

Dimensional and Age Structure of Populations of Epiphytic Lichen *Hypogymnia physodes* (L.) Nyl. under Conditions of Atmospheric Pollution

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Abstract—Atmospheric pollution (SO₂ and heavy metals) causes consistent changes in the dimensional and age structure of local *Hypogymnia physodes* populations growing on fir trunks. The age states were distinguished according to the quality of soralia and the degree of their development. Upon an increase in pollution, the frequency distributions of thallus weight and length shift toward smaller individuals, although their type remains relatively stable (exponential for weight, lognormal for length). Upon transition from the background to the impact zone, the spectrum of age states shifts from highly fertile to minimally fertile and sterile individuals.

The population-oriented approach developed for higher plants (Uranov, 1975; *Tsenopulyatsii rastenii* ..., 1988; Zhukova, 1995) is rarely applied to lichens, especially epiphytic. There are only a few investigations of their structure and population dynamics in unaffected habitats (Istomina, 1996; Armstrong, 1976; Roades, 1983; Hyvärinen, 1992), although the methodology of population analysis applied to such a specific object as lichens may help to obtain interesting results. The purpose of this work was to analyze the response of epiphytic lichens to stress (atmospheric pollution) using the population-oriented approach.

It should be noted that, by using the term “population” in relation to lichens, we adhere to its “mild” interpretation (Gilyarov, 1990), which generally coincides with the definition by Fahselt (1996): in lichens, population is a local group of thalli of the same species, which is more or less separated from other similar groups. Such “mildness” is justified, because at the modern level of knowledge about mechanisms of hereditary information transfer the concept of population in lichens cannot be substantiated genetically (Fahselt, 1996). This fact also determines a certain specificity of methodical approaches. The absolute age of foliose thalli is difficult to determine, and indirect methods developed for this purpose are based on criteria of size increment (Armstrong, 1976) and substrate age (Degelius, 1964; Hale, 1974; Nienburg, 1919, cited from Hale, 1973). Hence, the linear size and weight or area of thalli are usually used as age markers in studies on population structure in lichens.

Studies on higher plants showed that anthropogenic factors may cause changes in all parameters of their populations, including productivity, natality, mortality,

and, as a consequence, density and age structure (Zaugol'nova, 1977). It is probable that similar phenomena take place in lichen populations as well, although no comprehensive investigations were conducted in this respect. The available data concern a decrease in fertility (LeBlanc, De Sloover, 1970; Feige, 1982; Sigal and Nash, 1983) and the rate of vegetative reproduction (Nash and Gries, 1991) under the influence of pollutants. In polluted areas, morphological changes of thalli (Ikonen and Karenlampi, 1976; Goyal and Seaward, 1982; Sigal and Nash, 1983) and a decrease in their growth rate (Feige, 1982) were observed.

MATERIALS AND METHODS

The work was performed on the western slope of the Middle Urals (the southern taiga subzone), in the region exposed to discharge from the Middle Ural copper-smelting plant (main pollutants are sulfur dioxide and heavy metals: Cu, Pb, Cd, Zn, Cr, As, etc.). The detailed characteristics of pollution and transformation of forest ecosystems in the region were described previously (Vorobeichik *et al.*, 1994; Vorobeichik and Khantemirova, 1994). Taking into account the results of our investigations on degradation of the epiphytic lichen cover (Mikhailova, 1996), test plots were laid in three zones: the impact zone (4 km west of the plant), the buffer zone (7 km), and the background zone (30 km). The plots were located in similar habitats, namely, in spruce–fir forests on gray forest soils in lower parts of the slope. Compared to the background area, the fallout of heavy metals (determined from contents in snow) in plots located in the buffer zone (4–7 km) and 1–2 km away from the plant (the zone of “lichen desert”) exceeded that in the background zone as follows: copper, by fac-

Table 1. Characteristic of epiphytic lichen cover on trunks of fir trees over 80 years of age in different load zones (figures in parentheses show sample size)

Parameter	Zone		
	background (31)	buffer (21)	impact (35)
Total species richness	11	7	8
Number of species per trunk	4.97 ± 0.19	2.52 ± 0.31	1.34 ± 0.22
Similarity with background zone in species number (according to Jaccard coefficient)	–	0.64	0.58
Total coverage, %			
on trunk base	46.22 ± 4.33	40.86 ± 7.62	19.13 ± 4.75
at a height of 1.3 m	20.77 ± 4.23	1.93 ± 1.12	2.4 ± 1.59
Trunk height to which <i>H. physodes</i> ascended, cm (on 0–180 cm section)	167.31 ± 6.07	14.90 ± 6.41	12.29 ± 6.57
<i>H. physodes</i> population density, ind./trunk*	207.20 ± 18.52	49.70 ± 17.46	12.23 ± 2.14
Density variation coefficient, %	19.99	111.07	110.83

