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Populations of epiphytic lichens under stress conditions: survival strategies

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Abstract: The effect of a copper-smelting plant on populations of *Hypogymnia physodes* and *Tuckermanopsis sepincola* was studied in the Middle Urals. A different population response was found between the two lichen species due to different life strategies. The pollution appears to decrease growth and developmental rate of *H. physodes* (a vegetatively reproducing strongly competitive species), resulting in a shift of population structure towards smaller, esorediate to low sorediate thalli. The background population of the sexually reproducing *Tuckermanopsis sepincola* consisted mainly of young, small thalli of a low fertility as a result of strong inter-species competition with *H. physodes*. At the polluted site, the sharp decrease in the abundance of *H. physodes* led to a shift in structure of the *T. sepincola* population towards larger and more fertile thalli. It may be concluded that *T. sepincola* benefits from air pollution by an indirect effect of the removal of a strong competitor, i.e. *H. physodes*.

Key words: air pollution, heavy metals, lichen population, life strategy, reproduction, SO_2

Introduction

Epiphytic lichens are widely recognized as being very sensitive to atmospheric pollutants. Numerous studies have described toxic influences on physiological and biochemical processes, on morphology and anatomy of selected species, on frequency of species and on lichen community composition (see De Wit 1983; Nash & Gries 1991; Gries 1996 for overviews). Very few studies, however, have considered these influences at the population level. Investigations of populations might provide valuable additional information. Population structure reflects the influence of stress on thallus development and reproduction, allowing an assessment of population vitality and the prediction of the fate of species under stressed conditions.

Studies of lichen population structure have been carried out in both non-polluted (Rhoades 1983; Istomina 1994; Gauslaa 1997; Ramstad & Hestmark 2001; Hestmark *et al.* 2005; Hilmo *et al.* 2005) and polluted environments (Mikhailova & Vorobeichik 1999; Suetina 2001). All these studies involved convenient model species (i.e. macrolichens with more or less discrete thalli) which helps to minimize theoretical and methodological problems. Studies of *Hypogymnia physodes* (L.) Nyl. populations near a copper smelter (Mikhailova & Vorobeichik 1999) revealed a shift of the population structure towards young (in terms of biological age) thalli. Entrapment of soredia released by individual thalli and by the whole population revealed a significantly lower production level of soredia at the polluted site compared to the background area (Mikhailova 2002). Moreover, a decrease in the rates of early development of *H. physodes* was shown in the polluted environment (Mikhailova & Scheidegger 2001). From these studies, the following general scheme of the response of the population to toxic load might be suggested. A direct toxic influence on *H. physodes* thalli leads to a slow down in their development. At the population level, this is reflected in a decline in the proportion of soredia-producing thalli. This, in turn, combined with a decline in

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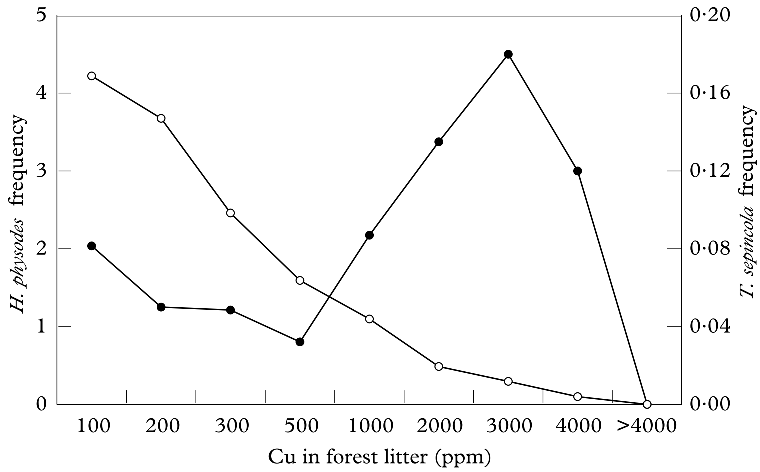

FIG. 1. Frequencies of *Hypogymnia physodes* (white) and *Tuckermanopsis sepincola* (black) on birch trunks along the pollution gradient. X-axis: upper limits of intervals. Frequency was measured according to Herzig and Urech (1991).

soredia production by individual thalli, leads to a sharp decrease in soredial flow from the population. This reduction in reproductive potential maintains the population density at a low level.

