Ontogenesis of the Lichen *Lobaria pulmonaria* (L.) Hoffm. in Plant Communities of the Boreal Zone

R. V. Ignatenko\textsuperscript{a,b, *}, V. N. Tarasova\textsuperscript{a}, and E. F. Markovskaya\textsuperscript{a}

\textsuperscript{a}Petrozavodsk State University, Petrozavodsk, 185910 Russia

\textsuperscript{b}Karelian Research Center, Russian Academy of Sciences, Petrozavodsk, 185000 Russia

*e-mail: ocean-9@mail.ru*

Received April 8, 2019; revised October 29, 2019; accepted November 7, 2019

Abstract—The paper describes the ontogenesis of the epiphytic lichen *Lobaria pulmonaria*. The studies were carried out in the Karelian forest communities with the period since the last disturbance ranging from 80 to 450 years. Based on the concept of a discrete description of plants and lichens, four periods and 14 age-related states have been distinguished in *L. pulmonaria*’s ontogenesis. Each ontogenetic state of *L. pulmonaria* is characterized by a certain thallus size as well as by the presence and the level of development of vegetative diaspores and apothecia on the thallus surface. The possible variants of the species ontogenesis are described.

Keywords: ontogenesis, lichens, *Lobaria pulmonaria*

DOI: 10.1134/S1062360420020046

INTRODUCTION

Investigation of the ontogenetic structure of a species is one of the important study directions in modern lichenology (Mikhailova and Vorobeichik, 1999; Suetina, 2001; Mikhailova, 2005; Suetina and Glotov, 2010, 2015; Ignatenko and Tarasova, 2017). The distinguishing of different age and quality thalli provides a better understanding into the rules of the ontogenetic development and formation of a lichen population’s structure at a certain time point as well as the forecasting of their future development (Mikhailova, 2005; Suetina and Glotov, 2010). Such an approach is especially important for the development of a protection strategy during a study of rare and endangered lichen species (Gauslaa, 1997; Scheidegger, 1998; Tarasova et al., 2008; Suetina and Glotov, 2010; Mikryukov, 2011; Fenko and Tarasova, 2016; Ignatenko, 2018; Ignatenko and Tarasova, 2018).

The large epiphytic cyanobiont *Lobaria pulmonaria* (L.) Hoffm., Lobariaceae, Ascomycotina is widespread in the boreal, temperate, mountain, and oceanic zones and regions (Yoshimura, 1971, 1998). This lichen is included into the Red Book of the Russian Federation (2008) and has the status of a vulnerable species with decreasing populations (2b). *L. pulmonaria* is a three-component lichen formed by a mycobiont (ascomycete), a primary photobiont (eukaryotic green algae *Dictyochloropsis reticulata* Tschermak-Woess (Tschermak-Woess, 1995)), and a secondary photobiont (nitrogen-fixing cyanobacterium *Nostoc* sp. (Tschermak-Woess, 1988)). *L. pulmonaria* is considered to be extremely sensitive to any type of anthropogenic impact and is confined to old forests of the moderate climatic zone (Andersson and Appelqvist, 1987; Rose, 1992; Gauslaa, 1994; Andersson et al., 2003; Liira and Sepp, 2009). According to some data, this large and well-known lichen is associated with other rare and endangered species, so it can be considered as an indicator (so-called umbrella species) of their presence in the community (Campbell and Frederen, 2004; Pykälä, 2004; Radies and Coxson, 2004; Ravera et al., 2006; Scheidegger and Werth, 2009; Nascimbene et al., 2010).

*L. pulmonaria* represents one of the most studied lichen species: the global database of a lichenological literature Recent Literature on Lichens (Culberson et al., 2019) contains 313 manuscripts with key words including the name of this species. In spite of this fact, there are still a lot of questions regarding its ontogeny. For example, Mikhailova (2005) described thalli of differing ontogenetic quality and divided them into different functional and age groups, from sterile to fertile (see Materials and Methods). This study did not include thalli with the length <0.2 cm; moreover, the fertile group position at the end of the functional–age range, right after the senile group, is rather questionable, as is combining of thalli belonging to different ontogenetic states into one sterile group. Other authors (Gorshkov and Semenova, 2008) developed a logical sequence of the ontogenetic age-related states of the species based on the concept of a discrete description of lichens (Suetina, 2001) corresponding to the classic plant ontogenesis scheme (Rabotnov, 1950; Uranov, 1975); however, the authors did not
consider thalli whose size was less than 0.5 cm and did not provide a detailed description of different age-related states.