Notes: * Thalli were counted on a 0–50 cm trunk section; for number of trees, see *Materials and Methods*.

tors of 1.68–5.97 and 3.17–26.33; lead, by factors of 1.56–5.05 and 3.92–27.63; cadmium, by factors of 1.41–5.90 and 3.22–22; and zinc, by factors of 1.68–3.8 and 3.06–10.78, respectively (Kaigorodova and Vorobeichik, 1996). The state of lichen cover is briefly characterized in Table 1.

Our investigation concerned the foliose lichen *Hypogymnia physodes*, which dominates in the epiphytic cover of main forest-forming species and has medium sensitivity to pollution (Mikhailova, 1996). In spruce–fir forests of the southern taiga subzone, this species reproduces only vegetatively (by soredia or, more rarely, fragments of thalli); in thinned stands, it sometimes forms apothecia on birch trunks.

Representative samples were taken from *H. physodes* cenopopulations of each test plot. In the background zone, all visible thalli (more than 1 mm in size, a total of 1049 specimens) were collected from trunk bases (0–50 cm from the ground) of five *Abies sibirica* Ldb. trees over 80 years of age. In the buffer and impact zones, where the density of cenopopulations was significantly lower, 496 and 486 thalli from 10 and 40 fir trees, respectively, were collected.

Every specimen placed into herbarium was cleaned from bark and weighed in the air-dry state on an analytic balance with an accuracy of 0.01 mg. The maximum linear dimension (length) was measured under a stereomicroscope with an accuracy of 0.1 mm. On every thallus the number of soralia of every four types was counted: the initial stage (disruption of the lower cortical layer), soralia on tubular, galeate, and labiate lobes.

With respect to the number and development of soralia, the following groups of thalli (age states) were distinguished: (1) *asorediate* (*as*), no soralia; (2) *cryptosorediate* (*cs*), all soralia at the initial stage of devel-

opment; (3) *hyposorediate* (*s*₁), soralia on tubular lobes and one or two on galeate and/or labiate lobes; (4) *mesosorediate* (*s*₂), up to ten soralia on galeate and/or labiate lobes; (5) *hypersorediate thalli* (*s*₃), more than ten soralia on galeate and/or labiate lobes.

RESULTS

The epiphytic lichen cover significantly changed under the effect of pollution (Table 1): in the impact zone, total coverage on the trunk base and 1.3 m above the ground decreased by factors of 2.4 and 8.7, respectively; number of species per trunk also decreased by a factor of 3.7. Changes in the abundance of *H. physodes* were even more apparent: compared to the background zone, its density in the impact and buffer zones decreased by factors of 16.9 and 4.2, and the maximum height to which lichens ascended, by factors of 13.6 and 11.2, respectively. The difference in density was even underestimated, as lichens in the background zone were recorded on only one-third of the trunk region generally occupied by them. In polluted areas, nonuniformity in the spatial distribution of lichen density increased 5.5 times.

The pattern of frequency distribution of thallus weight (Fig. 1a) was close to exponential, and that of length (Fig. 1b) was close lognormal. However, the strict goodness-of-fit test for continuous distribution showed that these hypotheses should be rejected: the values of Kolmogorov–Smirnov test for compound hypothesis (Tyurin and Makarov, 1995) in all cases differed from zero at a high significance level ($p < 0.01$). At the same time, when continuous distributions were transformed into discrete distributions with few gradations, the hypothesis of correspondence between the observed and expected distributions could be accepted in most cases. Thus, the values of χ^2 test for the com-