The aim of the present study was to investigate the response of populations of two lichen species, *H. physodes* and *Tuckermanopsis sepincola* (Ehrh.) Hale, to emissions from a copper smelter and to consider the survival strategies in this stressful environment.

Material and Methods

The study was conducted in the southern taiga subzone in the Middle Urals (56°51′N 59°48′E). The forest cover consists of mostly secondary stands with mixed coniferous and deciduous trees as well as birch and aspen stands (Kolesnikov *et al.* 1973). The climate is moderately continental, with an annual average rainfall of 400–600 mm and a of snow depth ≥40 cm. The mean annual temperature is +1°C; mean January and July temperatures are −16°C and +17°C, respectively. The duration of the frost-free period is 90 days (Prokaev 1976).

The area studied is affected by the emissions of a copper-smelting plant, which has been functioning since 1940 emitting particulate and gaseous pollutants in the ratio 1:8·44. Sulphur dioxide constitutes 98·7% of the gaseous pollutants, and copper, zinc, arsenic, and lead make up 46·9, 31·5, 11·5, and 10·1% of the particulate pollutants, respectively (Vorobeichik *et al.* 1994). Damage to the biota around the smelter has been described in a range of publications (e.g. Vorobeichik & Khantemirova 1994; Vorobeichik *et al.* 1994; Scheidegger 1998; Scheidegger & Mikhailova 2000).

Hypogymnia physodes, which has been studied previously, was chosen as an asexually reproducing species and a strong competitor dominating in all epiphytic communities in the area studied (Mikhailova & Vorobeichik 1999; Mikhailova & Scheidegger 2001; Mikhailova 2002). For comparison, *Tuckermanopsis sepincola* was selected as a sexually reproducing species and a weak competitor. Sample plots were selected on the basis of frequency data for the species under consideration (I. N. Mikhailova, unpublished). The highest pollution level tolerated by both species corresponds to a Cu forest litter content of *c.* 4000 ppm (Fig. 1). However, their response pattern is different. The frequency of *H. physodes* gradually decreases with increasing level of pollution, while the frequency of *T. sepincola* peaks just before the maximum tolerable load. Plots were therefore established both in the low-polluted part of the gradient (17 km from the smelter, Cu forest litter content *c.* 200 ppm, the background plot), and in the heavily polluted zone, near the *T. sepincola* frequency peak (5 km from the smelter, Cu forest litter content *c.* 3000 ppm, the polluted plot). Both plots were in the secondary birch stands (mixed *Betula pubescens* and *B. pendula*) derived from fir (*Abies sibirica*) and spruce (*Picea obovata*) forests after clearcuts. Within plots of 75 × 100 m (background plot) and 50 × 100 m (polluted plot), the circumference at breast height was recorded for all birch trees with circumference values >30 cm (540 and 443 trees at background and polluted plots, respectively). All *T. sepincola* thalli were collected from each tree and their height above the ground was recorded. Two estimates of lichen population density were used: the proportion of trunks colonized and the average number of thalli per trunk. In addition, the frequency of three other common macrolichens (*H.*

physodes, *Vulpicida pinastri* and *Cladonia coniocraea*) was recorded on each trunk using a sample grid of 10 units (adapted to fit half the circumference of each trunk) at two height classes (0–0·5 and 1·0–1·5 m above ground) (Herzig & Urech 1991).

