Litterfall, growth, and turnover of arboreal lichens after partial cutting in an Engelmann spruce – subalpine fir forest in north-central British Columbia

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Abstract: Dynamics of canopy lichens were investigated for 2 years after group and single-tree selection harvesting in a *Picea engelmannii* Parry ex Engelm. – *Abies lasiocarpa* (Hook.) Nutt. forest in north-central British Columbia. Litterfall was collected in 1-m^2 traps set on the forest floor and estimates of *Alectoria sarmentosa* (Ach.) Ach. and *Bryoria* spp. litterfall adjusted for decomposition in the snowpack. Growth rates of *A. sarmentosa* and *Bryoria fuscescens* (Gyeln.) Brodo & D. Hawksworth were measured by repeatedly weighing samples maintained in mesh enclosures in the canopy. Standing crop of canopy lichens was measured in concurrent studies. There appeared to be a small postharvest pulse of litterfall in the single-tree selection area, but it was largely masked by natural variation. Ninety percent of the lichen litterfall was deposited within 10 m of the nearest tree. Annual relative growth rates of *A. sarmentosa* and *B. fuscescens* ranged from 2.7% to 10.4% and from 2.4% to 9.1%, respectively. Growth rates of both species were as high in the single-tree selection area as in the unlogged control area but were reduced along the edges of group selection openings. Growth and turnover (annual litterfall as a percentage of standing crop) of *Alectoria* were approximately in balance, but growth of *Bryoria* exceeded turnover. In situ decomposition of *Bryoria* may account for the difference.

Résumé : La dynamique des lichens de la canopée a été étudiée pendant 2 ans après une coupe de jardinage par arbre ou par groupe d'arbres dans une forêt de *Picea engelmannii* Parry ex Engelm. et *Abies lasiocarpa* (Hook.) Nutt. située dans le centre nord de la Colombie-Britannique. La chute de litière a été collectée dans des trappes de 1 m^2 installées sur la couverture morte et des estimations de chute de litière de *Alectoria sarmentosa* (Ach.) Ach. et de *Bryoria* spp. ont été ajustées pour tenir compte de la décomposition dans le couvert de neige. Les taux de croissance de *A. sarmentosa* et de *Bryoria fuscescens* (Gyeln.) Brodo & D. Hawksworth ont été mesurés à plusieurs reprises en pesant des échantillons conservés dans des filets dans la canopée. La biomasse de lichens dans la canopée a été mesurée dans des études parallèles. Il semble y avoir eu une faible augmentation de chute de litière après la récolte dans la zone de jardinage par arbre, mais elle était masquée en grande partie par les variations naturelles. Quatre-vingt dix pour cent de la chute de litière de lichens était déposée à moins de 10 m de l'arbre le plus près. Les taux annuels relatifs de croissance de *A. sarmentosa* et de *B. fuscescens* variaient respectivement de 2,7 à 10,4% et de 2,4 à 9,1%. Les taux de croissance des deux espèces étaient aussi élevés dans la zone de jardinage par arbre que dans la zone témoin non coupée mais étaient plus faibles en bordure des ouvertures dans la zone de jardinage par groupe. La croissance et le recyclage (la chute annuelle de litière exprimée en pourcentage de la biomasse) étaient approximativement en équilibre mais la croissance de *Bryoria* excédait le recyclage. La décomposition in situ de *Bryoria* pourrait expliquer la différence.

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Introduction

Epiphytic lichens are a substantial component of the nonwoody biomass in some forest ecosystems and contribute significantly to canopy nutrient capital and turnover (Pike

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1978; Boucher and Stone 1992; Rhoades 1995). Some mammals, such as woodland caribou (*Rangifer tarandus caribou*) (Edwards and Ritcey 1960; Rominger et al. 1996; Terry et al. 2000) and flying squirrel (*Glaucomys sabrinus*) (Maser et al. 1985; Zabel and Waters 1997), are consistently dependent on this reservoir of energy and nutrients in parts of their range. Others, including black-tailed deer (*Odocoileus hemionus columbianus*), white-tailed deer (*Odocoileus virginianus)*, and mule deer (*Odocoileus hemionus hemionus*), use arboreal lichens intermittently, especially when snow conditions reduce the availability of vascular forage plants (Stevenson and Rochelle 1984; Hodgman and Bowyer 1985; Waterhouse et al. 1991).