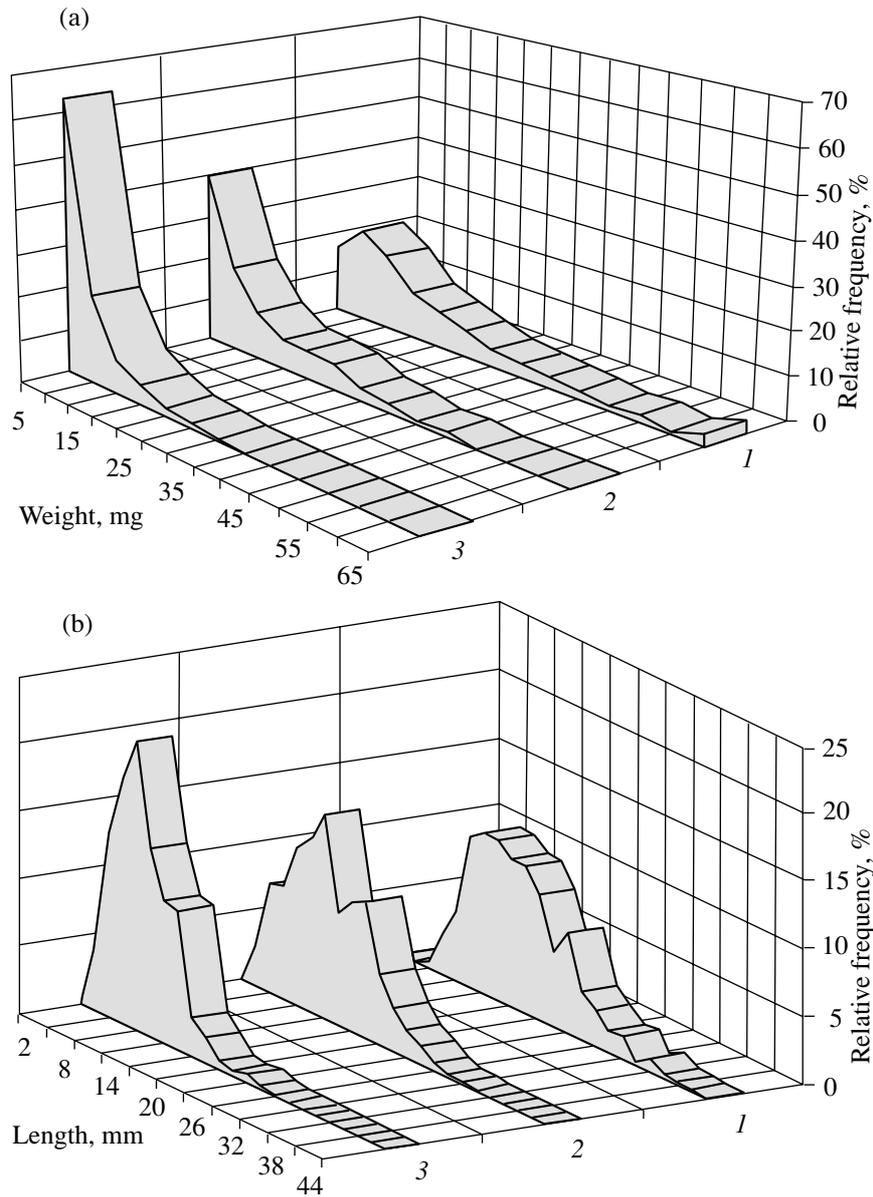


Fig. 1. Frequency distributions of (a) thallus weight and (b) length in *H. physodes* populations of (1) background, (2) buffer, and (3) impact zones.

pound hypothesis of correspondence between the observed and expected (exponential) distribution of thallus weight were 14.71 in the background zone ($df = 8$, $p = 0.065$), 13.74 in the buffer zone ($df = 7$, $p = 0.056$), and 14.10 in the impact zone ($df = 10$, $p = 0.168$). The values of χ^2 for the correspondence of length distribution to the expected (lognormal) distribution were 12.78 in the background zone ($df = 10$, $p = 0.236$) and 17.00 in the impact zone ($df = 8$, $p = 0.03$). For the buffer zone, such a hypothesis was rejected at any number of gradations. Similarity between the observed and expected distributions was also confirmed by the values of analytical and order estimates (Table 2). Thus, at the exponential distribution, the mode and coefficients of

variation, skewness, and kurtosis are equal to 0, 100%, 2, and 6, respectively (Aivazyan *et al.*, 1983), which is sufficiently close to the values obtained for weight distribution (except the mode in the background zone).¹

The distribution of logarithms of length was close to normal distribution (corresponding to the lognormal distribution of initial values), according to the test of the ratio between mean arithmetic deviation and mean square deviation: at normal distribution, this ratio is 0.7979 (Bol'shev and Smirnov, 1983), which is close to

¹ The lower frequency of the first class, compared to the modal class, may be partly accounted for by incomplete collection of small thalli.

