

Mass loss of epiphytic lichen litter in a boreal forest

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We measured the persistence of fallen epiphytic macrolichen litter as a part of developing a method for estimating epiphyte abundance from biomass of lichen litter. Annual mass loss in two pendulous, fruticose (alectorioid) lichens and three foliose lichens was determined with litterbags in an old *Picea abies* forest in north-eastern Sweden. Disturbance by animals caused high mass loss in alectoroid lichens during winter. Alectoroid lichens lost weight significantly faster than foliose species. In both *Alectoria sarmentosa* and *Bryoria fuscescens*, 17% of the original mass remained after one year (intact samples) compared to 39% in *Lobaria pulmonaria*, 44% in *Hypogymnia physodes* and 58% in *Platismatia glauca*. Half lives of epiphyte litter ranged from four months in *Alectoria* and *Bryoria* to 14 months in *P. glauca*. It is concluded that both growth form and extent of animal disturbance strongly influence the persistence of epiphyte lichen litter on the ground.

Key words: epiphytes, herbivory, lichen abundance, lichen decomposition, macrolichens, nutrient cycling

INTRODUCTION

High biomass of epiphytic lichens is a characteristic feature of many old-growth forest ecosystems in temperate and boreal areas. Standing crop of lichens may reach 1–3 tonnes ha⁻¹ d.w. (Boucher & Stone 1992) while litterfall rates up to 320 kg ha⁻¹ yr⁻¹ were reported (Pike 1971, Stevenson 1986). Consequently, where epiphytic lichens are abundant, they may play an important role in the nutrient cycling in forest ecosystems (Pike 1978, Boucher & Nash 1990, Knops *et al.* 1991, 1996, Esseen *et al.* 1996).

Our knowledge about the structure, dynamics and function of epiphytic lichen communities is

relatively limited, partly because of the few available biomass data. Determining epiphyte biomass by direct sampling in the forest canopy is both difficult and time consuming (Boucher & Stone 1992). Most studies have therefore only dealt with a single or a small number of stands. A more rapid method, suitable for large-scale surveys of epiphytes, is to estimate standing crop from the biomass of lichen litter on the forest floor (McCune 1994). The litterfall method has been used in recent studies in both temperate (Peck & McCune 1997) and boreal forests (Dettki & Esseen unpubl.). However, the method has several potential sources of error, for example, litterfall rates vary both within and between years (Esseen 1985,

Boucher & Nash 1990) and decomposition rates may differ among species (e.g., McCune & Daly 1994). Thus, to fully apply the litterfall method we must know both the relationship between epiphyte litter and standing crop, and the longevity of lichen litter on the forest floor.

Annual decomposition of epiphytic macrolichen litter was investigated in temperate forests (Pike 1971, Vogt *et al.* 1983, Guzman *et al.* 1990, McCune & Daly 1994, Knops *et al.* 1996) but only a couple of studies were made in the boreal zone (Taylor & Jones 1990, Biazrov 1994). In the present paper, we describe the pattern of mass loss during one year in litter of foliose and fruticose lichen epiphytes in a boreal Norway spruce (*Picea abies*) forest. For comparison we compiled data from previous studies on epiphytic lichen decomposition.

MATERIAL AND METHODS

Study area

The study was done in Långrumpskog (63°42'N, 19°33'E), a 43 ha large nature reserve located 40 km SW of Umeå, north-eastern Sweden. The site is in the middle boreal zone at an altitude of 100 m above sea level. The terrain is flat and the soil is relatively nutrient poor. The forest consists of mixed conifer stands on dry and mesic soils and swamp forest, dominated by spruce. The stand has a multi-layered canopy and has been unaffected by major disturbances since 1700 AD (Segerström *et al.* 1994). Maximum tree age is 250–300 years. *Picea abies* and *Pinus sylvestris* were about equally abundant in the area where the lichen decomposition experiment was performed. The most important species in the field layer were *Vaccinium myrtillus* and *V. vitis-idaea* with *Deschampsia flexuosa* and *Linnaea borealis* as subdominants. The ground layer was dominated by bryophytes such as *Dicranum* spp., *Hylocomium splendens*, *Pleurozium schreberi*, and *Ptilium crista-castrensis*.

The epiphyte vegetation was dominated by lichens with green-algal photobionts. The most abundant species were fruticose, pendulous (alectorioid) lichens, such as *Alectoria sarmentosa*, *Bryoria capillaris*, *B. fuscescens*, *B. nadvornikiana*, *Usnea filipendula*, and *U. subfloridana*, and ubiquitous foliose species, such as *Hypogymnia physodes*, *H. tubulosa* and *Platismatia glauca*. Lichen nomenclature follows Santesson (1993).