Because high biomass of arboreal lichens tends to be associated with old forests, concerns have been raised about the impact of forest harvesting on the diversity, abundance,

and functioning of lichen communities, and researchers have begun to investigate forestry practices that might contribute to the conservation of canopy lichen communities (e.g., Peck and McCune 1997; Sillett and Goslin 1999). In British Columbia, guidelines have been developed for the use of partial cutting systems to maintain arboreal lichen production for mule deer (Armleder et al. 1986) and for mountain caribou (Stevenson et al. 1994, 2001).

Despite the importance of epiphytic lichens in ecosystem functioning, their rates of production and loss are not well known in either natural or managed forests. Even less well known are turnover rates of epiphytic lichens: measurements of the gain or loss of biomass in relation to standing crop during a given time period. In those rare situations in which rates of growth, rates of loss, and standing crop are all known, it is possible to evaluate whether the system is in a steady state.

Most often, turnover rates of epiphytic lichens have been estimated in mature forests, and researchers have assumed a steady state. If gains are assumed to equal losses, then data on either production or losses may be used to estimate turnover. For example, Pike (1978) estimated arboreal lichen biomass, production, and nutrient capital in four forest ecosystems. Different methods, including sequential photography (Rhoades 1977), measurements of epiphyte production on twigs of known ages (Pike 1971), biomass accumulation and litterfall in a chronosequence of stands (Lang et al. 1980), and estimated losses through treefall and litterfall (Edwards et al. 1960), were used to estimate production in different stands. Annual turnover rates calculated by Pike (1978) ranged from 6.6% for a spruce–fir forest dominated by *Alectoria sarmentosa* to 28.8% for a Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) forest in which *Lobaria oregana* was the predominant lichen.

A steady state cannot be assumed in managed stands, as basic ecological parameters such as lichen growth rates, litterfall rates, and standing crop may each be affected differently by forest management practices. An understanding of changes in the ecological parameters that constitute turnover will enhance our ability to predict future lichen availability in managed stands.

Given the difficulty in obtaining data on biomass and production of epiphytic lichens, it is not surprising that the responses of epiphytes to attempts to conserve them through special management practices are not yet well understood. Effects of partial cutting on epiphyte biomass have been studied in Sweden (Esseen et al. 1996) and western North America (Rominger et al. 1994; Stevenson 2001; Coxson et al. 2003). Jull et al. (1999) and Quesnel and Waters (2000) have measured lichen litterfall in small harvest openings in western redcedar (*Thuja plicata* Donn ex D. Don) – western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) stands managed to maintain winter range for mountain caribou. Most of these studies have focused on the effects of partial cutting on a single aspect of lichen ecology. None has included a combination of measurements that would allow estimation of epiphyte turnover rates and how they are affected by partial cutting.

Evaluating the impact of forestry practices on canopy lichen communities also requires an appreciation of the fine-scale mosaic (on the order of metres) within which lichens and bryophytes respond to environmental variability (Campbell and Coxson 2001; Fenton et al. 2003). Thus, while the application of forestry practices may appear to be homogeneous at the stand level, arboreal lichens on a given branch within a tree canopy may experience a range of disturbance severities, as direct (e.g., physical removal during logging) and indirect (e.g., microclimatic changes) disturbance factors interact with canopy structural variables. As documented by Fenton et al. (2003) for forest floor bryophyte communities, we cannot assume that small patch community distribution of nonvascular plants will be uniform before harvesting within a given stand or treatment or that each patch will experience the same suite of disturbance impacts. We have therefore adopted an experimental approach of establishing sample plots on individual trees that are statistically independent and far enough apart to be ecologically independent, within harvest treatments. Establishing individual-tree sample plots as the basic unit of replication provides greater accuracy in determining changes in lichen community response (Lindenmayer 1999) at a scale appropriate to the study of canopy lichens.

