

Decomposition of hair lichens (*Alectoria sarmentosa* and *Bryoria* spp.) under snowpack in montane forest, Cariboo Mountains, British Columbia

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Abstract: Montane old-growth forests on the windward slopes of interior mountain ranges in British Columbia support high loadings of arboreal lichens. These lichens represent a major source of readily labile plant material and potentially play an important role in ecosystem nutrient dynamics. Given the role of winter storms in scouring lichens from within the canopy and the extended length of winter snowpack, from November through to May or even early June, in these ecosystems, the decomposition of lichen litterfall should be heavily influenced by placement within the snowpack. We have examined this factor by placing litter bags containing samples of the hair lichens, *Alectoria sarmentosa* and *Bryoria* spp., on top of the winter snowpack in the Cariboo Mountains. Samples were set out in early- (8 Nov.) mid- (16 Jan.) and late- (22 Mar.) winter and subsequently retrieved on spring snow-melt (22 May). Lichen samples that were buried in the lower snowpack all winter long (196 days) lost two-thirds of their original mass. In contrast lichens placed on the snowpack in mid- (127 days) or late-winter (61 days) lost only 6–15% of their total mass, far less than would be predicted on the basis of time in snowpack alone. Spot measurements showed that the snowpack environment effectively buffers litter samples from extreme winter conditions. All lichen samples placed within the snowpack showed much higher C/N ratios on removal, indicating rapid leaching of readily soluble cellular constituents in the snowpack environment. These findings indicate that the snowpack environment plays a major role in decomposition processes in these high-elevation forests and reinforces our view that lichens are a readily labile nutrient source within these ecosystems.

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Introduction

Lichens form an important component of high elevation forested ecosystems in north-central British Columbia, with canopy lichen loading reaching 400 kg ha⁻¹ (Campbell & Coxson 2001). Lichens of the genus *Alectoria* and *Bryoria*, in particular, are major constituents within the canopy, where they provide important forage values for ungulate populations such as mountain caribou (Edwards & Ritcey 1960; Rominger *et al.* 1996). Although previous research has

examined ecological attributes of *Alectoria* and *Bryoria* (Esseen 1985; Stevenson 1985; Goward, 1998), our knowledge of decomposition dynamics of lichen litterfall is more limited (Wetmore 1982; Guzman *et al.* 1990; Greenfield 1993; McCune & Daly 1994).

Rates of lichen litter fall from within the canopy vary annually and seasonally, with highest rates typically observed during the fall and winter period (Esseen 1985; Grier 1988). The significance of wintertime decomposition of various litter types has been well documented (Bleak 1970; McBrayer & Cromack 1980; Moore 1983; Coxson & Parkinson 1985; Bird *et al.* 1987; Taylor & Jones 1990), where it has been

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found that decomposition during the winter period can account for a considerable portion of annual mass loss (Moore 1984; Esseen 1985; Esseen & Renhorn 1998; Taylor & Jones 1990).

Although these studies provide evidence that litterfall decomposition under snow does occur, they are less conclusive with regard to the rate at which lichen litter may decompose during the winter period. Most decomposition studies measuring overwinter mass loss place litter samples on the forest floor surface at the end of the fall period, subsequently retrieving subsamples at regular intervals in order to follow decomposition processes. This methodology provides a realistic estimation of decomposition rates in ecosystems where litterfall is concentrated in one major pulse at the end of the growing season. Lichen litterfall, on the other hand, accumulates on the snow surface throughout the winter period, with repeated pulses deposited during successive storm events. This pattern of litter accumulation results in differential placement of litterfall within the snowpack, with each horizon of buried lichen litter potentially experiencing a different sequence of temperature and wetting events.

In order to understand the effect of this temporal and spatial separation of lichen litterfall within the snowpack, we have placed litter-bag samples on top of the winter snowpack during three separate periods (early-winter, mid-winter and late-winter), mimicking natural litter loading processes. Rates of decomposition and changes in nutrient composition were subsequently examined on retrieval of litter-bag samples at the time of spring snowmelt. This experimental design provides a closer approximation to natural processes of lichen litterfall during the winter period, allowing for a more detailed assessment of decomposition rates within the snowpack environment.

