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Does snail grazing affect growth of the old forest lichen *Lobaria pulmonaria*?

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Abstract: Grazing marks from snails are frequently observed in populations of the old forest epiphyte *Lobaria pulmonaria*. However, grazing marks are more numerous in thalli from deciduous broad-leaved forests than in thalli from boreal *Picea abies* forests, due to higher populations of lichen-feeding molluscs in deciduous stands. Here we tested for deleterious effects of snails on the lichens by transplanting 600 more or less grazed *L. pulmonaria* thalli from deciduous forests to snail-free *P. abies* forests. Subsequent measurements showed that growth rates were as high in thalli with many grazing marks as those without, suggesting that growth of mature lobes of *L. pulmonaria* are not inhibited by the recorded grazing pressure imposed by lichen feeding snails.

Key words: epiphytic lichens, herbivory, lichen growth, molluscs

Introduction

Many lichens are long-lived, sessile organisms (Jahns & Ott 1997) forming canopies that are often inhabited by numerous small herbivores (Gerson & Seaward 1977; Seaward, 1988). It has been inferred that to sustain viable populations and complete a life cycle comprising several years, lichens depend on a strong herbivore defence (Lawrey 1983; Gauslaa 2005) and/or a low nutritional value, particularly because they often dominate habitats with few plants (Seaward 1988). Nevertheless, grazing by invertebrates such as molluscs, oribatid mites, and some insects seems to be common on lichens in the field (e.g. Lawrey 1980; Baur *et al.* 1995, 2000), as shown by the frequent presence, at least in humid regions, of tiny grazing marks. While the

influence of lichen-foraging reindeer and caribou on lichen communities is well demonstrated from a landscape perspective (e.g. Cooper & Wookey 2001; Boudreau & Payette 2004), invertebrate grazing is much less spectacular, and often overlooked. Few studies have compared invertebrate grazing pressure on lichens in different ecosystems. Invertebrate grazing may vary on a small spatial scale within a lichen thallus (e.g. Lawrey 1983; Baur *et al.* 1995; Prinzing & Wirtz 1997; Benesperi & Tretiach 2004), but very little is known about how such small scale grazing damage may affect lichen growth and performance.

This study focuses on the foliose old forest lichen *Lobaria pulmonaria*, which is rare or threatened in many parts of the world, mostly as a result of industrial forestry (e.g. Campbell & Fredeen 2004) and air pollution (e.g. Gilbert 1986; Gauslaa 1995). Grazing by the slug *Lehmannia marginata* on *L. pulmonaria* has occasionally been reported (Coker, 1967). In a Swiss transplantation experiment, nearly 50% of the inoculated *L. pulmonaria* lobes were lost due predominantly to browsing by invertebrates, i.e. slugs and arthropods (Scheidegger *et al.* 1995). It is possible that grazing can also

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aggravate the adverse effects of other environmental stresses (i.e. pollution, forest management). To the best of our knowledge, however, nothing is known about the effects of invertebrate grazing on subsequent lichen growth.

The main objective of this study was to establish a correlation, if any, between lichen growth rates and grazing damage. Our study is partly based on an earlier experiment in which surface area and dry matter increments in *L. pulmonaria* thalli collected in snail-rich deciduous forests were assessed after a 100 day transplantation period in boreal *Picea abies* stands with few lichen-feeding snails (Gauslaa *et al.* 2006). Since there are few actual reports of snail occurrence on *L. pulmonaria* (Coker 1967), we recorded also the snail community on *L. pulmonaria* in the deciduous stands. Later, we extended our study to include assessments of snail grazing marks on *L. pulmonaria* collected in boreal *Picea abies* rainforests, in which *L. pulmonaria* is locally abundant on twigs. Grazing marks in thalli from deciduous forests were compared to those in the set of *L. pulmonaria* thalli from *Picea abies* forests, thereby allowing for wider generalizations concerning the frequency of snail grazing in the field.