In the laboratory, *T. sepincola* thalli were air dried, cleaned of bark fragments under a stereomicroscope, and weighed. Sections of 20 apothecia were cut to investigate hymenium development. Apothecia less than 0·5 mm diameter were shown to contain immature or single mature asci. In larger apothecia, the hymenium was fully mature and the number of spores produced was roughly proportional to the area of the apothecial disc. As the area of the apothecial disc increases, the shape of apothecia changes from flat to convex. Each thallus was subsequently referred to one of the following functional groups:

1. young sterile thalli (st);
2. subfertile thalli (s/fert), bearing flat apothecia <0·5 mm in diameter;
3. fertile 1 (fert1), bearing flat apothecia of 0·6–1·5 mm in diameter
4. fertile 2 (fert2), bearing flat apothecia larger than 1·5 mm and/or convex apothecia under 1 mm.
5. fertile 3 (fert3), bearing flat and/or convex apothecia larger than 1·5 mm.
6. subsenile (s/sen) thalli, decaying in old parts;
7. senile (sen) thalli, bearing young lobes (regenerative structures) originating from decaying parts of the old lobes.

Standard statistical procedures were applied including calculation of Spearman rank order correlation coefficient, the Kolmogorov–Smirnov non-parametric test, the χ^2 and *t*-tests. Thalli under 0·1 mg were excluded from analysis of thallus mass, although were used to analyse spectra of developmental stages.

Results

Colonization of trees by macrolichens

In the background plot, *Cladonia coniocraea* and *Vulpicida pinastri* are the most frequent macrolichens and the first colonizers of the trunks. Almost all registered trees were colonized by *C. coniocraea* (98·3%) and *V. pinastri* (94·3%). Both species were restricted to the base of the trunks, and no significant correlation was found between species frequency and tree size so that their frequencies remain more or less stable during the life of the host tree. *Hypogymnia physodes* was found on 69·5% of the trunks. Colonization also starts from the base of the trunks, with further expansion over the basal part and also higher up the trunk. Species frequency on trunks therefore increases with

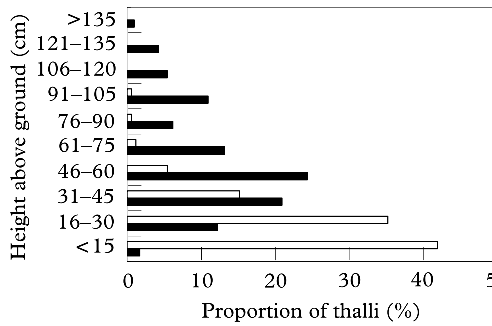

FIG. 2. Vertical distribution of *Tuckermanopsis sepincola* thalli on birch trunks at background (black) and polluted (white) sites.

increasing tree size [Spearman rank order correlation coefficient (*r*) is 0·41, $P<0·05$].

In the polluted plot, the proportion of trees colonized by the species was lower: 76·7% of the trunks by *C. coniocraea*, 3·4% by *V. pinastri*, and 4·7% by *H. physodes*. The frequency on trunks of *V. pinastri* and *H. physodes* was extremely low, not exceeding 5%. Statistically significant correlations were found between the frequency of all species and tree size ($r=0·34$, $r=0·22$ and $r=0·16$ (all $P<0·001$), for *C. coniocraea*, *V. pinastri*, and *H. physodes*, respectively).

Population density of *T. sepincola* and its vertical distribution on trunks

In the background plot, *T. sepincola* was found on 20·6% of birch trunks with an average number of thalli per trunk of 3·5. A very low but statistically significant positive correlation was found between tree size and number of thalli per trunk ($r=0·16$, $P<0·05$). In the polluted plot, the two estimates of population density (23·3%, 4·5 thalli per trunk) slightly exceeded those from the background plot. The differences are, however, not statistically significant.

The vertical distribution of *T. sepincola* on trunks is shown in Fig. 2. More than 90% of thalli in the polluted plot were present below 50 cm whereas in the background plot, the species reaches a maximum height of 152 cm above the ground, with a frequency peak at 30–75 cm. The Kolmogorov–Smirnov test confirmed a significant differ-

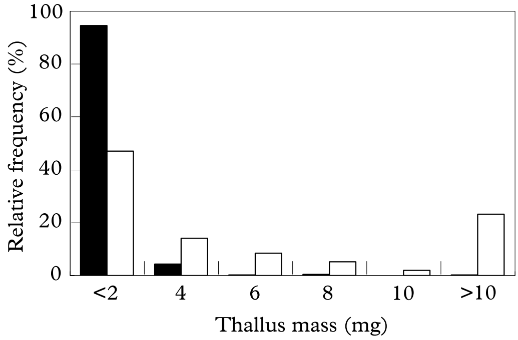

FIG. 3. Dimensional structure of the populations of *Tuckermanopsis sepincola* at background (black) and polluted (white) sites.

ence in the vertical distribution of thalli in the two plots ($P<0{\cdot}01$).