The performed analysis showed the lack of a complete description of the ontogenetic development of *L. pulmonaria* as well as the lack of any morphometric indices of thalli at the early ontogenetic stages. Obviously, the existing data require generalization, unification, and establishment of correlations between the groups and states distinguished by different authors as well as the study of their dimensional structure, morphogenesis, and ecological features.

**MATERIALS AND METHODS**

The study was carried out in 2014–2016 in the forest communities of the Republic of Karelia, including middle taiga (Kivach Nature Reserve, Vodlozero National Park, Kizhsky protected area, and Petrozavodsk urban district) and northern taiga (Kostomuksha Nature Reserve and Paanayarvi National Park) subzones.

Data were collected using a network of permanent 1-ha sample plots (PSPs). For each PSP, the complete geobotanical descriptions of phytotocoenoses were made (Andreeva et al., 2002), including the evaluation of a canopy density (using an Ipatov’s densitometer) and the relative sum of the cross-sectional areas of live, dead, and fallen tree trunks (using a Bitterlich’s relascope) as well as the ground cover description. To evaluate the age of disturbances in plant communities, the study of the age structure of spruce (*Picea* spp.) coenopopulations was used (Stavrova et al., 2016).

In total, we described 33 PSPs located in different forest types with the age of disturbance varying from 80 to 450 years. In the middle taiga subzone, all studied phytocoenoses belonged to the same ecodynamic series representing the regenerative dynamics of a bilberry–green moss spruce forest. These phytocoenoses included (1) middle-aged bilberry–grass aspen forest (80–110 years), (2) mixed grass–bilberry spruce–aspen communities (150–190 years); (3) subclimax bilberry–green moss spruce forests (210–260 years), and (4) conditionally climax communities (410–450 years). No middle-aged aspen forests were registered in the course of reconnaissance routes (~110 km) in the northern taiga subzone. In this area, spruce communities are usually recovered via birch forests. Therefore, the studies were carried out in only two types of forest phytocoenoses: mixed grass–bilberry spruce–birch communities (180–200 years) and subclimax bilberry–green moss spruce communities (210–270 years).

The total count of *L. pulmonaria* thalli on all substrates (branches and trunks of live and dead trees) was carried out at a height of 0–2 m above the ground with a simultaneous registration of habitat characteristics (tree parameters and microconditions). Each thallus was measured with a 25 × 25-cm frame to record its total area (cm$^2$) and classified with a certain functional–age group according to Mikhailova (2005): sterile (*st*) without reproductive structures; hyposorediate (*s1*) with marginal soralia; mesosorediate (*s2*) with abundant marginal and single laminal soralia; hypersorediate (*s3*) with abundant laminal soralia; fertile (*fert*) with apothecia; subsenile (*s*/sen), which are partially destroyed in the center and have regenerative structures on old lobes; and senile (sen) with dying lobes and regenerative structures formed after a decay of a large thallus.

To study thalli with the area of <1 cm$^2$, bark samples were collected from the trunks of at least five trees on each PSP; the samples were harvested from the places of growth of large thalli (at a distance of 2–10 cm) and from the sites with no visualized thalli (the opposite sides of trunks, at the moss-free areas). The harvesting was performed based on the permit no. 18 of the Federal Service for Supervision of Natural Resources for collecting of fauna and flora objects belonging to the species listed in the Red Book of Russia (March 28, 2016).

Substrate samples were studied under laboratory conditions using a MicroMed MS2 binocular. The following thallus parameters were registered (in the case of their presence): length and width (mm); presence of rhisines and roughnesses; presence and number of hollows; shape (flat/nonflat, rounded, etc.); number of lobes; color; film; and pits.