Methods

The study was conducted in an area of old-growth forest adjacent to the Purden Mountain Ski Resort

(122°54'W, 53°54'N), located approximately 65 km east of Prince George, British Columbia. This region, transitional between the Interior Cedar-Hemlock (ICH) and Engelmann Spruce-Subalpine Fir (ESSF) biogeoclimatic zones, is characterized by relatively cold, moist winters and short cool growing seasons, with mean annual temperature ranging from -2 to $+2^{\circ}\text{C}$ and precipitation up to 2200 mm (Meidinger & Pojar 1991). The climax tree species are *Picea engelmannii* (Engelmann Spruce) and *Thuja plicata* (Western Red-cedar) and the shrub layer is dominated by *Oplopanax horridus* (devil's club). The study area where the samples were placed was at 1167 m in elevation and has a northeast aspect. This site was chosen because it is a high elevation ecosystem known to maintain abundant lichen communities, receives a high amount of snow fall (50–70% of total precipitation; Meidinger & Pojar 1991) and is easily accessible by road during winter.

Live branches bearing the arboreal lichen species *Alectoria sarmentosa* and *Bryoria* spp. (predominantly *B. pseudofuscescens*, but including *B. capillaris*, *B. fremontii*, *B. fuscescens*, and *B. glabra*) were collected from the canopy of adjacent forest stands. Collections were made in early October, after snowfall had begun, but before a permanent snow cover had been established. Lichens were removed from branches or twigs, separated by genus (*Alectoria sarmentosa* or *Bryoria* spp.) and oven dried in paper bags at 65°C for 24 h. As weighed lichen mass can change in response to fluctuations in atmospheric humidity (McCune *et al.* 1996) lichens were placed over Drierite for a minimum of 5 h after they were removed from the oven, allowing the thalli to cool and equilibrate before being weighed. Samples of between 1–3 g in weight were subsequently placed in 10×19 cm 1 mm^2 nylon mesh litter bags.

Natural litterfall loading was mimicked by placing litter bags on top of the snowpack at three different times during the winter period: on 8 November 1999, 16 January and 22 March 2000, representing early-winter, mid-winter and late-winter litterfall respectively. The snow depth at time of placement is listed in Table 1. On each placement date, a total of twenty replicate litter bags of each species in total were placed in canopy gaps (to avoid the drip zone of tree canopies). These bags were divided into groups of four, each group placed within a separate canopy gap. Placement locations were marked with bamboo stakes. Ten additional litter bags of each species were brought to the field on 8 November and then returned to the lab where they were stored until all bags were recovered from the field. These samples served as controls to determine mass loss due to sample handling. All of the litter bags were collected on 22 May, on snow melt at this site.

From January to April snow depth and ambient temperatures were measured once a month during the mid-day period, recording the snow temperature profile at 10 cm increments. Snowfall accumulation and air temperature data were also obtained from the adjacent Purden Mountain Ski Resort for the period of December to early April.

TABLE 1. Monthly temperature and snow measurements at study site during winter period at Purden Mountain

| Month | Mean monthly air temperature (°C)* | Field sampling dates | Air temperature (°C)‡ | Snowpack temperature (°C)§ | Snow depth (cm) | |
|----------|------------------------------------|----------------------|-----------------------|----------------------------|-----------------|-------------|
| | | | | | Canopy gaps | Open field* |
| November | na | Nov. 8 | 4.5 | na | 5 | na |
| December | -2.6 | na | na | na | na | 70 |
| January | -8.3 | Jan. 16 | -16.5 | -4.2 | 56 | 132 |
| February | -8.8 | Feb. 21 | 1.4 | 0.5 | 52 | 138 |
| March | na | Mar. 22 | 0 | -0.1 | 53 | na |
| April | na | Apr. 19 | 5.9 | 0.9 | 40 | na |
| May | na | May. 22 | 7 | na | 0 | na |

*From climate station at Purden Mtn ski area.

‡Air temperature at 1 m above snowpack at noon on indicated field sampling dates.

§Snowpack temperature at base of snowpack at noon on field sampling dates.

Following collection of litter bag samples, the enclosed lichen material was oven dried for 24 h at 65°C, subsequently placed over Drierite for 24 h, followed by weighing on an electronic balance. Mass loss during the field incubation periods was calculated by comparison of initial and final masses. Decomposition rates during each of the winter periods was derived by taking the difference between overall mass loss (full winter period) and mass loss during mid- and late-winter periods.

Total carbon and nitrogen content of retrieved lichen litter was measured using a Fisons NA1500 NC elemental analyser, based on assays of dried samples that had been previously ground in a mortar and pestle.

Paired *t*-tests (Bonferonni method) were used to compare initial and final masses to determine if significant mass loss had occurred, based on a significance level of $P < 0.05$, and to compare mass loss between *Alectoria* and *Bryoria* samples. A three-way ANOVA Tukey HSD test was carried out to determine the significance of mass loss between early-mid- and late-winter litterfall samples.