Functional structure of the *T. sepincola* population

The frequency distributions of thallus mass were close to exponential in both stands but in the background population there was a significant shift towards smaller thalli (Fig. 3). ($P<0{\cdot}001$, Kologorov–Smirnov test). The relationship between the thallus mass and the frequency of the functional groups is shown in Fig. 4 (subsenile and senile thalli are not included). Small thalli are mainly sterile or subfertile. With increasing thallus mass, the percentage of sterile thalli gradually decreases, and that of fertile thalli increases until they predominate.

Spectra of functional groups of thalli are shown in Fig. 5. In the background plot, young sterile thalli prevail (54·3%). Fertile thalli are surprisingly rare (*fert1*+*fert2*+*fert3*= 18·3%); among them, *fert1* prevails. In the polluted plot, 53·1% are fertile with subfertile and fertile 1 thalli dominant with almost equal frequencies of 27·9 and 28·1%, respectively. There is a clear difference in the proportion of sterile thalli with 54·3% in the background plot and 13·9% in the polluted plot.

Log-linear analysis of the '2 zones × 7 stages' table by χ^2 test showed that the difference between spectra of functional groups is highly significant ($P<<0{\cdot}0001$). Pair-wise comparisons of proportions of the groups after arcsine transformation also showed significant differences in all combinations (at the least, at $P<0{\cdot}004$) except for the proportion of senile thalli.

Discussion

In the background plot, *T. sepincola* is a frequent pioneer species of open lichen communities on the bases of trunks. During subsequent successional stages, rapid growth of other species (mainly *C. coniocraea* and *H. physodes*) leads to a dense lichen cover on trunk bases, and *T. sepincola* thalli are often overgrown by adult thalli of *H. physodes* or its juvenile lobes. However, high mortality rates are compensated for by high dispersal ability so that *T. sepincola* is not eliminated from communities, but colonizes new microsites on trunks (usually slightly above the densely covered part of the trunk). In the course of time, fast-growing *H. physodes* also reaches these microsites, once more replacing *T. sepincola*. Thus, the background population is kept 'permanently young' and its density is sustained by the surprisingly low number of thalli with reduced fertility. In the birch stands of the Middle Urals, *T. sepincola* can be regarded as a pioneer species (*r*-strategist) which occupies free microsites because of its high dispersal ability and tendency to be excluded from communities by stronger competitors.

In the polluted plot, *T. sepincola* thalli are exposed to a strong toxic load, resulting in a range of visible signs of damage in many thalli (growth abnormalities, irregular shape of apothecia, changes of colour, wrinkled central part of thalli, etc). However, the absence of the competitor species allows successful development of thalli, which is evident from the population structure with a high proportion of fertile thalli. So, the most important effect of air pollution on the *T. sepincola* population is not a toxic influence on thalli (as it is for *H. physodes*), but its indirect effect of the removal of competitor species. Changes in preferred microsites may be a possible mechanism for avoidance of the toxic influence. Basal parts of trunks

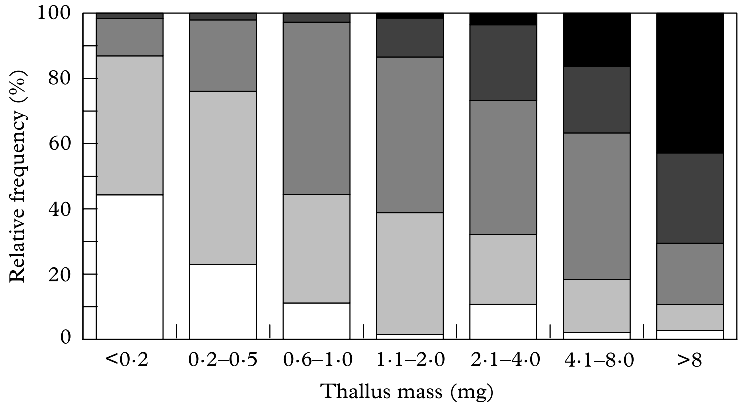

FIG. 4. Relationship between thallus mass of *Tuckermanopsis sepincola* and spectrum of functional groups in the population from the polluted site (see text for explanations). □ st, ▒ s/fert, ▒ fert 1, ▒ fert 2, ■ fert 3.