The growing season (average temperature above 3°C) is 173 days. Mean annual temperature is 2.7°C and annual precipitation is 650 mm at a meteorological station 50 km from the study site. During the course of the study, the ground was snow-covered between 15 November 1990 and 15 May 1991.

Methods

We determined mass loss in five lichens commonly occurring in the boreal forests of Fennoscandia. Two were alectorioid: *Alectoria sarmentosa* and *Bryoria fuscescens*, and three were foliose: *Hypogymnia physodes*, *Lobaria pulmonaria* and *Platismatia glauca*. Lichen thalli were collected from branches of *Picea abies* and stems of *Salix caprea* (in the case of *L. pulmonaria*) two weeks before the start of the experiment. The thalli were cleaned of bark fragments and other non-lichen material. One to a few thalli were dried in a desiccator over silica gel for 24 hours, and weighed to the nearest 1 mg. The thalli (total weight 0.3–2.1 g) were then put into litterbags (20×20 cm) made of 1.5 mm nylon mesh, along with a numbered plastic tag. A total of 450 litterbags (90 per species) were distributed at 15 stations along a 420 m transect, with a 30 m distance between the stations, in a part of the reserve with level ground and mesic soil. On 7 November 1990, we had marked a 4 × 4 m² square at each station, and then placed there 30 litterbags (six per species). The litterbags were placed loosely on the bryophyte carpet, which sometimes required clipping of the field layer. One randomly selected litterbag per species was taken from each of the 15 stations on 23 May, 19 July and 13 September 1991. On 31 October, the same year we collected the remaining 225 litterbags for determination of annual mass loss. Samples were carefully cleaned of non-lichen material, such as needles and bryophytes, dried in a desiccator for 24 hr and weighed.

Calculations

The single exponential decay function ($X = e^{-kt}$) was used to estimate the decay constant (k) as preferred by Wieder & Lang (1982). We fitted the function: $\ln(X) = -kt$ by linear regression (using a fixed intercept model), where X was the proportion of initial lichen mass (X_0) remaining at time t (in years), i.e. $X = X_t/X_0$. Half-life ($0.693/k$) and the time required for 95% mass loss ($3/k$) were calculated from the exponential equation following Olson (1963). One-way ANOVA was used to assess differences in annual mass loss between the species. The analysis was made on arcsine transformed data ($\arcsin \sqrt{X}$) following Zar (1984).

RESULTS

All lichen samples lost weight during the course of the study. Small thallus fragments were frequently found below the litterbags, especially in *Hypogymnia physodes*. Most thalli had become dull in colour and particularly the alectorioid species were compressed by the snow pack. *Lobaria pulmonaria* became pale while *Platismatia glauca* turned reddish-brown. Fungal hyphae occurred on

the lower side of many thalli.

The most rapid mass loss occurred during winter and spring (Fig. 1). At the first sampling occasion (23 May 1991), we found that a large proportion of the litterbags of the two alectorioid species had been disturbed by animals during winter. No snow remained at this occasion but the ground was still frozen. The bags had one to three small holes in the mesh (mainly on the underside) and most of the lichen material had been removed. In *Alectoria sarmentosa*, 47% ($n = 90$) of the litterbags bore evidence of animal disturbance as compared to 58% ($n = 90$) in *Bryoria fuscescens*. In May 1991, 97% of the biomass was lost in the disturbed bags of *A. sarmentosa* ($n = 8$) and 88% in *B. fuscescens* ($n = 9$, Fig. 1). After one year, only 1% of the original mass remained in disturbed samples of alectorioid lichens (Table 1). No signs of animal disturbance were observed during subsequent sampling or in any of the foliose species.

Most (ca. 90%) of the mass of alectorioid lichens had disappeared after one year as compared to 42%–61% mass loss in foliose lichens in the litterbags (Table 1). The alectorioid lichens lost weight much faster than the foliose lichens (Fig. 1); 17% and 39%–58% of intact samples remained after one year, respectively (Table 1). Annual mass loss in intact samples differed significantly among species ($F_{4,175} = 102.8$, $P < 0.001$; ANOVA). The species can be divided into three groups that differ in mass loss ($P < 0.05$; Scheffé's multiple range test): (1) *Alectoria sarmentosa* and *Bryoria fuscescens*,