Material and Methods

Six hundred healthy *Lobaria pulmonaria* (L.) Hoffm. thalli (5–30 cm², 50–500 mg dry weight) were collected on 1 July 2004 from *Acer platanoides*, *Fraxinus excelsior* and *Ulmus glabra* in old forests at Kvelde, Vestfold, S Norway (59°12'N 9°57'E, 200 m a.s.l.). The thalli were collected both from the main stems and thick branches. Five hundred and forty additional thalli (5–23 cm², 50–315 mg d. wt) were collected in boreal *Picea abies*-dominated rainforests in Nord-Trøndelag at Overhalla (64°27'N 11°53'E, 15 m a.s.l.) and Namsos (64°25'N 11°25'E, 20 m a.s.l.), sampled from thin twigs of *P. abies* and scattered stems of *Salix caprea*.

All lichens were transported in closed bags to the laboratory on the same day as field collection. Molluscs on the lichen thalli samples were removed the following morning, counted and identified. No snails were observed on the lichen thalli collected in *P. abies*-dominated stands. However, as an estimate of mollusc population size, the sampling may be inaccurate because the daytime collection of lichens probably underestimated the number of molluscs present since these creatures are mostly active at night. Furthermore,

molluscs occurring on the tree bark were not collected. Grazing impact in both sets of thalli was assessed using an ordinal scale: 0, no grazing marks; 1, grazing marks covering <1% of the thallus area; 2, 1–4%; 3, 4–10%; 4, >10%. According to our field and laboratory experience with small herbivores and lichens, we consider the grazing marks observed on the samples collected to be produced by molluscs (Fig. 1). Oribatid mites make small cavities, especially on the lower side. However, we cannot identify the mollusc species by means of the grazing marks.

The subsequent transplant experiment, including measurements of size, growth, etc., has been described in detail in Gauslaa *et al.* (2006). The 600 *L. pulmonaria* lobes from the deciduous forests were transplanted into three successional boreal forest stands with *Picea abies* (old forest, young forest and clear-cut) for 100 days (July–October). Prior to their transplantation, all thallus lobes were randomized, and replicates for the three forest types were selected at random. The % cover of grazing marks estimated on the 5-graded scale did not differ between lobes transplanted into the three successional forest stands. Similarly, there was no significant difference in thallus biomass, area, and dry matter per area (Table 1), suggesting that the pooled dataset from all successional stands can be used to detect possible effects of grazing on subsequent lichen growth rates. Growth is given in % dry matter (DM) gain = $(DM_{\text{end}} - DM_{\text{start}}) \times 100 / DM_{\text{start}}$. No snails were observed on lichen lobes in the *P. abies* forests during transplantation, and no additional grazing marks were observed following transplantation, suggesting that lichens were relieved from snail grazing pressure during the entire period over which growth was measured.

Results

Five species of snails were found on *L. pulmonaria* thalli collected from broadleaved deciduous forests (Table 2). The species *Balea perversa* and *Helicigona lapicida* were most frequent, *Cochlodina laminata*, *Clausilia bidentata* and *Cepaea hortensis* occurred in smaller numbers. No snails were found on the *L. pulmonaria* thalli collected from the *P. abies* forests.

Approximately 82% of the 600 thalli from deciduous forests had clearly visible grazing marks. Among the 540 thalli from the *P. abies* forests, by contrast, less than 10% had grazing marks (Fig. 2). However, the percentage of the total thallus area directly affected by grazing was low, even in deciduous forests with a high frequency of grazing marks (Fig. 2). Only 12% of thalli from the deciduous forest had >10% cover of grazing