Initial stages of *L. pulmonaria*’s ontogenesis (latent period, protothallus, and pregeneric prototrophallus states) were not studied, so their description was made with allowance for the published data common for all lichens (Suetina, 2001, 2006; Semenova, 2005; Suetina and Glotov, 2015). Juvenile and immature age-related states were described based on the results of study of thalli, whose area did not exceed 1 cm$^2$. Descriptions of the subsequent ontogenetic states, from virginile to senile ones, partially or completely coincided with the available published data (Mikhailova, 2005; Gorshkov and Semenova, 2008). For example, the following (complete or partial) correspondence was established between the functional and age groups determined according to Mikhailova (2005) and the ontogenetic states determined in this study: sterile–virgin 1, hyposorediate–virgin 2a, mesosorediate–virgin 2b, hypersorediate–virgin 2s, fertile–generative, subsenile–subsenile, senile–senile.

The size structure of “juvenile–senile” ontogenetic states was studied based on the linear sizes (length and width) and thallus area.

The results were statistically treated by regression analysis using the following linear function equation: $y = ax + b$ (Andreeva et al., 2002; Ivanter and Kolosov, 2003). In the case of any correlations, the lines on diagrams were built in accordance with the regression equation. In the case of the lack of any reliable
changes, the diagram represented a horizontal line at the level of the average value. The average values of *L. pulmonaria* thallus characteristics were compared among themselves using a nonparametric Mann–Whitney U test (Ivanter and Korosov, 2003).

The analysis was performed based on the description of 4528 thalli grown on 676 substrate units (separate standing or lying trees and shrubs; Table 1).

## RESULTS AND DISCUSSION

The full life cycle of *L. pulmonaria*, including its development from a single spore to the thallus formation, starts from the germination of a fungal askospore and includes the processes of lichenification with an eukaryotic green alga *Dictyochloropsis reticulata*, dolichenification with a cyanobacterium *Nostoc* sp., apothecia formation, senescence, and the thallus’s death.

No sexual reproduction of algae and cyanobacteria is observed within a lichen thallus; it is typical only for a fungal component. Sexual spores of *L. pulmonaria* are formed in open-type ascomata (apothecia). Red-brownish apothecia (2–4 mm in diameter) are formed on the upper surface of a thallus along its edges (Denison, 2003). Each apothecium contains asci with spores, whose number exceeds tens of thousands. As spores mature, they are poured out of the asci and spread by air and water flows to colonize new substrates. However, at this stage, populations of this species pass through a “bottle neck” determined by the fact that germinating fungal hyphae have to meet a required alga for the subsequent lichenification process (Walser et al., 2001). In this study, we did not observe prototallus (spore germination) and proterotallus (licheni- nation) age-related states because of their microscopic size, short duration of the process, and technical difficulty of the species identification. However, available data (Suetina, 2001, 2006; Semyonova, 2005; Suetina and Glotov, 2015) and a common logic of the ontogenesis suggest the presence of these states at least in those coenopopulations in which generative thalli are present.

The data obtained in this study (Table 2) make it possible to correct the existing scheme of *L. pulmonaria*’s ontogenesis (Gorshkov and Semenova, 2008). For example, four age-related states can be distinguished in the pregenerative period: juvenile, immature 1, immature 2, and immature 3.

### Juvenile and immature states.

At the initial ontogenic stages, *L. pulmonaria* thalli, whose area is less than 1 cm², undergo a number of consecutive (qualitatively differing) morphological states (the number of tested thalli is indicated in parentheses): (1) crustose thallus of a rounded, prominent, or tear-shaped form (209); (2) foliose thallus representing an oval (length to width ratio is 3 : 2) flat plate (182); (3) elongated foliose thallus (length to width ratio is 7 : 3) without hollows or with one hollow (214); (4) strongly dissected thallus with two or more hollows, pitted grooves (“pulmonary” rugosity) and/or the first embryonic lobes with forming cephalodia (214). Our study showed that the transition from the rounded to dissected form via the consecutive series of morphological states is associated with an increase in the average length and width of *L. pulmonaria* thalli (Figs. 1a, 1b; Table 3) and their areas (Figs. 2a—2g; Table 4). It is important that the maximum length and width of thalli reach 0.15 and 0.12 cm, respectively, for rounded thalli; 0.45 and 0.24 cm, respectively, for oval thalli; 0.82 and 0.71 cm, respectively, for elongated thalli; and 1.04 and 0.86 cm, respectively, for dissected thalli.