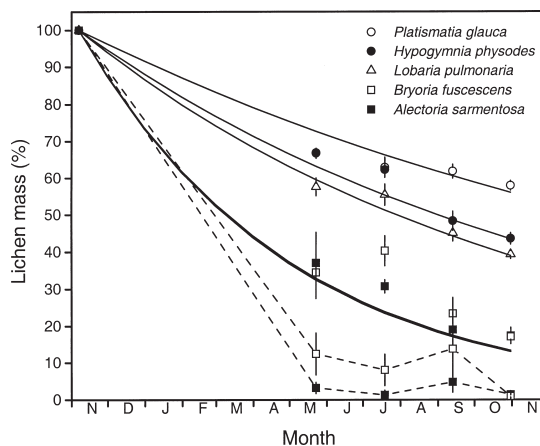


Fig. 1. Mass loss (% of initial mass, $\bar{X} \pm SE$) of five epiphytic lichens in litterbags during one year, from 7 November 1990 to 31 October 1991. Solid lines denote intact samples (curves represent fitted exponential decay functions) and broken lines denote samples disturbed by animals. Number of samples (per species) was 15 in May, July and September and 45 in October.

and (2) *Hypogymnia physodes* and *Lobaria pulmonaria*, and (3) *Platismatia glauca*, in order of decreasing mass loss (Table 1).

The decay constant (k) ranged from 2.08 in *Alectoria sarmentosa* to 0.59 in *Platismatia glauca*. Estimated half-lives of intact samples ranged from 4 months in *Alectoria* and *Bryoria* to 14 months in *Platismatia glauca* (Table 1). The high correlation coefficients indicate that the negative exponential model is suitable for describing the de-

Table 1. Mass remaining in litterbags after one year and decomposition parameters for epiphytic lichen litter. Cases followed by the same letter are not statistically different at $P < 0.05$ (Scheffé's multiple range test on intact litterbags).

Species	Initial mass (g d.w.) $\bar{X} \pm SE$	Percent remaining after one year $\bar{X} \pm SE$	Decay constant k	Correlation r	Half time (years) $0.693/k^1$	95% time (years) $3/k^1$
<i>Alectoria sarmentosa</i>	0.91 \pm 0.04	10.3 \pm 1.7 ($n = 45$)				
Disturbed bags		1.4 \pm 0.7 ($n = 20$)				
Intact bags ^a		17.4 \pm 2.2 ($n = 25$)	2.08	0.88 ($n = 47$)	0.33	1.44
<i>Bryoria fuscescens</i>	1.00 \pm 0.03	8.5 \pm 1.4 ($n = 45$)				
Disturbed bags		0.9 \pm 0.3 ($n = 24$)				
Intact bags ^a		17.1 \pm 1.6 ($n = 21$)	2.06	0.84 ($n = 38$)	0.34	1.46
<i>Lobaria pulmonaria</i> ^b	1.40 \pm 0.05	39.4 \pm 1.1 ($n = 45$)	0.96	0.98 ($n = 90$)	0.72	3.13
<i>Hypogymnia physodes</i> ^b	0.80 \pm 0.02	43.6 \pm 1.8 ($n = 44$)	0.85	0.95 ($n = 89$)	0.81	3.53
<i>Platismatia glauca</i> ^c	1.20 \pm 0.02	58.0 \pm 1.3 ($n = 45$)	0.59	0.96 ($n = 90$)	1.17	5.08

¹⁾ following Olson (1963).

composition of epiphytic lichens in litterbags. The single exponential function assumes that the relative rate of decomposition remains constant over time (Wieder & Lang 1982). This model was less useful for describing the pattern of mass loss in bags disturbed by animals.

DISCUSSION

Factors affecting lichen decomposition

The persistence of lichen litter on the forest floor is influenced by both internal factors, such as the physical and chemical properties of the lichen thallus, and external factors, such as climate, decomposing organisms and site characteristics (Wetmore 1982, Moore 1984, Greenfield 1993, Parinkina *et al.* 1993). Decomposition includes both mechanical breakdown, mainly caused by invertebrates, and chemical decomposition brought about by microbial activity. It is likely that secondary lichen chemicals with antibiotic properties are important in determining the rate of decomposition (Lawrey 1986, Guzman *et al.* 1990), but experimental data are scarce.