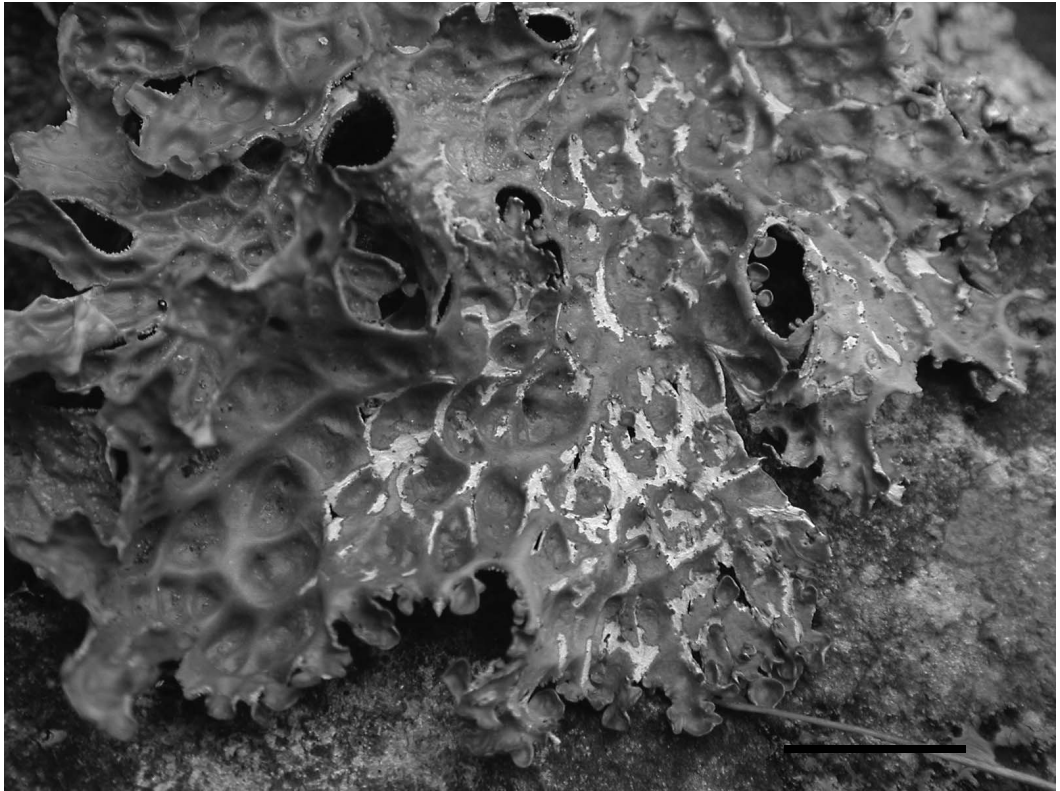


FIG. 1. *Lobaria pulmonaria*, thallus showing fresh grazing marks with exposed medulla (pale areas). Scale=1 cm.

TABLE 1. Pre-experiment characteristics* of *Lobaria pulmonaria* thalli selected for the three forest categories.

	Young forest	Old forest	Open area	P†
Thallus dry weight (g)	0.167 ± 0.006	0.168 ± 0.005	0.170 ± 0.005	ns
Thallus area (cm ²)	11.6 ± 0.3	11.9 ± 0.3	12.0 ± 0.3	ns
Thallus dry matter per area (g m ⁻²)	141 ± 1	139 ± 1	141 ± 1	ns
Maximal photochemical quantum yield (F_V/F_M)	0.723 ± 0.001	0.720 ± 0.002	0.722 ± 0.001	ns
Grazing marks, classes (0–4)	2.03 ± 0.09	2.02 ± 0.09	1.87 ± 0.09	ns

*means ± standard errors ($n=200$) are given; † P -values according to an ANOVA.

marks, and only two thalli had >25% cover. Thus, although grazing was frequent in the deciduous forests, it was spatially limited within a thallus. The most severe grazing marks were located on the reticulated ridges of the upper surface. The upper cortex and the algal layer had been eaten, leaving the white medulla exposed (Fig. 1). However, some small grazing marks were restricted to

the upper cortex only, leaving most algal cells intact. Regardless of grazing pattern, the lichen thallus was able to repair snail damage during the subsequent transplantation period. Old grazing marks were observed, presumably from previous years, in which green algal cells had already recolonized the algal deficient patches, and cortical repair was well advanced.

TABLE 2. Snail species collected from *Lobaria pulmonaria* thalli during sampling of donor material in deciduous forest prior to transplantation.

Snail species	Number of individuals
<i>Balea perversa</i>	43
<i>Helicigona lapicida</i>	15
<i>Cochlodina laminata</i>	8
<i>Clausilia bidentata</i>	5
<i>Cepaea hortensis</i>	3