The studied traits, which first appear in the course of ontogenesis, include setas (downiness), rhizines (on the bottom side of the thallus), and roughnesses (on the upper part of the thallus); later the hollows are formed, and only then clearly visible pitted grooves appear.

Based on the obtained results and published data on the ontogenesis of plants and lichens (Rabotnov, 1950; Uranov, 1975; Suetina, 2001; Gorshkov and Semenova, 2008; Suetina and Glotov, 2010; Suetina and Yamberdova, 2010; etc.), all studied microscopic thalli belonged to two age-related states of the pregenerative ontogenetic period. Rounded prominent thalli are referred to the juvenile (*j*) state, while the other three sequentially developed morphological phases belong to the immature (*im*1, *im*2, *im*3) states.

In the juvenile state, thalli do not have any traits typical for an adult organism. During the period from the immature 1 to immature 3 states, *L. pulmonaria* forms foliate blastema, linear sizes and areas of thalli are increased (Tables 3, 4; Figs. 2a—2d), and the typical species-specific traits begin to appear and develop. It is important that cephalodia begin to form in the lichen thallus during the immature 3 state, which evidences a completion of the lichenification process and formation of a three-component system: a fungus, a green alga, and cyanobacteria. Cornejo and Scheidegger (2013) described the process of cephalodia formation in young *L. pulmonaria* thalli. The authors noted

### Table 1. Volume of the analyzed material

<table>
<thead>
<tr>
<th>Data type</th>
<th>Number</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of sample areas</td>
<td>33</td>
</tr>
<tr>
<td>Number of registered trees and shrubs</td>
<td>676</td>
</tr>
<tr>
<td>Number of described <em>L. pulmonaria</em> thalli with the area &gt;1 cm²</td>
<td>3709</td>
</tr>
<tr>
<td>Number of described <em>L. pulmonaria</em> thalli with the area &lt;1 cm²</td>
<td>819</td>
</tr>
<tr>
<td>Number and area of crust samples</td>
<td></td>
</tr>
<tr>
<td>harvested from substrates for the study of microthalli, pieces/cm²</td>
<td>632/11967</td>
</tr>
</tbody>
</table>
that these structures in young thalli can be both internal and external.

As our studies showed, juvenile and immature thalli of *L. pulmonaria* were observed only in those habitats where macrothalli were grown, i.e., they were located in close proximity to large (probably parental) thalli. No thalli with an area <1 cm$^2$ were observed from the opposite side of trunks. It is important that, in the case of forest communities of the middle taiga subzone, an increase in the total area of thalli growing

**Table 2. Ontogenetic states of *Lobaria pulmonaria***

<table>
<thead>
<tr>
<th>Period</th>
<th>Ontogenetic states and their indices</th>
<th>Traits</th>
</tr>
</thead>
<tbody>
<tr>
<td>Latent</td>
<td>Fungal spore (sp)</td>
<td>Four-cell spindle-shaped colorless spore</td>
</tr>
<tr>
<td>Pregenerative</td>
<td>Prothallus (pr)</td>
<td>Germination of mycelial hyphae from spores</td>
</tr>
<tr>
<td></td>
<td>Proterothallus (prt)</td>
<td>Hyphae wind around green alga cells and formation of rudimentary thallus</td>
</tr>
<tr>
<td></td>
<td>Juvenile thallus (j)</td>
<td>Rounded, prominent, and tear-shaped (crustose thallus)</td>
</tr>
<tr>
<td></td>
<td>Immature 1 (im1)</td>
<td>Foliose thallus in the form of oval flat plate</td>
</tr>
<tr>
<td></td>
<td>Immature 2 (im2)</td>
<td>Elongated thallus with 0–1 hollows</td>
</tr>
<tr>
<td></td>
<td>Immature 3 (im3)</td>
<td>Strongly dissected thallus (hollows &gt;2 cm in depth), presence of pitted grooves (typical “pulmonary” rugosity) and/or first rudimentary lobes; formation of cephalodia</td>
</tr>
<tr>
<td></td>
<td>Virginile 1 (v1)</td>
<td>Thallus has a typical adult form, including well-formed lobes with pitted grooves and ribs; it is sterile and does not form reproductive structures</td>
</tr>
<tr>
<td></td>
<td>Virginile 2a (v2a)</td>
<td>Thallus with marginal soralia; cephalodia become clearly visible on the top and/or bottom surface of the thallus</td>
</tr>
<tr>
<td></td>
<td>Virginile 2b (v2b)</td>
<td>Thallus with abundant marginal and single laminal soralia</td>
</tr>
<tr>
<td></td>
<td>Virginile 2c (v2c)</td>
<td>Thallus with abundant laminal soralia and clearly visible cephalodia; isidia are formed</td>
</tr>
<tr>
<td>Generative</td>
<td>Generative (g)</td>
<td>Large thallus with apothecia and abundant laminal soralia, isidia present on old parts of the thallus</td>
</tr>
<tr>
<td>Post-generative</td>
<td>Subsenile (ss)</td>
<td>Partially destroyed thallus with isidia and lobules (regenerative structures unable to the expansion) on its old parts</td>
</tr>
<tr>
<td></td>
<td>Senile (s)</td>
<td>Decay of a large thallus, presence of numerous necrotic lesions, dying lobes with nonexpanding regenerative structures</td>
</tr>
</tbody>
</table>

