

Reproductive Parameters of *Lobaria pulmonaria* (L.) Hoffm. in the Urals

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Abstract—The capacity of species for expansion and colonization of new habitats is a key condition for the maintenance of their populations. In this study, specific features of the reproductive potential have been analyzed in *Lobaria pulmonaria* populations growing under contrasting climatic conditions. Certain ecological determinants governing the development of this lichen species have been revealed.

Keywords: epiphytic lichens, *Lobaria pulmonaria*, soredia production, reproductive strategy, population potential, Northern Urals, Southern Urals.

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Studies on the reproductive biology of lichens under different ecological conditions can shed light on the causes of their substrate and phytocenotic preferences (Gauslaa, 1997) as well as on population mechanisms of their tolerance or sensitivity to technogenic impact (Mikhailova and Vorobeichik, 1999). Studies on the population structure of rare and endangered lichen species are a necessary prerequisite for predicting their future and developing an effective conservation strategy (Mikhailova, 2005).

Lichenologists have long been paying special attention to the distribution of the tree lungwort, *Lobaria pulmonaria* (L.) Hoffm. (Lobariaceae, Ascomycotina). This lichen is on the Red Data List in Russia and is also regarded as an endangered species in most countries of Central Europe. The poor state of its populations is explained by a high regional level of atmospheric pollution and deterioration of habitats, as well as by specific features of reproduction and life cycle. The process of colonization of new phorophytes is a weak link in the *L. pulmonaria* life cycle (Scheidegger, 1995; Walser et al., 2001), primarily because of a small range of diaspore dispersal and very low survival of soredia.

Success in the spread of lichens largely depends on the reproductive strategy of a given species (Mikhailova, 2005) and, in particular, by the size of the pool of diaspores it produces (Scheidegger and Werth, 2009). However, it is still unclear whether or not these parameters differ between populations of the same species. To find the answer, it is necessary to study lichen pop-

ulations growing under contrasting conditions. The territory of the Urals offers unique opportunities for such research.

Potential habitats for *L. pulmonaria* in the Urals are in old-growth forests located in protected or hardly accessible areas and not affected by timber harvesting (primeval forest islands, forests in mountain or remote areas, etc.).

In this study, the reproductive potential of a population is understood as its potential capacity for growth under optimal environmental conditions, with its functional and age composition being retained. Since *L. pulmonaria* is characterized by the prevalence of vegetative reproduction, its reproductive potential is largely accounted for by the amount of vegetative diaspores (soredia) it produces. By analogy with r- and K-strategies (Pianka, 1970), the reproductive strategy of a population is characterized by the amount of energy invested into reproduction as a proportion of total energy expenditures. For lichens, this proportion may be expressed as the “cost” of soredia formation (the ratio of soredia weight to the weight of the maternal thallus).

The purpose of this study was to verify two hypotheses: (1) the degree of *L. pulmonaria* development depends both on habitat conditions and on characteristics of phorophytes on which this lichen grows, and (2) the reproductive strategy of the species and its reproductive potential may differ depending on habitat conditions.

Table 1. Characteristics of *L. pulmonaria* populations included in the study

Code	Population	Coordinates	Elevation a.s.l., m	Coverage, cm ²	Main phorophyte species	Dominant forest types
Northern Urals						
I	Loz'va	61.2973 N, 60.1676 E	146–162	93 (62–372)	<i>Betula</i> spp. (41%), <i>Picea obovata</i> Ledeb. (44%)	Abieto-Piceetum oxalidosum, A-P. polytrichosum, Pinetum vaccinatum, P. polytrichosum, P. sphagnosum
II	Vishera-1	60.9838 N, 58.9152 E	436–824	929 (409–1858)	<i>Sorbus aucuparia</i> L. (99%)	
III	Vishera-2	60.4279 N, 58.0787 E	220–268	1162 (723–1419)	<i>Populus tremula</i> L. (41%), <i>S. aucuparia</i> L. (52%)	
Southern Urals						
IV	Bashkiria-1	54.2952 N, 57.6281 E	369–411	620 (204–1239)	<i>Tilia cordata</i> Mill. (92%), <i>Acer platanoides</i> L. (8%)	Aceretum magnoherbosum, Tilietum magnoherbosum, T. herbosum, Pinetum herbosum
V	Bashkiria-2	54.1817 N, 57.6350 E	388–435	310 (171–1859)	<i>T. cordata</i> Mill. (97%)	
VI	Bashkiria-3	54.1771 N, 57.6086 E	333–367	300 (79–929)	<i>T. cordata</i> Mill. (94%), <i>P. tremula</i> L. (6%)	

Note: Median values of *L. pulmonaria* coverage (with 95% confidence interval in parentheses) are shown.

