoses in northern Karelia, the largest number of thalli was recorded on the trunks of the main substrates, where the projective cover of bryophytes was 10–20%. In the south of the region, with an increase in the total coverage of bryophytes from 3 to 60%, the number of *L. pulmonaria* thalli on aspen trunks increases 3 times (from 3 to 9 pcs.) and the average thallus area decreases 2 times (from 115 to 65 cm^2) (Ignatenko 2018).

Conclusions

As a result of the studies, it becomes apparent that populations of *L. pulmonaria* in the northern taiga forests of Karelia are vulnerable to changes in environmental conditions and need a special protection. The absence of suitable substrates and peculiar climatic conditions leads to a decrease in the density of populations, which probably has a significant effect on the genetic diversity of the species in the region.

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