The physical structure of the lichen thallus, i.e. thallus anatomy and thallus morphology, strongly affects the rate of lichen decomposition. For example, *Evernia mesomorpha*, a species with a loose medulla, decomposed more rapidly than species with a compact medulla (Wetmore 1982). In the present study we found significantly higher mass loss in alectorioid lichens than in foliose ones. Fruticose lichens, especially alectorioid ones, have much higher surface area to mass ratios than foliose lichens, and consequently, larger area available to attack by decomposer organisms. Alectorioid species are also more easily fragmented than foliose ones, which further accelerates the rate of mass loss. With the exception of *Lobaria pulmonaria*, the sequence of increasing decomposition constants (k) in Table 1 corresponds rather well to increasing surface area to mass ratio, from *Platismatia glauca* to *Alectoria sarmentosa* and *Bryoria fuscescens*.

The higher nitrogen content in *Lobaria pulmonaria* (2.3%–2.8%, Millbank 1982; 2.5%, Solberg 1970) compared to *Hypogymnia physodes* (1.3%, Kubin 1990; 0.8%, Lang *et al.* 1980) and *Platis-*

matia glauca (1%, Lang *et al.* 1980) may possibly explain its relatively high decay rate. According to Crittenden and Kershaw (1978), the high nitrogen content and low C/N ratio in nitrogen-fixing cyanobacterial lichens will result in greater decomposition rates than in non-fixers.

Comparison with previous studies

Lichens decompose at roughly the same rate as other non-lignified plant litter (Pike 1978, Moore 1984) but faster than most tree litter components (Taylor & Jones 1990). It should be noted, however, that litterbags may underestimate actual decomposition as bags exclude large invertebrates and other animals (Biazrov 1994, McCune & Daly 1994). The available data suggest that decomposition rates of terrestrial lichens are lower than in epiphytic species. Reports of annual mass loss in terrestrial lichens range from 5% in *Cladonia stellaris* (Rosswall *et al.* 1975, Moore 1984,) to 33% in *C. portentosa* (Gloaguen *et al.* 1980). This can be compared with an average annual loss of 61% (range 5%–100%) for epiphytic species based on the data compiled in Table 2. Few generalisations can be made about the decomposition of epiphytic lichens because of the limited data available and differences in measurement techniques. However, decomposition appears to be higher in fruticose lichens than in most foliose species (Table 2). Notable exceptions are the slow decay (5%) found for *Ramalina menziesii* in central coastal California (Knops *et al.* 1996), characterised by a dry Mediterranean climate, and the high mass loss (93%) in *Sticta hypochra* (Guzman *et al.* 1990), a species with a cyanobacterial photobiont.

Our data on lichen decomposition in a boreal forest in Sweden are similar to those of McCune and Daly (1994) from a temperate rainforest in Oregon. Both studies found faster mass loss in *Hypogymnia* than in *Platismatia*. The only exception was the slower decomposition of *Alectoria sarmentosa* in litterbags (41% mass loss) found by McCune and Daly (1994). However, the rapid decomposition of alectorioid lichens in our study (83% annual loss in intact samples) is consistent with two other works. Taylor and Jones (1990) reported 71% loss of original mass in a mixture of *Alectoria* spp. and *Usnea* spp. from November

to June in a mature *A. balsamea* stand in boreal Quebec. Similarly, Vogt *et al.* (1983) observed 76% mass loss in *Alectoria* spp. in the first year and almost 100% by the end of the second year in a mature *Abies amabilis* stand in western Washington. Our results confirm the rapid mass loss in lichens under deep snow found in these two studies. We conclude that alectorioid lichen litter has a rapid turnover in forests.

Animal impact

Epiphytic lichens are highly attractive to several animal species. For example, alectorioid lichens, available on standing trees, on treefalls and as litterfall (Edwards *et al.* 1960), constitute preferred food of ungulates such as caribou (Rominger *et al.* 1996), reindeer (Danell *et al.* 1994), and deer (Stevenson & Rochelle 1984). The persistence of lichen litter on the ground may thus be strongly affected by the extent of animal disturbance. Re-

cently, McCune and Daly (1994) reported high mass losses in bare *Alectoria sarmentosa* and other species due to herbivory and that litterbags may significantly reduce losses of lichen material. In our study, even litterbags were not sufficient to prevent animal disturbance. The high mass loss in both *A. sarmentosa* and *Bryoria fuscescens* during winter was remarkable, particularly as abundant litter of the same species was also present at the site. Losses were most probably caused by voles. The holes in the mesh were typical of vole damage and no other animals are active under snow in these forests. The most likely candidate is Bank vole (*Clethrionomys glareolus*). This species regularly consumes epiphytic lichens, and *Alectoria* and *Bryoria* spp. constitute an important part of the diet (28%–54%) at most seasons of the year (Hansson 1979, 1985), especially in old *Picea abies* forests in northern Fennoscandia (Viro & Sulkava 1985). Bank vole has the peculiar habit of storing large quantities of *Bryoria* spp. in tree holes and on branches (Pulliainen & Keränen 1979), particularly during years with high

Table 2. Decomposition of epiphytic lichen litter during the first year (in litterbags).