Table 2. Parameters of frequency distributions of *H. physodes* thallus length and weight in different load zones

Parameter	Length, mm			Weight, mg		
	background	buffer	impact	background	buffer	impact
Analytical estimates:						
arithmetic mean	18.04	13.28	9.72	18.64	11.95	5.52
geometric mean	16.78	11.89	8.80	12.38	5.89	2.79
standard deviation	6.90	5.83	4.20	17.68	13.06	6.48
variation coefficient, %	38.25	43.90	43.21	94.85	109.29	117.39
skewness	0.82	0.41	0.78	2.20	2.02	2.58
kurtosis	0.75	-0.28*	0.91	6.71	6.00	10.10
Order estimates:						
median	17.20	12.60	9.20	13.24	7.39	3.34
mode	15.10	12.10	8.10	8.65	0.71	0.69
minimum	4.70	2.80	1.20	0.05	0.04	0.03
10% decile	10.20	5.60	4.70	3.60	0.71	0.49
25% quartile	12.80	9.20	6.80	6.73	2.49	1.25
75% quartile	22.0	17.30	12.20	24.23	17.57	7.55
90% decile	27.20	21.40	15.40	40.67	29.51	13.64
maximum	45.70	32.10	27.10	129.15	98.15	52.15
range:						
-interlimit	41.00	29.30	25.90	129.10	98.11	52.12
-interdecile	17.00	15.80	10.70	37.07	28.80	13.15
-interquartile	9.20	8.10	5.40	17.50	15.09	6.30
median deviation	4.50	4.10	2.70	7.74	5.67	2.55
variation coefficients:						
-median	38.75	48.19	43.46	86.58	113.63	113.07
-quartile	39.65	47.62	43.48	97.96	151.29	139.82
-decile	38.55	48.89	45.33	109.21	151.96	153.59
Skewness coefficients:						
-quartile	0.043	0.160	0.111	0.256	0.350	0.337
-decile	0.176	0.114	0.159	0.480	0.536	0.567

* Difference from zero is nonsignificant; other coefficients of skewness and kurtosis significantly differ from zero ($p < 0.001$).

the recorded values (0.8078, 0.7918, and 0.7856 for the background, buffer, and impact zones, respectively, in all cases, $p < 0.1$). Thus, it is probable that we were dealing with contaminated theoretical distributions (i.e., a small part of the population was distributed according to a different law), but, due to a large sample size, this contamination had a strong influence on the decision to accept the corresponding null hypothesis. Determining the actual form of the contaminating function was beyond the scope of this study.

Thus, the observed frequency distributions of length and weight of thalli are strongly asymmetrical and, in the first approximation, may be described by lognormal and exponential laws. In any case, the abnormality of these distributions suggests that common analytical

statistics should be used cautiously, with preference given to order estimates and nonparametric tests.

Comparison of frequency distributions in different load zones by any nonparametric test (e.g., Kruskal–Wallis test) showed that they differ at a very high significance level ($p \ll 0.0001$). This was primarily associated with a consistent change in parameters of distribution shift: all statistics characterizing the central tendency of a trait (analytical and mean order estimates) regularly decreased upon the transition from the background to the impact zone. A similar decrease was observed for limits and percentiles (Table 2). The absolute parameters of distribution scale (mean square and median deviations) also decreased significantly. At the same time, relative parameters of the scale (variation coefficients) proved to be significantly more stable. To

estimate significance of differences in analytical coefficients of variation, we used the test for skewed distributions (Zhivotovskii, 1991):

$$U = \frac{|\ln C_1 - \ln C_2|}{\sqrt{V_1 + V_2}},$$

$$V_i = \frac{1 + 2C_i^2 + E_i/2 - A_i C_i}{2n_i}, \quad i = 1, 2,$$

where C_i , A_i , and E_i are coefficients of variation (in fractions of a unit), skewing, and kurtosis of the i th sample, and n is sample size. The results showed that the difference in coefficients of variation in thallus weight between the background zone and the buffer zones is nonsignificant ($p < 0.1$), the same applies to that between the buffer and impact zones ($p < 0.5$), and only the difference between the background and impact zones is significant ($p < 0.02$). In the case of thallus length, variation coefficients in the buffer and impact zones did not differ ($p < 0.5$), but the corresponding difference was significant for the background and buffer zones ($p < 0.001$) and the buffer and impact zones ($p < 0.01$). At the same time, even statistically significant differences between coefficients of variations in different pairwise comparisons had values of about 10–20%, which does not appear substantial. Thus, if the so-called scale effect is excluded, parameters characterizing the scale of distributions in different load zones appear to be relatively stable.