Partial-cut harvesting in 1998 at the Pinkerton Mountain silvicultural systems site, the first in a replicated set of silvicultural systems trials in north-central British Columbia (Jull et al. 2001), provided the opportunity to evaluate postharvest changes in canopy lichen dynamics, including lichen growth rates, rates of lichen litterfall, and changes in standing biomass (the latter measurements from Coxson et al. 2003). Target lichen groups assessed included *Alectoria*, *Bryoria*, and foliose lichens. We addressed three major questions. (*i*) What were the short-term effects of partial cutting on litterfall at Pinkerton Mountain? Specifically, we expected that litterfall would be greater in the winter immediately after logging than in the subsequent winter in the partial cuts but not in the control area. (*ii*) Were the growth rates of the lichens affected by increased exposure after partial cutting at Pinkerton Mountain? We expected that the growth rates of *Alectoria sarmentosa* (Ach.) Ach., but not *Bryoria* spp., would be adversely affected by increased exposure. (*iii*) What were the turnover rates (litterfall as a proportion of standing crop) of arboreal lichens at Pinkerton Mountain? An advantage of taking multiple measures of canopy lichen dynamics was that we could assess whether turnover and growth rates were in balance in the unlogged and single-tree selection portions of the study area. These intensive measurements allow an initial assessment of the efficacy of partial cutting in maintaining canopy lichen communities within the study area and will set a baseline for comparative measures as other replicate sites are developed within this set of silvicultural systems trials.

Materials and methods

Study area

The study area (53°37′38″N, 121°25′33″W) is located in the Cariboo Mountains approximately 90 km east-southeast of Prince George, British Columbia (Fig. 1), in the wet cold subzone of the Engelmann Spruce – Subalpine Fir Zone (Meidinger and Pojar 1991). Mean annual precipitation in this subzone is 1408 mm, of which approximately 56% falls as snow (DeLong et al. 1994).

Fig. 1. Location of the Pinkerton Mountain study area and layout of the harvest block.
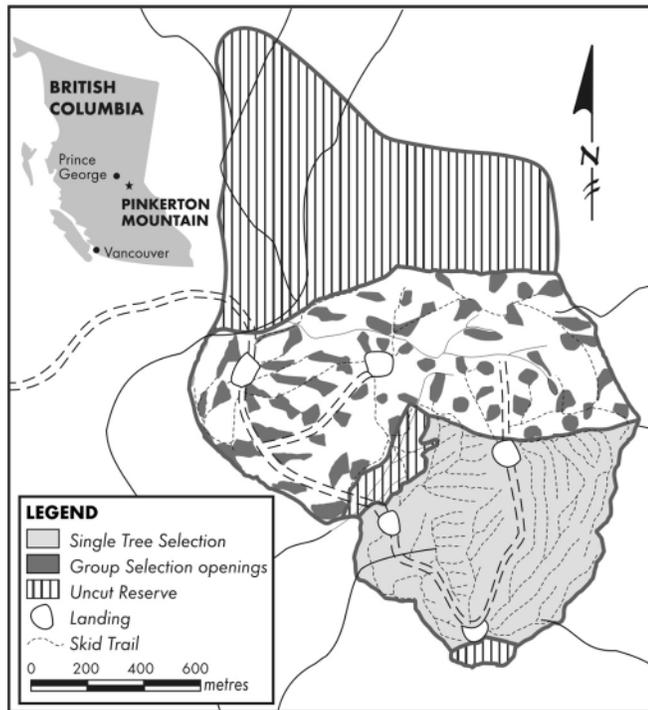
The mesic to subhygric site is on a moderate, southwest-facing slope between 1350 and 1475 m elevation. The lichen studies were concentrated in a level, relatively homogeneous portion of the study area at about 1450–1475 m. Vegetation in the shrub layer is dominated by *Rhododendron albiflorum* (white-flowered rhododendron), while *Valeriana sitchensis* (sitka valerian), *Veratrum viride* (Indian hellebore), *Rubus pedatus* (five-leafed bramble), and *Gymnocarpium dryopteris* (oak fern) are the most common herbs. The epiphyte community is dominated by *Bryoria* spp., which are most abundant in the middle and upper canopy, *A. sarmentosa*, mainly in the lower and middle canopy, and foliose species such as *Hypogymnia* spp., *Parmelia sulcata*, and *Platismatia glauca*, which are distributed throughout the canopy profile. Preharvest distribution and abundance of these groups were similar throughout the study area (Coxson et al. 2003).