**Fig. 1.** Average length (a) and width (b) of different morphological forms of *Lobaria pulmonaria* thalli from the studied Karelian phytocoenoses. Thallus forms are indicated in the following way: 1, rounded; 2, oval; 3, elongated; 4, dissected. Statistically significant differences between average values at $p < 0.01$ are indicated with different Latin letters.
on Populus tremula trunks from 50 to 750 cm² results in a 30-fold increase in the density of juvenile and immature thalli (from 0.01 to 0.3 thallus/cm²; Fig. 3).

**Virginile states.** As in plants, the formation of a typical stable life form in lichens occurs in the virginile (v) ontogenetic state (Suetina and Yamberdova, 2010). For example, in the virginile 1 (v1) state of the pregerminative period, L. pulmonaria thalli have a typical adult appearance, including well-formed lobes, pitted grooves, and ribs, but they are sterile and do not form reproductive structures. At this state, the area of the majority of thalli (75%) does not exceed 10 cm² (Fig. 2e; Table 4). During the further transition to the virginile 2a (v2a) state, the area of a thallus increases; it varies

---

**Fig. 2.** Area of Lobaria pulmonaria thalli in different ontogenetic states.
from 1.3 to 30 cm² in 74% of specimens, averaging 14 cm² (Fig. 2f). Lobe edges form vegetative diaspores, which occupy up to 10% of a thallus area; ribs become more prominent. Cephalodia become more visible as brown or dark-brown prominences on the top and/or bottom surface of the thallus. In the virginile 2b (v2b) state, the majority of thalli (71%) has an area between 10 and 70 cm² (Fig. 2g), averaging ~30 cm². A large number of vegetative propagules are formed on thallus edges, and single laminar soralia appeared. The percentage of the area occupied by vegetative diaspores in relation to the total thallus area varied from 10 to 30%. A pre-generative period is finished by the virginile 2c (v2c) ontogenetic state. In this state, the area of a thallus greatly varied from 6.25 to 3437 cm² (Table 4; Fig. 2h), averaging 265.9 cm². For 78% of the studied thalli, their area exceeded 40 cm². Soralia were abundant at the thallus edges and ribs, and their area exceeded 30% of the total thallus area. Cephalodia were well visible on the top and/or bottom thallus surface, and the old parts of a thallus began to form isidia.

Generative state. *L. pulmonaria* is reproduced and spread mainly by vegetative diaspores; apothecia (fruiting bodies) are developed rather rarely (Gauslaa, 2006; Edman et al., 2008; Jüriado et al., 2011). It is considered that apothecia are formed only in genetically heterogeneous populations (Zoller et al., 1999). In the case of the studied forest communities of Karelia, apothecia were observed only in 4% of thalli. Generative (g) thalli were characterized by sufficiently large sizes; ~60% of thalli had an area exceeding 100 cm² (Fig. 2i). Note that apothecia were formed on thalli characterized by abundant soralia and clearly manifested ribs. Old parts of thalli had isidia.