Results

Snowpack accumulation at the Purden Mountain site commenced in mid-November, reaching a maximum depth of 55 cm on the forest floor (1.4 m in adjacent open sites) during January and February, with final snowmelt under the forest canopy not occurring until late May (Table 1). Spot measurements of temperature profiles showed a rapid attenuation of air temperatures within the snowpack environment under mid-winter conditions, with conditions at the base of the snowpack up to

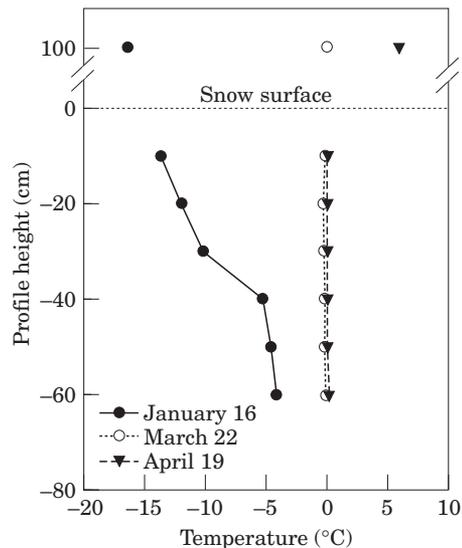


FIG. 1. Temperature profile in snowpack under canopy at Purden Mountain, British Columbia, on 16 January, 22 March, and 19 April 2000.

15°C warmer than air temperature. By late winter snowpack conditions were basically isothermal, near to 0°C at all depths (Fig. 1).

Significant mass loss occurred in both *Alectoria* and *Bryoria* during each of the three decomposition treatment periods (*t*-test $P < 0.001$, $\alpha = 0.05$) (Table 2). Percent mass loss increased with the time the bags were buried in the snow, ranging from 65% for litter bag samples held under snowpack all

TABLE 2. Mean percent mass loss in lichen litterfall samples* placed on winter snowpack in early-winter (Nov. 8), mid-winter (Jan. 16), and late-winter (Mar. 22). Litterfall samples were removed on snowmelt (May 22)

| Species | Litterfall placement period (number of days in field) | | | | | | | | | | | |
|------------------|---|-----|----------|--------------------|-----|----------|------------------|-----|----------|------------------|-----|----------|
| | Control (0) | | | Early-winter (196) | | | Mid-winter (127) | | | Late-winter (61) | | |
| | Mean | SE | <i>n</i> | Mean | SE | <i>n</i> | Mean | SE | <i>n</i> | Mean | SE | <i>n</i> |
| <i>Alectoria</i> | 1 | 0.9 | 10 | 66.8 | 7.1 | 20 | 8.6 | 1.9 | 20 | 6.8 | 1.4 | 20 |
| <i>Bryoria</i> | 0.3 | 0.1 | 10 | 65.2 | 9.6 | 20 | 14.9 | 3.2 | 19 | 12.8 | 2.2 | 20 |

*Mean, standard error (SE) and sample size (*n*) are provided for each sample set.

winter long, to only 6–15% for samples that were placed on mid- and late-winter snowpack. Early-winter litterfall samples had a significantly higher mass loss than did mid-winter and late-winter litterfall samples (ANOVA $P < 0.001$, $\alpha = 0.05$). There were no significant differences in mass loss between samples placed in snowpack in the mid-winter versus late-winter period (ANOVA $P > 0.1$). Mass losses of the two hair lichen species were similar for samples that were buried under snow all winter. Mass loss of *Bryoria* was slightly greater in samples placed on snowpack in mid- to late-winter, however, these differences were not significant (*t*-test $P > 0.1$). Mass loss attributed to handling was small, less than 1.5%.

Partitioning of the rates of mass loss for each of the winter periods show much higher decomposition rates in early-winter, compared to mid- or late-winter measurements (Fig. 2). Mass loss from the early-winter sample set was significantly greater than either of the mid- or late-winter sample sets ($P < 0.001$), which were not significantly different, one from another ($P > 0.1$).

A major result of placing lichen litter-bag samples under the snowpack was the decline in total nitrogen content, falling by near half in both *Alectoria* and *Bryoria* (Table 3). Percent carbon content, on the other hand, was relatively unchanged, compared to control samples, resulting in higher carbon/nitrogen ratios in lichen samples from under the snowpack.