The use of variation coefficients based on order estimates helped to further clarify the situation. Median (C_m), quartile (C_q), and decile (C_d) coefficients of variation were calculated in the following way (Zhivotovskii, 1991):

$$C_m = 1.481\tilde{s}/\tilde{x}, \quad C_q = 0.741R_q/\tilde{x},$$

$$C_d = 0.39R_d/\tilde{x},$$

where \tilde{s} is median deviation, \tilde{x} is median, and R_q and R_d are interquartile and interdecile ranges. In general, the range of variation did not strongly differ between the load zones, but it was slightly greater in the impact and buffer zones than in the background zone. This concerns the variation of both the distribution as a whole (as estimated from C_m) and its central and peripheral parts (as follows from C_q and C_d).

The tendency toward an increase in skewness and kurtosis of weight distribution was observed upon transition from the background to the impact zone, especially when quartile (A_q) and decile (A_d) coefficients of skewing were compared (Zhivotovskii, 1991):

$$A_q = (Q_2 + Q_1 - 2\tilde{x}) / (Q_2 - Q_1),$$

$$A_d = (D_2 + D_1 - 2\tilde{x}) / (D_2 - D_1),$$

where Q_2 (D_2) is the upper quartile (decile), and Q_1 (D_1) is the lower quartile (decile). The peaked pattern of weight distribution became more acute, as followed

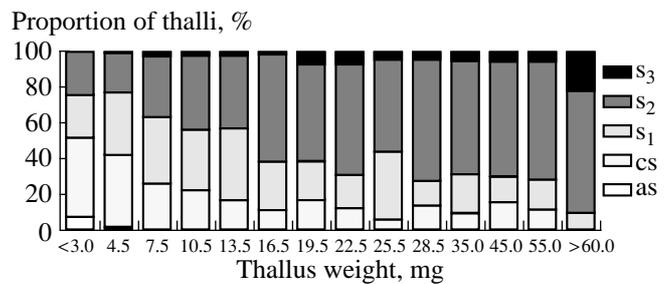


Fig. 2. Relationship between the spectrum of age states and thallus weight in the background zone. For designations of stages, see Materials and Methods.

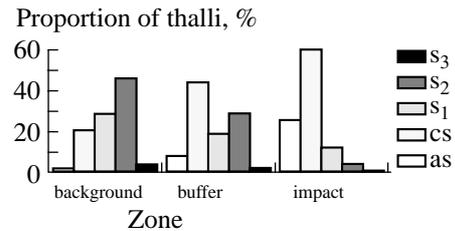


Fig. 3. Age spectrum of *H. physodes* populations in different zones. For designations, see Fig. 2.

from an increase in the proportion of the modal class (Fig. 1a) from 22.1% in the background zone to 39.7 and 63.4% in the buffer and impact zones, respectively. Thus, weight distributions in the buffer and impact zones had more acute peaks and were stronger shifted toward smaller thalli, compared to that in the background territory. In the case of length distribution, no consistent changes in skewness and kurtosis were revealed.

Age spectrum. The relationship between the frequency of “age states” and thallus weight in the background territory is shown in Figure 2 (plots for the buffer and the impact zone are similar). The increase of thallus weight was accompanied by a consistent change in age spectrum, with initially prevailing cryptosorediate thalli being replaced as dominants by mesosorediate thalli; asorediate thalli were found only in the smallest size groups. This fact confirmed that the identified groups can be rightfully regarded as age states, rather than manifestations of ecological polymorphism.

The age composition of the cenopopulation from the background territory (Fig. 3) was characterized by the prevalence of mesosorediate thalli (46%), which indicated that their development at the first three stages was rapid and the fourth stage had the longest duration. In cenopopulations of the buffer and impact zones, the spectrum was shifted to the prevalence of cryptosorediate thalli (44 and 60 %, respectively); compared to the background zone, there was also an obvious increase in the frequency of asorediate thalli (from 0.7 to 25.3 %) and a decrease in that of hypersorediate thalli (from 3.9 to 0.2 %).

Loglinear analysis of the "3 zones \times 5 stages" table by the χ^2 test showed that the differences between age spectra of cenopopulations from different zones are highly significant ($p \ll 0.0001$). Pairwise comparisons of proportions by means of arcsine transformation also confirmed that differences in all combinations are significant (to say the least, at $p < 0.002$), except for that in the proportion of hypersorediate thalli in the buffer and impact zones ($p < 0.1$).

DISCUSSION

Dimensional structure of the populations.

Assuming that thallus weight in our case demonstrates stronger correlation with the absolute age than thallus length, we can confirm the prevalence of young thalli in populations of all load zones.² The rapid decrease in the number of thalli with age suggests either their high mortality at early developmental stages (probably because of intraspecific competition) or their fusion and the formation of complex thalli.