MATERIAL AND METHODS

Lichens were collected in two regions, in the Northern Urals and the Southern Urals. In the Northern Urals, samples were taken from the eastern macroslope, in the Loz'va River basin (Ivdel' city district, Sverdlovsk Region) (Table 1, population I), and from the western macroslope, in the Vishera State Nature Reserve (Krasnovisherskii district, Perm Region) (populations II and III). In the Southern Urals, samples were taken from the western macroslope in the Beloretsk district of the Republic of Bashkortostan (populations IV–VI). Climatic conditions in the two regions differ considerably. In the Northern Urals, the annual average air temperature is -2.0°C , with monthly average temperatures in January and July being about -19 and 15°C ; the warm season is 160–170 days long, and annual average precipitation varies from 660 to 1000 mm. In the Southern Urals, the annual average air temperature is 1.5°C , average January and July temperatures are -15.8 and 17.0°C , the warm season is 188–193 days long, and annual average precipitation is in the range of 667–1100 mm (Dubinin et al., 2010).

To evaluate the relationship between the degree of *L. pulmonaria* development and ecological determinants, subpopulations of this lichen on 117 phorophyte trees were described in the Loz'va model population from the Northern Urals. Descriptions included data on the total coverage of thalli (cm²) and their reproductive status, which was determined from the prevailing degree of their development on the tree stem: fertile (in the presence of apothecia, fruiting bodies produced by the fungal partner of the lichen symbiosis), sorediate (in the presence of soredia and isidia, vegetative diaspores including both symbionts of the lichen), or sterile (in the absence of apothecia

and soredia). For phorophytes, we recorded stem diameter at breast height (DBH), life state (live, damaged, or dead tree), and illumination level arbitrarily determined as high (light) or low (shade). Factors determining the degree of lichen development were identified by log-linear analysis with the Statistica v. 8.0 program package (Stat Soft Inc.). Contingency tables were tested for heterogeneity using the likelihood ratio test (G^2) in the AtteStat v. 12.1.5 program (Gaidyshev, 2004). Phorophyte trees were divided into three size groups with respect to DBH (for each species individually) and into two species groups (coniferous and deciduous). We also distinguished three dimensional classes of lichen coverage (by area): less than 100, 100–1200, and more than 1200 cm².

Broadleaf forests of the Southern Urals and mountain taiga forests of the Northern Urals were chosen as model phytocenoses for the assessment of soredia production (Table 1). In each of the six populations, we examined 20 trees to measure the total coverage of *L. pulmonaria* and collected ten thalli of different dimensional classes (from 4 to 600 cm²). The material was dried to air-dry weight, and all soredia from each thallus were removed under a Zeiss Stemi 2000-C binocular microscope using a brush and a scalpel. After removing extraneous matter (fragments of tree bark, moss, etc.), the thallus and soredia were weighed on a Kern 770 analytical balance to an accuracy of 0.1 mg. Comparisons between populations with respect to soredia production (by weight) were made by means of analysis of covariance (Separate-slopes model of ANCOVA for regression coefficients unequal between populations), with thallus weight taken to be the covariate. Multiple comparisons of soredia production between populations were made by the Tukey method.

RESULTS

Reproductive structure of populations and coverage.

The majority of plant communities with *L. pulmonaria* were represented by old-growth forests (average tree age 80–120 years) located at elevations ranging from 146 to 824 m a.s.l. (Table 1). These were mainly fir–spruce and pine forests in the Northern Urals and linden and maple forests in the broadleaf forest subzone of the Southern Urals. The highest *L. pulmonaria* coverage was recorded in the Vishera-2 population: on 30% of phorophyte trees, it reached 1000–2000 cm². In all populations studied, sorediate subpopulations prevailed. The proportion of fertile subpopulations was usually less than 10%, reaching a peak of 27.72% in the Vishera-2 population (Fig. 1). Populations from the Southern Urals (Bashkiria-1 and Bashkiria-2) contained no fertile thalli.