Species	Photobiont ¹⁾	Mass loss (%) ²⁾	Ecosystem	Source
Fruticose				
<i>Alectoria</i> spp.	G	76	temperate <i>Abies amabilis</i> forest	Vogt <i>et al.</i> (1983)
<i>Alectoria</i> and <i>Usnea</i> spp.	G	71 ³⁾	boreal <i>Abies balsamea</i> forest	Taylor & Jones (1990)
<i>Alectoria sarmentosa</i>	G	41 (100)	temperate <i>Pseudotsuga menziesii</i> rainforest	McCune & Daly (1994)
<i>Alectoria sarmentosa</i>	G	83	boreal <i>Picea abies</i> forest	this study
<i>Bryoria fuscescens</i>	G	83	"	"
<i>Ramalina menziesii</i>	G	5	temperate <i>Quercus douglasii</i> woodland	Knops <i>et al.</i> (1996)
<i>Ramalina menziesii</i>	G	80 ⁴⁾	temperate oak-ash forest	Pike (1971)
<i>Usnea subfloridana</i>	G	100 ⁴⁾	"	"
Foliose				
<i>Hypogymnia inactiva</i>	G	41 (97)	temperate <i>Pseudotsuga menziesii</i> rainforest	McCune & Daly (1994)
<i>Hypogymnia physodes</i>	G	56	boreal <i>Picea abies</i> forest	this study
<i>Hypogymnia physodes</i>	G	39 ⁵⁾	hemiboreal <i>Tilia-Picea</i> forest	Biazrov (1994)
<i>Hypogymnia physodes</i>	G	67 ⁵⁾	"	"
<i>Platismatia glauca</i>	G	23 (87)	temperate <i>Pseudotsuga menziesii</i> rainforest	McCune & Daly (1994)
<i>Platismatia glauca</i>	G	42	boreal <i>Picea abies</i> forest	this study
<i>Lobaria oregana</i>	G + CB	43 (67)	temperate <i>Pseudotsuga menziesii</i> rainforest	McCune & Daly (1994)
<i>Lobaria pulmonaria</i>	G + CB	61	boreal <i>Picea abies</i> forest	this study
<i>Lobaria pulmonaria</i>	G + CB	81 ⁴⁾	temperate oak-ash forest	Pike (1971)
<i>Pseudocyphellaria berberina</i>	G	77	temperate <i>Nothofagus</i> rainforest	Guzman <i>et al.</i> (1990)
<i>Pseudocyphellaria divulsa</i>	G	43	"	"
<i>Pseudocyphellaria glabra</i>	G	46	"	"
<i>Pseudocyphellaria nitida</i>	G	88	"	"
<i>Sticta hypochra</i>	CB	93	"	"

¹⁾ G = green algae, CB = cyanobacteria; ²⁾ bare samples in parenthesis; ³⁾ in 217 days; ⁴⁾ estimated from Pike (1971): fig. 31; ⁵⁾ in 190 days.

vole population density. A single store may consist of several hundred lichen balls, each with a dry weight of 0.1–0.3 g (Pulliainen & Keränen 1979). Voles show regular population fluctuations in boreal Fennoscandia with a pronounced three- to four-year periodicity and in 1990–91 there was a peak in population density in our study area (B. Hörnfelt pers. comm). Therefore, the losses of lichen material due to animal disturbance were probably exceptionally high in this study.

CONCLUSIONS

In conclusion, both growth form and extent of animal disturbance are important for the persistence of epiphyte lichen litter on the forest floor. Differences in mass loss rate among lichen species must be taken into account to reduce bias in estimates of lichen biomass in the canopy based on lichen litter. For example, our data suggest that the abundance of alectoroid lichens will be considerably underestimated if the rapid decay of these lichens is ignored. Some of the bias can be removed by using the decay constants presented in this paper. However, lichen decomposition may differ considerably among sites and between years. Further, removal of lichen material by animals is often unpredictable and may still lead to inexact and biased estimates. Despite the limitations of the litterfall method, as discussed in detail by McCune (1994) and Peck and McCune (1997), the method is often the only viable alternative for estimating epiphyte biomass in a large number of stands. The litterfall method is best suited for comparative studies in cases where large differences in lichen biomass are expected, such as between young and old-growth forests.

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