The former explanation is traditional for population ecology (survival curves like the "oyster curve"), whereas the latter is specific for lichens. The principal possibility of fusion of juvenile lobes was demonstrated by Armstrong (1984, cited from Armstrong and Smith, 1992). There is published data on the formation of thalli from groups of fused soredia (the "arachnoidal" stage of juvenile development in *H. physodes*; Schuster, 1985) and the development of young *H. physodes* thalli on decomposing parts of old thalli (Kiss, 1982). On the other hand, there is no conclusive evidence that this process is common in nature.

The exponential distribution of thallus weight was observed for epiphytic *Lobaria oregana* (Roades, 1983). However, contrary to our data, the distribution of thallus diameter described for *H. physodes* (Hyvärinen, 1992) and epilithic *Parmelia glabratula* subsp. *fuliginosa* (Armstrong, 1988) is close to exponential distribution. This is probably explained by differences in the experimental scheme (complete census in our study and selective census used by these two authors). Moreover, our results are difficult to compare with published data because the authors of all the papers cited above did not apply strict statistical criteria to the analysis of distribution.

The consistent shift of frequency distributions in response to increasing load is primarily associated with elimination of large thalli, and, hence, the prevalence of small specimens in cenopopulations of polluted habitats is more obvious. This can be caused by two processes resulting from atmospheric pollution: (1) a decrease in growth rates of thalli and (2) increased mortality of large thalli. Some publications provide evi-

dence in favor of the former cause (Feige, 1982), but we have no reasons to reject the latter. Hence, we cannot definitely attribute the above shift to any of these two processes.

The patterns of frequency distribution of test parameters in different load zones proved to be relatively stable. This unexpected fact sharply contrasts with a decrease in the absolute size of thalli and especially with the catastrophic reduction of lichen population density. If any "rapid" changes have occurred in populations under the effect of toxic load, it would be logical to suppose the existence of a significant difference in the pattern of frequency distributions, e.g., the change from positive to negative skewness upon inhibition of reproduction. Hence, the stability of distribution patterns is indirect evidence that under conditions of long-term pollution (in our case, about 60 years), lichen populations are in a steady state; i.e., mortality is counterbalanced by reproduction, and population size remains relatively constant.

Age structure of populations. It is necessary to note that we analyzed a truncated sample from the age spectrum of the population, which did not include the early stages of thallus development, invisible to the unaided eye, and discolored dying specimens that fell apart during sampling (in terms of plant demography, subsenile and senile individuals).

As a criterion for distinguishing age states, we chose the production of vegetative diaspores by a thallus, estimated from the number of soralia, the rate of their development, and the numerical ratio of soralia on lobes of different types. It is logical to suppose that soralia at the initial stages of development produce the minimal number of soredia, those on tubular lobes occupy an intermediate position, and soralia on galeate and labiate lobes, having the largest area, produce the greatest number of soredia. Therefore, thalli of the same age state make a more or less similar contribution to the process of population reproduction. As in vascular plants, the age states of lichens characterize the biological age of individuals and are related to their absolute age only indirectly.

The obvious shift of age spectrum upon increasing load provides evidence for the so-called rejuvenation of cenopopulations in the buffer and impact zones (we emphasize once again that only the biological age is discussed). This process may lead to a decrease in the total flow of *H. physodes* diaspores in the ecosystem, which, in turn, may be one of the factors responsible for the reduced abundance of lichens in polluted territories.

There are at least two possible explanations for this shift of the age spectrum. (1) The formation of soralia may decrease the resistance of thalli because this process involves the loss of photobiont cells, which can significantly reduce photosynthetic activity, and the destruction of lower cortex that has a protective function. Hence, thalli carrying more soredia may have

² This assumption is based on two reasons: (1) In the considered period of time, neither central nor peripheral parts of a thallus die off with age, and (2), due to a significant vertical division of thalli, they grow in volume as well as in area.

lower resistance to pollutants, which accounts for their higher mortality and subsequent elimination. (2) Pollutants may inhibit the formation of soralia. Atmospheric pollution was shown to have an adverse effect on the rate of cell division in algae (Nash and Gries, 1991), and this can cause a significant decrease in the intensity of soredia formation.

The data on vascular plants differ from our results. Thus, the "aging" process manifested in the shift of age spectrum to senile and subsenile specimens was observed under conditions of atmospheric pollution with heavy metals and SO₂ in cenopopulations of bilberry (Deyeva and Maznaja, 1993) and snakeweed (Khantemirova, 1996). However, there are only a few such investigations, and it remains uncertain whether this phenomenon may be regarded as a general rule, all the more so since cenopopulations of higher plants exposed to anthropogenic impact of other type (e.g., pas-cual load) also demonstrated rejuvenation (Zaugol'nova, 1977).