Relationship between the degree of *L. pulmonaria* development and ecological determinants (the example of the Loz’va population). The observed contingency table was heterogeneous ($G^2 = 26.06, p = 0.037$) (Table 2). It was found that the reproductive status of subpopulations depended on lichen coverage and phorophyte species (coniferous or deciduous): $R^2 = 0.95, p \ll 0.001$; maximum likelihood $\chi^2 = 14.88, df = 22, p = 0.867$. Moreover, statistical significance was also confirmed for factor interactions (only two-way): reproductive status with coverage ($p < 0.001$) and phorophyte species ($p = 0.037$) and of phorophyte species with illumination level ($p = 0.027$). As expected, illumination of tree stems proved to be lower in coniferous than in deciduous species ($G^2 = 4.84, p = 0.028$). In turn, lichen coverage was found to have an effect on the proportion of fertile subpopulations: as coverage increased to values of the second or third class, this proportion increased to 40% ($G^2 = 19.01, p < 0.001$). In addition, the proportion of fertile subpopulations also depended on tree species, being three times

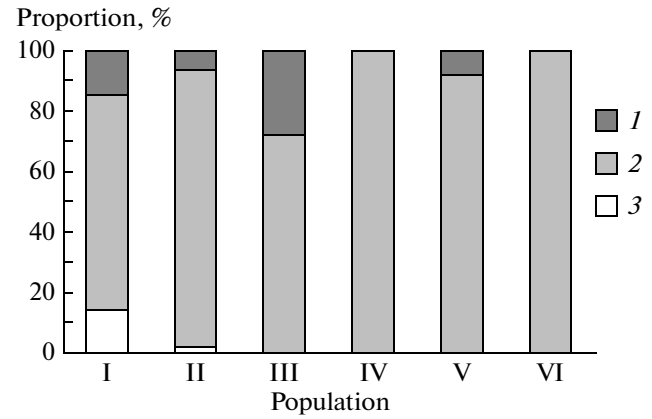


Fig. 1. Reproductive structure of *L. pulmonaria* populations: (1) fertile, (2) sorediate, and (3) sterile thalli. Here and in Fig. 2, populations are designated by Roman numerals as in Table 1.

greater on deciduous than on coniferous trees ($G^2 = 6.56, p = 0.037$).

Soredia production. In each population, we calculated the weight of soredia per “standard” thallus weighing 2 g (Fig. 2). The results showed that soredia production differed between populations ($F(5,48) = 2.72, p = 0.030$), with differences being significant either between populations from the two study regions (Loz’va vs. Bashkiria-2, $p = 0.003$; Vishera-1 vs. Bashkiria-2, $p = 0.003$) or between populations from the same region (Loz’va vs. Vishera-1, $p = 0.023$; Bashkiria-2 vs. Bashkiria-3, $p = 0.033$). Factor interaction of thallus weight and population was also statistically significant ($F(6) = 12.62, p \ll 0.001$), indicating that the dependence of specific soredia production on thallus weight differs between populations.

With the effect of thallus weight excluded, the highest soredia production was observed in populations Vishera-1 and Bashkiria-3 (Fig. 2). However, the cov-

Table 2. Distribution of *L. pulmonaria* subpopulations with respect to their reproductive status, coverage, phorophyte tree species, and illumination conditions (the example of Loz’va population)

Parameters of subpopulations	Phorophyte tree species		Illumination conditions		Total number of thalli
	deciduous	coniferous	light	shade	
Reproductive status:					
sterile	9	14	5	18	23
sorediate	59	29	39	49	88
fertile	6	0	3	3	6
Class of coverage, cm ² :					
<100	10	10	7	13	20
100–1200	51	30	29	52	81
>1200	13	3	11	5	16
Total number of thalli	74	43	47	70	117

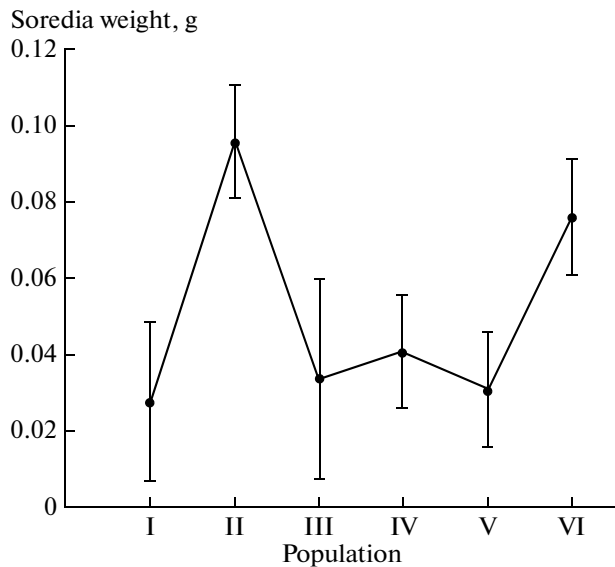


Fig. 2. Average weights of soredia (with 95% confidence intervals, $n = 10$) produced by a “standard” *L. pulmonaria* thallus weighing 2 g. Populations are arranged according to their geographic location (in the north–south direction).