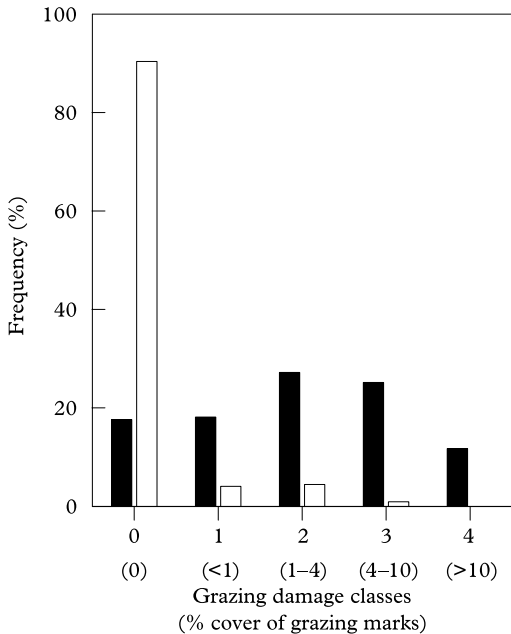


FIG. 2. Frequency of epiphytic *Lobaria pulmonaria* thalli in the five classes of snail grazing damage. Grazing was classified by given classes (abscissa) of estimated percent cover of grazing marks. The lichen material was collected in temperate broadleaved deciduous forests (■; $n=600$) and in boreal *Picea abies* forests (□; $n=540$).

Snail grazing prior to transplantation did not adversely affect subsequent lichen growth measured as dry matter gain (Figure 3; $P>0.05$; ANOVA, data not shown). Even the two thalli with the highest cover of grazing marks (>25%) had a mean dry matter growth as much as 20%. Percent area growth was also analysed (ANOVA) with no significant differences between the various

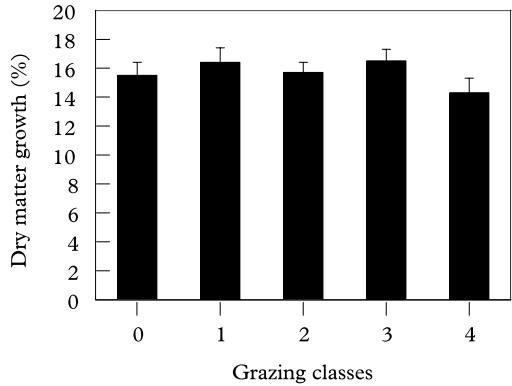


FIG. 3. Dry matter growth (means \pm 1 SE) in *Lobaria pulmonaria* thalli from temperate deciduous forests during a 100 days transplantation period subjected to different levels of grazing prior to transplantation. Lichen growth did not differ significantly ($P<0.05$) between different grazing classes (ANOVA). Grazing classes: 0, no grazing marks ($n=105$); 1, grazing marks covering <math><1\%</math> of the thallus area ($n=108$); 2, 1-4% ($n=162$); 3, 4-10% ($n=150$); 4, >10% ($n=70$).

grazing classes (data not shown). Finally, lichen dry matter gain was analysed in a two-way ANOVA with grazing classes and forest type as factors, showing no significant effects of grazing and no significant interaction (data not shown).

Discussion

Lichens are a significant dietary component for some snail species (e.g. Kerney & Cameron 1979; Benesperi & Tretiach 2004; Turner 1994). Nevertheless, as this study has shown, frequent snail grazing is not necessarily detrimental to established thalli of *L. pulmonaria*, even in snail-rich environments (Figs 2-3). Grazing was usually spatially limited to small portions of a lichen thallus. It has been shown that a high content of secondary compounds deters excess grazing in many lichen species (Lawrey 1983), also evidenced by experiments in which the content of lichen compounds was artificially removed by acetone (Reutimann *et al.* 1987; Gauslaa 2005). Thus removal or reduction of compound content may trigger a significant or complete consumption of many lichens by snails, at least under

laboratory conditions (Gauslaa 2005). The selective grazing of the upper cortex and the photobiont layer on the reticulated ridges can therefore be taken as evidence that these portions have a lower content of herbivore-deterrent compounds relative to adjacent thallus structures. *Lobaria pulmonaria* lacks the widespread cortical lichen compounds usnic acid and atranorin, but contains the medullary compounds stictic and norstictic acids (e.g. Krog *et al.* 1994). However, the total content of acetone-soluble compounds is not particularly high in *L. pulmonaria* compared to many other lichen species (Gauslaa 2005), and the intrathalline spatial distribution of compound deposits in this particular lichen is to our knowledge not known.