CONCLUSIONS

This study is ideologically close to the field of population plant ecology developed by A. A. Uranov's school, primarily with respect to identification of age states in lichens. It should be noted, however, that the life of vascular plant populations has been investigated significantly better and at a higher methodological level (Zhukova, 1995) than that of lichens. Hence, we decided that arbitrary application of methods traditionally used in plant demography (calculating age parameters, plotting the base spectrum, etc.) to the new object is untimely. Compared to the advanced level of population analysis in higher plants, attempts at applying it to lichens can be regarded only as the initial stage of investigations. That is why there are more questions than answers in our study. However, its results suggest that investigations in this field are promising.

One of the main difficulties in applying the population approach to lichens concerns the isolation of individual thalli. The appropriate choice of the object (foliose lichen with more or less discrete thallus), substrate (thalli developing on smooth fir bark have more regular shape and are easier to collect), and phytocenotic conditions (low illumination prevents the formation of very dense populations and, hence, promotes the development of separate thalli) allowed us to solve this problem. However, the process of isolating individual thalli in cases of crowded growth remains subjective, and another source of errors is deformation of drying thalli and changes in their size during the period of storage before measuring. Nevertheless, we believe that any significant distortion of results under the effect of these factors is hardly probable.

We found that exposure to atmospheric pollution leads to consistent changes in the dimensional and age structure of lichen populations. Upon transition from

the background to the impact zone, frequency distributions of thallus weight and length shift toward specimens of smaller sizes, and the age spectrum shifts toward the prevalence of less fertile (asorediate and cryptosorediate) thalli. At the same time, the form of frequency distributions remains relatively stable in all zones. The population of the impact zone is at the technogenic limit of *H. physodes* distribution in the region of our studies. This fact suggests that rejuvenation of populations under the effect of toxic load is the key process determining the fate of this species in polluted territories.

The population-oriented approach to the analysis of anthropogenic changes of the lichen cover adds nothing new to the data on its degradation, which can be obtained by the traditional indication methods. Moreover, being extremely labor-consuming, this approach can hardly have any important role in applied bioindication research. Its significance is different: it provides the possibility of gaining better knowledge about causes and mechanisms of changes occurring in lichen communities under the effect of environmental pollution.

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REFERENCES

- Aivazyan, S.A., Enyukov, I.S., and Meshalkin, L.D., *Prikladnaya statistika: Osnovy modelirovaniya i pervichnaya obrabotka dannykh* (Applied Statistics: Fundamentals of Modeling and Initial Data Processing), Moscow: Finansy i Statistika, 1983.
- Armstrong, R.A., Studies on the Growth Rates of Lichens, in *Lichenology: Progress and Problems*, London, 1976, pp. 309–322.
- Armstrong, R.A., Substrate Colonization, Growth, and Competition, *CRC Handbook of Lichenology*, Cleveland, 1988, vol. 2, pp. 3–16.
- Armstrong, R.A. and Smith, S.N., Lobe Growth Variation and the Maintenance of Symmetry in Foliose Lichen Thalli, *Symbiosis*, 1992, vol. 12, pp. 145–158.
- Bol'shev, L.N. and Smirnov, H.B., *Tablitsy matematicheskoi statistiki* (Tables of Mathematical Statistics), Moscow: Nauka, 1983.
- Degelius, G., Biological Studies of Epiphytic Vegetation on Twigs of *Fraxinus excelsior*, *Acta Hort. Göteborg*, 1964, vol. 27, pp. 11–55.
- Deyeva, N.M. and Maznaja, E.A., The State of Bilberry in Polluted and Unpolluted Forests of the Cola Peninsula, *Aerial Pollution in Cola Peninsula*, Apatity, 1993, pp. 308–311.
- Fahsel, D., Individuals, Populations, and Population Ecology, in *Lichen Biology*, Cambridge, 1996, pp. 181–198.