erage of *L. pulmonaria* in the former population was more than three times greater than in the latter (Mann–Whitney test, $U = 308.5$, $p \leq 0.001$; see Table 1). This is evidence for differences in the reproductive strategy of this species: in population Bashkiria-3, this strategy is aimed at abundant production of vegetative diaspores rather than at an increase in biomass. Thus, the “cost” of soredia formation in this population is higher than in population Vishera-1. A similar situation is observed with some other populations. For example, the average weight of soredia in populations Vishera-2 and Bashkiria-1 is almost the same ($p = 0.999$), but their coverage differs by a factor of almost two.

DISCUSSION

The wide distribution of lichens, even in specific habitats, implies their high ecological plasticity (Mikhailova, 2005). Hence, it appears that changes in ecological preferences of lichen species in different parts of their ranges reflect their adaptations to local conditions. These conditions, in turn, may depend both on general parameters of tree stand (illumination level, humidity, etc.) and on species-specific features of phorophyte trees. In particular, this concerns physicochemical characteristics of tree bark (hardness, water-holding capacity, acidity, contents of inorganic and organic nutrients, etc.), which account for different degrees of lichen growth preference and have an effect on their physiology and biochemistry. The results of this study show that parameters of substrates largely determine characteristics of *L. pulmonaria* thalli growing on them. Of special interest is the

dependence between the degree of *L. pulmonaria* development on the phorophyte tree species (coniferous or deciduous). Moreover, the relationship between the coverage of this lichen and the presence of fruiting bodies confirms the hypothesis that *L. pulmonaria* is a heterothallic species, i.e., the sexual process can take place only between genetically different thalli (Zoller et al., 1999), since the probability of emergence of different genotypes increases as the lichen colony on a phorophyte expands in area.

The colonizing potential of a lichen species determines the size of its population and is directly connected with reproductive processes. Therefore, the dispersal of vegetative and generative diaspores provides a basis for ecological and evolutionary processes influencing the dynamics and genetic structure of populations. Since the environment of epiphytic lichens (i.e., phorophyte trees) is highly variable in time and space, lichens must “follow their phorophytes” in order to survive (Snall et al., 2003). This is why the production of a sufficient amount of diaspores is an important prerequisite for the spread of lichens and colonization of new phorophytes.

As a rule, the amount of diaspores produced by a lichen increases with an increase in thallus weight and size, and populations with a high coverage may potentially have a greater reproductive resource (the pool of soredia or ascospores). However, high productivity cannot ensure the efficiency of dispersal or reproduction, since maturation of soredia depends on climatic conditions in a given region, and their germination and attachment to the substrate additionally depend on the properties of phorophyte trees.

Moreover, clonal colonization is effective only if the genotype of the clone is well adapted to given environmental conditions (Scheidegger and Werth, 2009). When the environment is variable, vegetative reproduction of the symbiotic system as a whole may prove less favorable for the population than sexual reproduction, which involves the process of relichenization, or restoration of symbiotic connections between a fungus and an alga (Genkai-Kato and Yamamura, 1999). In this course, the fungus can establish symbiosis with a different algal genotype, which can provide for the improvement of its adaptive properties. Therefore, the presence of reproductively active individuals in a population is evidence for its high potential and a prerequisite for its sustainable existence.

The study region is diverse in terms of climatic and orographic conditions, vegetation pattern, and anthropogenic influences. Therefore, the observed differences may depend on many factors accounting for ecological preferences of *L. pulmonaria*, including the type of landscape, altitudinal gradient, forest type, the level of atmospheric pollution, and the current and past practice of forest management. Nevertheless, the regularities described above confirm our working hypotheses. Moreover, the observed variation in the reproductive strategies of populations may reflect their

genetic structure, and information on this structure is important for gaining a deeper insight into the ecology and distribution of lichens and, hence, for developing an effective strategy of their conservation.

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