The preharvest stand was uneven aged, with trees up to approximately 350 years old. The trees were unevenly distributed and much of the stand was composed of clumps of trees with overlapping crowns separated by natural gaps. The preharvest basal area was 36–39 $m^2 \cdot ha^{-1}$, composed of subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) (78%) and Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) (22%).

The site is located in the winter range of mountain caribou, an ecotype of the woodland caribou that has been red-listed by the provincial government as a candidate for endangered or threatened status (B.C. Ministries of Sustainable Resource Management and Water, Land and Air Protection 2002). The land use plan currently in effect specifies that conservation of caribou habitat is a priority in the area and that alternative silvicultural systems are preferred over clear-cutting (Anonymous 1999). The Pinkerton Mountain

study area is part of a larger, replicated set of silvicultural systems trials (Jull et al. 2001) that comprise two sites in the Engelmann Spruce – Subalpine Fir Zone and three at lower elevations in the Interior Cedar–Hemlock Zone (Meidinger and Pojar 1991).

Two uneven-aged silvicultural systems were used at Pinkerton Mountain: group selection and single-tree selection (Fig. 1). In the 59-ha group selection area, trees were removed in discrete groups with a mean opening size of 0.25 ha. As much as possible, naturally occurring clumps of trees were either removed entirely or retained, resulting in irregularly shaped harvest openings. In the 40-ha single-tree selection area, trees were removed from across the range of diameter classes to achieve a target diameter distribution; trees larger than 52.5 cm diameter at breast height were retained unless they had to be felled to clear skid trails. A 25-ha area immediately adjacent to the block was designated as a control area and left unlogged. The prescription for both harvest units was for 30% timber removal. The resulting postharvest basal area was 23–27 $m^2 \cdot ha^{-1}$ in both treatment units.

Harvesting took place in March and April 1998 on a settled snowpack. Operational details of the planning, prescription, and harvesting are given in Stevenson et al. (1999).

Litterfall measurements

Litter was collected in litterfall traps with a collection surface area of 1 m × 1 m. The traps were constructed of nylon screen stapled to a frame of one-by-twos (boards approximately 2 cm × 4 cm) and reinforced at the corners with 0.25-in. (6.3-mm) plywood gussets.

In October 1998, 40 litterfall traps were installed at random locations along a 300-m transect in each of the three treatment units at Pinkerton Mountain. The transects were located on cruise lines that had been systematically laid out across the contours prior to harvesting. Shrubs were clipped at ground level from the area where the trap was to be placed, and where necessary, the forest floor was levelled so that the traps could be placed horizontally. Landscape fabric was placed under the traps to prevent damage to the screen from new vegetation. Overhanging shrubs were clipped at the point where they intercepted the vertical projection of the traps.

We measured the distance from the centre of each litterfall trap to the nearest main canopy tree (>15 m high). Trees that had been dead long enough to lose their fine branches and some bark (Stage 4 and higher of Thomas et al. 1979) were excluded, as they typically bear much lower lichen biomass than living or recently dead trees.

Litter was collected from the 120 traps immediately after snowmelt in late June – early July 1999, in early October 1999, in June 2000, and again in early October 2000. It was placed in labelled paper bags and air-dried for storage. Litter was sorted into five categories: fruticose lichens (*Alectoria* and *Bryoria* functional groups), foliose lichens, noncanopy material (e.g., insects, rodent droppings, shrub leaves), very fine material (material that was too small to sort), and other (e.g., wood, needles, bark, cones). The proportion of the fruticose lichens composed of *Alectoria* was estimated; the remainder was *Bryoria*. The very fine material was allocated

to the other categories by estimating proportional occurrence.