- Feige, G.B., *Niedere Pflanzen – speziell Flechten – als Bioindikatoren*, *Decheniana, Beihefte* (Bonn), 1982, vol. 26, pp. 23–30.
- Gilyarov, A.M., *Populyatsionnaya ekologiya* (Population Ecology), Moscow: Mosk. Gos. Univ., 1990.
- Goyal, R. and Seaward, M.R.D., Metal Uptake in Terricolous Lichens: 2. Effects on the Morphology of *Peltigera canina* and *Peltigera rufescens*, *New Phytol.*, 1982, vol. 90, pp. 73–84.
- Hale, M.E., Growth, in *The Lichens*, London: Academic, 1973, pp. 473–492.
- Hale, M.E., *The Biology of Lichens*, London: Edward Arnold, 1974.
- Hyvärinen, M., Adaptivity of the Thallus Structure of *Hypogymnia physodes* to Microclimatic Conditions, *Lichenologist*, 1992, vol. 24, pp. 267–279.
- Ikonen, S. and Karenlampi, L., Physiological and Structural Changes in Reindeer Lichens Transplanted around a Sulfite Pulp Mill, *Proc. Kuopio Meeting on Plant Damage Caused by Air Pollution*, Kuopio, 1976, pp. 37–45.
- Istomina, N.B., The Biology of *Lobaria pulmonaria* (L.) Hoffm. and *Menegazzia terebrata* (Hoffm.) Massal. in Southern Taiga Forests of European Russia, *Cand. Sci. (Biol.) Dissertation*, Moscow, 1996.
- Kaigorodova, S.Yu. and Vorobeichik, E.L., Changes in Certain Properties of Gray Forest Soil Polluted with Emissions from a Copper-smelting Plant, *Ekologiya* (Ekaterinburg), 1996, no. 3, pp. 187–193.
- Khantemirova, E.V., Structure of Cenopopulations of Snakeweed under Conditions of Technogenic Pollution, *Ekologiya* (Sverdlovsk), 1996, no. 4, pp. 307–309.
- Kiss, T., Aspects and Types of Competition between Lichen Species in Epiphytic Communities, *Acta Bot. Hung.*, 1982, vol. 28, pp. 113–126.
- LeBlanc, F. and De Sloover, J., Relation between Industrialization and the Distribution and Growth of Epiphytic Lichens and Mosses, *Can. J. Bot.*, 1970, vol. 48, pp. 1485–1496.
- Mikhailova, I.N., Epiphytic Lichen Communities in Forests of the Middle Urals under Conditions of Technogenic Pollution, *Cand. Sc. (Biol.) Dissertation*, Ekaterinburg, 1996.
- Nash, T.H. III, and Gries, C. Lichens as Indicators of Air Pollution, *The Handbook of Environmental Chemistry*, Berlin, 1991, vol. 4, part C, pp. 1–29.
- Rhoades, F.M., Distribution of Thalli in a Population of the Epiphytic Lichen *Lobaria oregana*, and a Model of Population Dynamics and Production, *Bryologist*, 1983, vol. 86, pp. 309–331.
- Schuster, G., Die Jugendentwicklung von Flechten—ein Indikator für Klimabedingungen und Umweltbelastung, *Bibliotheca Lichenologica*, 1985, vol. 20.
- Sigal, L.L., and Nash, T.H. III, Lichen Communities on Conifers in Southern California Mountains: An Ecological Survey Relative to Oxidant Air Pollution, *Ecology*, 1983, vol. 64, pp. 1343–1354.
- Tsenopopulyatsiia rastenii (ocherk populyatsionnoi biologii)* (Plant Cenopopulations: An Essay on Population Biology), Zaugol'nova, L.B., Zhukova, A.A., Komarova, A.S., and Smirnova, O.V., Eds., Moscow: Nauka, 1988.
- Tyurin, Yu.N. and Makarov, A.A., *Analiz dannykh na komp'yutere* (Computer-aided Data Processing), Moscow: Finansy i Statistika, 1995.
- Uranov, A.A., Age Spectrum of Cenopopulations as a Function of Time and Energy Wave Processes, *Biol. Nauki*, 1975, no. 2, pp. 7–34.
- Vorobeichik, E.L. and Khantemirova, E.V., Response of Forest Biocenoses to Technogenic Pollution: Dose–Effect Relationships, *Ekologiya* (Sverdlovsk), 1994, no. 3, pp. 31–43.
- Vorobeichik, E.L., Sadykov, O.F., and Farafontov, M.G., *Ekologicheskoe normirovanie tekhnogennykh zagryaznenii nazemnykh ekosistem* (Ecological Standards for Technogenic Pollution of Terrestrial Ecosystems), Nauka, 1994.
- Zaugol'nova, L.B., Analysis of Cenopopulations as a Method for Studying Anthropogenic Effects on Phytocenoses, *Bot. Zh.*, 1977, vol. 62, no. 12, pp. 1767–1779.
- Zhivotovskii, L.A., *Populyatsionnaya biometriya* (Population Biometrics), Moscow: Nauka, 1991.
- Zhukova, A.A., *Populyatsionnaya zhizn' lugovykh rastenii* (The Life of Meadow Plant Populations), Ioshkar-Ola: Lanar, 1995.