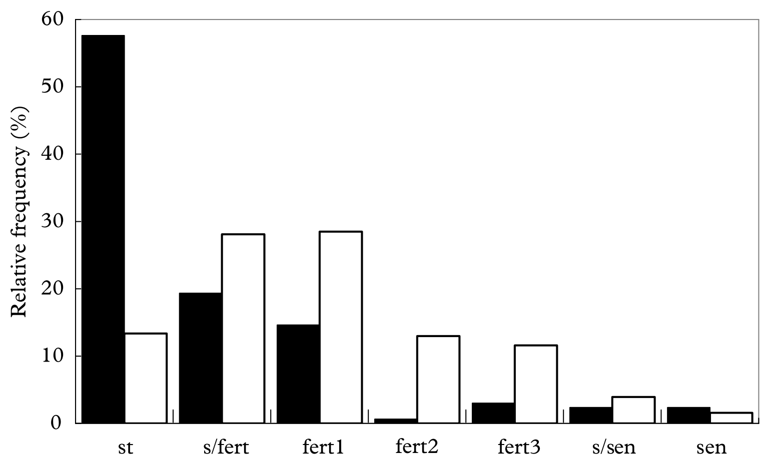

FIG. 5. Spectra of functional groups of *Tuckermanopsis sepincola* thalli in populations from background (black) and polluted (white) sites (see text for the explanations).

are to a certain extent protected from pollutants by the understorey and by snow cover.

Thus, two species with different reproductive strategies have a different population structure both in background conditions and at the border of 'the lichen desert'. *Tuckermanopsis sepincola* proves more successful when exposed to an abiotic stress factor (toxic load). Adult thalli of *H. physodes* can survive the existing level of toxic load, but their soredia production is suppressed so that a population of only a very low density can be sustained. The high 'cost' of soredia production might be determined by the necessity of high rates of division of algal cells, which can be suppressed by pollutants. Spore production might not be so affected by the existing level of pollutants, and this probably plays a decisive role for the survival of *T. sepincola* under stress conditions.

Different patterns of population response to the toxic load have also been shown for higher plants. For example, a shift towards older individuals ('ageing' of populations) under the pollution from a copper smelter was shown for populations of *Vaccinium myrtillus* (Deyeva & Maznaja 1993) and *Polygonum bistorta* (Khantemirova 1996).

On the other hand, populations of *Crepis tectorum* were shown to be 'getting younger' near the source of atmospheric fluorides (Trubina & Makhnev 1999). 'Rejuvenation' of plant populations can be caused by a decline in developmental rates. The *r*-strategist *C. tectorum* becomes almost a *k*-strategist because of its increasing longevity and decline in seed production (Trubina & Makhnev 1999). Declines in inter-species competition in the polluted environment was suggested as an important factor leading to an increase in density of a *V. myrtillus* population (Deyeva & Maznaja 1993). Thus, although it is hardly possible to determine the mechanisms of population response to stress in either plants or lichens, some common features are evident.

Because of an insufficiency of empirical data on population structure of different lichen species and the lack of molecular data, we refrain from any generalizations to predict the stress response of lichen species on the basis of their life strategy. The most attractive hypothesis would be that pioneer organisms, which are adapted to surviving in stressed environments, are by definition able to survive pollution stress. One of the most important features of *r*-strategists is early reproduction and high reproductive rates, features of great importance also to survive exposure to pollution, where high mortality rates of spores and young developmental stages are highly probable. The lack of molecular data hinders assessment of the importance of reproductive mode in determining the level of genetic variation within lichen species and, hence, the possibilities and rates of evolution of resistant lichen populations.

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