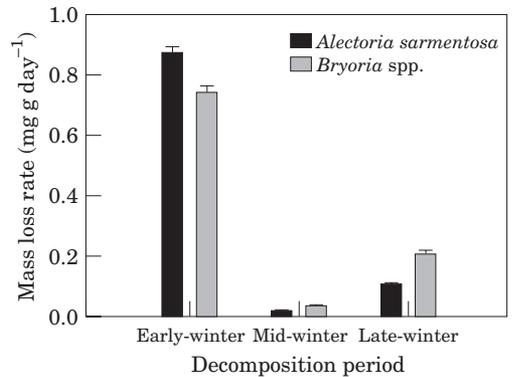


FIG. 2. Mass loss rate (mg g day^{-1}) of lichen litterfall (*Alectoria sarmentosa* and *Bryoria* spp.), isolated for the periods of early- (8 Nov. to 15 Jan.), mid- (15 Jan. to 21 Mar.), and late-winter (22 Mar. to 22 May). One standard error is denoted by bars.

Discussion

In northern ecosystems where nutrient availability is limited, litterfall decomposition is a fundamental component of nutrient cycling, soil formation and ecosystem productivity (Lousier & Parkinson 1976; Pike 1978; Moore 1983; Harmon *et al.* 1990; Taylor *et al.* 1991). Although arboreal lichens represent a small component of standing biomass in most forested ecosystems, their relatively labile nature, combined with high rates of annual turnover, and for some species, the capacity to fix atmospheric nitrogen, places a disproportionate importance on their ecosystem contribution

TABLE 3. Changes in mean percent carbon* and nitrogen content* in lichen litterfall samples placed on winter snowpack in early-winter (Nov. 8), mid-winter (Jan. 16), and late-winter (Mar. 22). Litterfall samples were removed on snowmelt (May 22)

| Species | Litterfall placement time (number of days in field) | | | | | | | | | | | |
|------------------|---|------|----------|--------------------|------|----------|------------------|------|----------|------------------|------|----------|
| | Control (0) | | | Early-winter (196) | | | Mid-winter (127) | | | Late-winter (61) | | |
| | Mean | SE | <i>n</i> | Mean | SE | <i>n</i> | Mean | SE | <i>n</i> | Mean | SE | <i>n</i> |
| % Nitrogen | | | | | | | | | | | | |
| <i>Alectoria</i> | 0.57 | 0.02 | 13 | 0.33 | 0.03 | 20 | 0.33 | 0.01 | 20 | 0.30 | 0.01 | 20 |
| <i>Bryoria</i> | 1 | 0.08 | 11 | 0.66 | 0.10 | 15 | 0.61 | 0.02 | 17 | 0.60 | 0.02 | 20 |
| % Carbon | | | | | | | | | | | | |
| <i>Alectoria</i> | 44.43 | 0.26 | 13 | 45.96 | 0.22 | 20 | 44.14 | 0.13 | 20 | 44.35 | 0.12 | 20 |
| <i>Bryoria</i> | 43.46 | 0.22 | 11 | 44.1 | 0.22 | 15 | 42.59 | 0.17 | 17 | 43.15 | 0.13 | 20 |
| C/N ratio | | | | | | | | | | | | |
| <i>Alectoria</i> | 78.4 | | | 139.9 | | | 132.5 | | | 147.3 | | |
| <i>Bryoria</i> | 43.4 | | | 66.7 | | | 70.0 | | | 72.3 | | |

*Mean, standard error (SE) and sample size (*n*) are provided for each sample set.

(Pike 1978; Lang *et al.* 1980; Nadkarni 1984).

Rates of lichen litterfall in north temperate ecosystems exhibit distinct annual and seasonal variation, with higher rates typically observed during the winter period, as a result of storms and ice accumulation (Esseen 1985; Grier 1988; Waterhouse *et al.* 1991). In particular, during the fall and winter period storms can dislodge and disperse large quantities of lichen material (Stevenson & Rochelle 1982; Esseen 1985; Grier 1988). In addition, freezing rain or wet snow can cover tree branches in amounts great enough to cause breakage (Grier 1988). Thus, lichen litter loading at the forest floor surface, may be quite episodic, with significant deposition of organic matter on snowpack surfaces.

The morphological characteristics of arboreal lichens, commonly highly branched with fragile thallus threads, contribute to their fragmentation (Esseen 1985; Stevenson 1985), and provide both mechanisms for dispersal and ecological inputs through litterfall. Esseen (1985) measured the amount of lichen litterfall in mature spruce stands in Sweden, reporting annual lichen litterfall for *Alectoria sarmentosa* and

Bryoria spp. of 14.3 and 10.4 kg ha⁻¹ respectively (Site A). Waterhouse *et al.* (1991) reported 2–20 kg ha⁻¹ month⁻¹ lichen litterfall in even-aged stands of Douglas fir in central interior of British Columbia. In an old-growth forest on Vancouver Island, Stevenson (1985) reported higher litterfall rates for *Alectoria* and *Bryoria* ranging from 10.5–16.1% of the total standing crop. Specifically, *Alectoria* winter litterfall measured by Stevenson & Rochelle (1984) on Vancouver Island, British Columbia, ranged from 2–151 kg ha⁻¹ over 180 winter days.