Subsenile and senile states. During the postgenerative period, subsenile (ss) thalli of *L. pulmonaria* began to be destroyed with the formation of isidia on old dying parts of a thallus; in addition, regenerative structures, which are not capable of expansion (lobules), were also generated. However, 50% of subsenile thalli had an area exceeding ≥100 cm² (Fig. 2j). In this ontogenetic state, the surface area of a thallus occupied by vegetative propagules exceeded >30%. The ontogenesis came to the end with the senile (s) state, characterized by the destruction of the greater part of a thallus;
the remaining lobes had large necrotic areas and regenerative structures incapable of expansion. The average percentage of the necrotic area was ~20% of the total thallus area. The majority (~60%) of senile thalli had an area varying from 20 to 50 cm² (Fig. 2k). At the same time, remaining thallus parts had vegetative propagules (soralia and isidia), which seemed to successfully expand up to a complete death of a thallus.

CONCLUSIONS

Based on the published data (Mikhailova, 2005; Gorshkov and Semenova, 2008) and the studied sampling of Lobaria pulmonaria thalli, the species ontogenesis was divided into four periods and 14 age-related states.

After the combining of fungal and algal components, a rudimentary thallus becomes rounded and tear-shaped (juvenile state); the thallus later becomes foliate and strongly dissected with a pitted and roughness surface. During the immature 3 state, the introduction of cyanobacteria into the thallus takes place. Thus, at the virginal state, thalli get an adult appearance but still remain sterile.

During the virginal 2 stage, the size of a thallus increases with the formation of soralia (which are developed first along lobe edges and then on their top surface) and isidia; additionally, cephalodia become clearly visible on the top and/or bottom surface of a thallus. Vegetative diaspores contain both fungal and green alga cells. After separation from the parental thallus, soredia are fixed on a tree trunk with fungal hyphae and form a new thallus. However, to provide its own survival, such thallus should incorporate a cyanobacterium into its body (Werth et al., 2006).

After the reaching of a large size and the abundant formation of soralia on the thallus surface, the thallus becomes potentially generative. A sexual reproduction process results in a formation of fruiting bodies (apothecia) on the thallus surface.

With time, the thallus destruction begins; at the same time, old lobes have isidia, which can grow and form lobules (nonexpanding generative structures; Mikhailova, 2005). The lichen life cycle ends by the destruction of a large thallus with a formation of numerous necrotic lesions. At the same time, a large number of vegetative propagules present on the surface of old subsenile and senile thalli that confirms the vegetation reproduction of this lichen is possible up to the end of its life cycle.

Mechanical impacts may result in the separation of both specialized vegetative diaspores and thallus fragments. Under favorable conditions, such thallus parts are able to attach to a substrate with the further formation of a new thallus. In this case, there is no need in the dolichenification process.

Thus, the life cycle of Lobaria pulmonaria provides several possible ways for a new thallus formation depending on the start position (ascospore, vegetative diaspore, or thallus fragment). Thalli formed by different ways may pass through the generative state or may not include it during their ontogenesis. Such a situation is determined by the fact that fruiting bodies are generated only in genetically heterogeneous populations, i.e., in the presence of heterothallic Lobaria pulmonaria thalli (Zoller et al., 1999). The formation of apothecia is influenced by the growing conditions, mainly by the time passed since disturbance; this factor determines the presence of conditions suitable for the development of coenopopulations and the duration of a colonization process (Ignatenko and Tarasova, 2018).

In the course of our study, we revealed that large Lobaria pulmonaria thalli have a high potential to form new