The recorded grazing did not reduce subsequent lichen growth after transplantation to a snail-free environment (Fig. 3). Lichens have a high regenerative potential after various types of serious physical destruction (Honegger *et al.* 1996). Viable myco- and photobiont cells have been retrieved even from faeces of lichen-feeding oribatid mites (Meier *et al.* 2002). Such regenerative capabilities may not only facilitate subsequent repair of grazing damage, maintaining high lichen growth despite grazing pressure, but suggest also that lichen-feeding invertebrates may act as dispersal agents.

Snail grazing was frequent on *L. pulmonaria* in deciduous forests, and rare in spruce forests (Fig. 2). In Fennoscandia, the recorded snails (Table 2) are associated with broadleaved deciduous woodlands, in which the two most frequent, *B. perversa* and *H. lapicida*, favour stony ground or calcareous scree (Waldén 1969; von Proschwitz 1994; Turner *et al.* 1998; Solhøy *et al.* 2002) that were present in the sampled deciduous forest, but not in the boreal rainforest. These requirements of *B. perversa* and *H. lapicida* are often fulfilled in deciduous forests with *L. pulmonaria* (e.g. Gauslaa 1985; Gauslaa 1995). The *Picea abies* forests of Nord-Trøndelag, in which the second dataset of *L. pulmonaria* was collected, are known to be poor or deficient in *Balea perversa* and *Helicigona lapicida* (Solhøy *et al.*

2002). The occurrence of fewer lichen-feeding climbers probably accounts for the lower frequency of grazing damage in such ecosystems (Fig. 2).

Among native Norwegian terrestrial molluscs, 18 of about 80 species regularly climb trees (T. Solhøy, pers. obs). Five of the 18 climbers are probably too small and/or too rare to have any significant grazing impact on lichens, while additional five climbing Clausiliids (doorsnails) are rare and two others may rarely graze lichens. Of the five species found in our study, *Cochlodina laminata* seems to feed on fungi on tree stumps rather than lichens (Fog 1979), and more rarely climbs vertical surfaces (Kerney 1999). *Balea perversa*, *Helicigona lapicida* and *Clausilia bidentata* are reported to consume various lichen species on trees and rocks (e.g. Boycott 1934; Evans 1972; Holyoak 1978; Waldén 1981; von Proschwitz 1994; Baur *et al.* 1995; Turner *et al.* 1998). *Cepaea hortensis* has also been recorded as a grazer of arboreal lichens (Stahl 1904), and consumed different lichen species in a feeding experiment (Gauslaa 2005). Finally, two mostly night active slugs (*Lehmannia marginata* and to a lesser extent *Malacolimax tenellus*) are climbers and could have produced some of the observed grazing marks, but slugs normally hide in sheltered sites during the daylight hours when our lichen thalli were collected, and so would have been overlooked in this study.

Our dataset did not allow within-forest variability of grazing marks to be tested. However, grazing in deciduous forests appeared to be more severe on bryophyte-covered boles than on branches higher in the canopy. Presumably this reflects the fact that boles are closer to the snails' sheltering places, and therefore represent a shorter creeping distance. In spruce forests, which mostly lack mossy trunks, snails necessarily have to travel longer distances to reach lichen-rich sites in the canopy. From the trunk they would have to follow the branches outward to reach the lichens on thin twigs. However, microhabitats closer to the ground and accessible to snails may be more shaded while the growth of *L. pulmonaria* has been

shown to be strongly limited by low light in a forest environment (Gauslaa *et al.* 2006). In closed forest ecosystems, most lichens are restricted to well-lit mid and upper canopies (e.g. McCune *et al.* 1997). Investments in lichen compounds depends on the photobiont's ability to produce photosynthates (Solhaug & Gauslaa 2004). Accordingly, a combination of reduced growth and increased grazing with increasing proximity to the ground suggests that lichen-feeding invertebrates may play a significant role in shaping the lower distribution limit of epiphytic lichens within forest canopies. Grazing and shade adversely affect the performance of seedlings of plants (Baraza *et al.* 2004).

Lichens and lichen-feeding snails coexist in many localities. Our study shows that snails frequently graze *L. pulmonaria* without significant adverse effects on the growth of full-grown, mature lobes, at least within the recorded grazing range. However, the regeneration of juvenile thalli may be more vulnerable to herbivory, as has often been shown to be the case for regenerating plants (Grubb 1977).

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