Given that decomposition is highly temperature dependent, it might be expected that litter trapped in snowpack would remain relatively immobilized, awaiting spring melt before significant decomposition could occur. However, many studies have reported that significant litter decomposition does occur under winter snowpack (Bleak 1970; McBrayer & Cromack 1980; Moore 1984; Taylor & Jones 1990). In particular, it has been suggested that wintertime decomposition can account for 60–90% of the annual mass loss and is therefore an important ecological process (Moore 1984; Taylor & Jones 1990). In a subalpine balsam fir forest

in Quebec, Taylor & Jones (1990) traced the decomposition of birch leaves, fir needles and fruticose lichen species (*Alectoria* spp. and *Usnea* spp.) exclusively through the winter period (November–May) and reported 10%, 13% and 70% mass losses respectively after 183 days in the field. Esseen & Renhorn (1998) found that nearly 40% of the original mass of the lichens *Alectoria sarmentosa* and *Bryoria fuscescens* (undisturbed samples) was lost during the winter and early spring period, for samples placed out in litterfall bags in early November and collected in late-May.

Our findings confirm these previous suggestions that rapid mass loss can occur under snow, with lichen samples losing up to two-thirds of their mass when placed on early-winter snowpack. The partitioning of our decomposition rates suggest that decomposition during the early winter period exceeds that of late winter conditions, even though lichens falling on late winter snowpack experience near isothermal snowpack conditions, with a melt-water slurry present between ice-crystals in the snowpack. This may reflect the importance of early-winter freeze-thaw periods, with diurnal freeze-thaw cycles observed on over 70% of all early-winter days (Campbell & Coxson 2001), in destroying cellular integrity. McBrayer & Cromack (1980) suggest that freeze-thaw cycles during the winter period are a major explanation for wintertime litterfall decomposition. Additionally, melt-water flushing experienced in spring-time by lichens in lower snow-pack positions (i.e. the early-winter litterfall cohort) should accelerate subsequent decomposition of these thalli (previously exposed to early-winter freeze-thaw events). During the mid-winter period, low temperatures are probably the most important limitation on decomposition activity.

Microbial activity within a snowpack is facilitated by the thermal properties of snow. An undisturbed snowpack acts as an effective insulator, buffering the soil from extreme air temperature fluctuations (McBrayer & Cromack 1980; Coxson & Parkinson 1987; Taylor & Jones 1990). During melt con-

ditions, ice crystals can be surrounded by a melt-water slurry, providing a favourable medium for bacterial and fungal growth (Witkamp 1963; McBrayer & Cromack 1980). Although this study provides only spot measurements from the snowpack environment, our results confirm previous findings on the insulative properties of snow. Our study site showed a long period in mid- to late-spring where the snowpack was relatively isothermal, near 0°C. This is consistent with the lag phase between the period of snow accumulation and the melt period in these sub-alpine environments, where snowpack melt can extend well into late May or early June, under steadily lengthening days (Campbell & Coxson 2001).

During periods of daily freeze-thaw cycles, water leaching from within the snowpack may remove large quantities of soluble materials (Bleak 1970). This can be expressed as an increase in carbon/nitrogen ratios in litterfall, as nitrogen rich cellular constituents (e.g. N-amino acids) are leached, leaving behind recalcitrant carbon skeletons. In this study, each of the sample sets showed a similar pattern of reduced nitrogen content, suggesting that leaching losses occur relatively soon after placement, as soon as mass transport of water through the snowpack was available.

The finely-branched morphology of the hair lichens may also play a role in facilitating this rapid leaching of cellular constituents. Moore (1984) reported 12–32% mass losses over two years for *Cladina stellaris*, a terrestrial lichen, compared to 70% mass losses over 183 days for fruticose mixed lichen species (*Alectoria* spp. and *Usnea* spp.) reported by Taylor & Jones (1989) and 67% mass losses observed in this study. Their findings and the results of this study suggest that the average mass losses are higher for the finely branched arboreal lichens than for more robust terrestrial lichens (Moore 1983; Taylor & Jones 1990).

The differential rates of lichen mass loss observed in this study indicate that the time period in which the lichen litter reaches the snow surface and subsequent placement of litterfall within the snowpack plays an

important role in determining decomposition rates. This confirms **McBrayer & Cromack's (1980)** conclusion that winter-time decomposition rates are not constant throughout the winter period.

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