<table>
<thead>
<tr>
<th>Ontogenetic state</th>
<th>Number of thalli</th>
<th>Thallus area</th>
<th>Area of necrotic lesions</th>
</tr>
</thead>
<tbody>
<tr>
<td>Minimum/maximum values, cm</td>
<td>Average value, cm</td>
<td>CV, %</td>
<td>Minimum/maximum values, cm</td>
</tr>
<tr>
<td>j</td>
<td>209</td>
<td>0.0001–0.048</td>
<td>0.0022 ± 0.0003</td>
</tr>
<tr>
<td>im1</td>
<td>182</td>
<td>0.0003–0.057</td>
<td>0.0065 ± 0.0007</td>
</tr>
<tr>
<td>im2</td>
<td>214</td>
<td>0.001–0.76</td>
<td>0.034 ± 0.0067</td>
</tr>
<tr>
<td>im3</td>
<td>214</td>
<td>0.001–0.89</td>
<td>0.095 ± 0.0075</td>
</tr>
<tr>
<td>v1</td>
<td>1136</td>
<td>0.3–69</td>
<td>7.9 ± 0.26</td>
</tr>
<tr>
<td>v2a</td>
<td>1117</td>
<td>1.25–443</td>
<td>27.0 ± 1.19</td>
</tr>
<tr>
<td>v2b</td>
<td>279</td>
<td>3.1–544</td>
<td>58.1 ± 3.97</td>
</tr>
<tr>
<td>v2c</td>
<td>192</td>
<td>6.25–3437</td>
<td>265.9 ± 34.84</td>
</tr>
<tr>
<td>g</td>
<td>156</td>
<td>12.5–3750</td>
<td>330.2 ± 41.04</td>
</tr>
<tr>
<td>ss</td>
<td>326</td>
<td>6.25–1937</td>
<td>292.7 ± 30.65</td>
</tr>
<tr>
<td>s</td>
<td>503</td>
<td>1.9–564</td>
<td>96.6 ± 5.59</td>
</tr>
</tbody>
</table>
viable thalli under suitable habitat conditions. Though only genetic studies made it possible to determine which diaspores (generative or vegetative) produced one or another juvenile or immature thalli, the obtained data allowed us to suppose that the greater part of the described juvenile and immature thalli was developed vegetatively, since fertile \textit{L. pulmonaria} thalli were rather rare in the studied communities.

The described ontogenetic scheme has some significant distinctions from the published data (Mikhailova, 2005; Gorshkov and Semenova, 2008). According to our data, the size of juvenile thalli did not exceed 0.15 cm in length and 0.12 cm in width, while the size of immature 1 thalli did not exceed $\leq0.45$ and $\leq0.24$ cm, respectively. Based on the principles of a discrete classification of age-related (ontogenetic) states in lichens (Suetina, 2006; Suetina and Glotov, 2015), the juvenile state should include only crustose but not lobe-like thalli (Gorshkov and Semenova, 2008); the latter, in our opinion, belong rather to the immature group. The moment of cephalodia development on thalli represents a very important trait, which has not been taken into account earlier.

The ability to form vegetative propagules is one of the main traits that appears in the course of lichen ontogenesis and, as a rule, remains during the whole life of a thallus. However, Gorshkov and Semenova (2008) took into account the presence of soredia only at the virginile 2a state. As in the case of I.N. Mikhailova’s study (2005), the key traits used for the determination of virginal states ($v1$, $v2a$, $v2b$, $v2c$) in our study included the abundance and location of soralia as well as the thallus area. It is known that the ontogenetic series from virginile 2a to virginile 2c states is characterized by an increase in the sorallia proportion and increase in the linear size of thallii (Mikhailova, 2005). Isidia are developed on old thallus lobes abundantly covered by soralia (virginal 2c state). It is important that vegetative propagules continue to exist on old dying thalli and are able to propagate. Gorshkov and Semenova (2008) used isidia and lobules as separate traits for distinguishing of the virginile 2b and virginile 2c ontogenetic states, respectively. Like I.N. Mikhailova (2005), we found that lobules are formed on old dying lobes of thalli belonging to the postgenerative period. Thus, the obtained data significantly supplement the existing scheme of the \textit{L. pulmonaria} ontogenesis.

ACKNOWLEDGMENTS

We are grateful to our relatives, friends, students, and teachers of the Department of Botany and Plant Physiology of the Petrozavodsk State University for their assistance in the collection of field samples. We are also grateful to the administration and employees of the studied natural reserves and protected areas for their assistance in the organization and conducting of field studies.

FUNDING

The study was financially supported by the “Complex Evaluation of the Recovery Potential of the Moss and Lichen Cover in the Course of Secondary Autogenic Successions in the Taiga Ecosystems of the Northwest of Russia” project (State Assignment no. 5.8740.2017/BCh).

COMPLIANCE WITH ETHICAL STANDARDS

The authors declare that they have no conflict of interest. This article does not contain any studies involving animals or human participants performed by any of the authors.

REFERENCES


Gauslaa, Y., Lie, M., Solhaug, K.A., et al., Growth and ecophysiological acclimation of the foliose lichen \textit{Lo-


*Translated by N. Statsyuk*