The litter was equilibrated in a laboratory in which the relative humidity was held constant at 60%. The lichens and fine material were weighed to the nearest 0.0001 g and the other material was weighed to the nearest 0.01 g. All mass data reported here are based on material weighed at 60% humidity. Lichens that have been oven-dried for 24 h at 60 °C weigh approximately 8.6% less than lichens equilibrated at 60% relative humidity; woody material (which dominated the "other" category) is about 6% lighter when it has been oven-dried (S.K. Stevenson, unpublished data).

Corrections for decomposition of lichen litter under snowpack

The biomass of the lichens collected from litterfall traps at the end of the winter underestimates the actual biomass of lichens falling to the forest floor during winter because lichens decompose in the snowpack. To correct for this source of error, we used decomposition data collected by Coxson and Curteanu (2002) at another montane site in the Prince George area. Coxson and Curteanu (2002) weighed samples of *A. sarmentosa* and *Bryoria* spp., inserted them in litter bags, and placed them on the snowpack at intervals during the winter. In spring, the samples were returned to the laboratory and weighed. Their data provide estimates of the decomposition rates of lichens in the two functional groups, *Alectoria* and *Bryoria*, that fall during the early-, mid-, and late-winter periods.

Because litterfall rates are related to wind and storms (Esseen 1985; Boucher and Nash 1990*a*), we used data from a wind tower in an adjacent clearcut (M. Jull and R. Sagar, unpublished data) to estimate the proportion of litter that fell during the early-, mid-, and late-winter periods. Early winter was defined as the date of the first persistent snow to 16 January, midwinter was 17 January – 20 March, and late winter was 20 March to snowmelt. Litter was allocated to each time period in proportion to the number of hours in which wind speed exceeded 20 km·h^{-1}.

For each of the two lichen functional groups, *Alectoria* and *Bryoria*, the corrected litterfall total for winter (L_c) was calculated according to the following formula:

$$[1] \qquad L_c = \frac{L_w}{\dfrac{P_E}{1/R_E} + \dfrac{P_M}{1/R_M} + \dfrac{P_L}{1/R_L}}$$

where L_w is the total weighed litterfall (grams per square metre), P is the proportion of total litterfall allocated to a given time period, R is the proportion of litter fallen during a given time period that remains at the end of winter (from Coxson and Curteanu 2002), and the subscripts E, M, and L represent the early-, mid-, and late-winter periods, respectively.

Canopy lichen biomass

To obtain estimates of the standing crop of canopy lichens in the immediate vicinity of the litterfall transect lines, we established 10 randomly located 0.015-ha circular plots along each transect line. We recorded the species and height class (medium: 5–15 m, large: >15 m) of each tree in the

plots. Mean lichen biomass values for each tree species – height class combination, as measured before harvesting by Campbell and Coxson (2001), were used to calculate estimates of canopy lichen biomass in each plot for the year 1998–1999. The data of Campbell and Coxson (2001) were obtained by climbing a set of sample trees and using a standard "clump" of lichen as a reference to estimate the biomass of *Alectoria*, *Bryoria*, and foliose lichens on each branch. The lichens from a subset of the branches were removed and weighed, and regressions describing the relationships between the estimated and measured lichen were used to correct the lichen estimates on all branches (Campbell et al. 1999; Campbell and Coxson 2001).

The lichen abundance estimates were repeated in summer 2000 on a subset of trees that had been identified as permanent sample trees and that had been excluded from destructive sampling (Coxson et al. 2003). The changes in lichen biomass on the permanent sample trees in each treatment unit, reported by Coxson et al. (2003), were used to calculate estimates of canopy lichen biomass for the year 1999–2000.

Lichen growth rates

Growth rates of *A. sarmentosa* and *Bryoria* spp. were assessed by repeatedly measuring the mass of thalli that were attached to artificial substrates in the canopy using methods similar to those of Denison (1988), Renhorn and Esseen (1995), and McCune et al. (1996).

Lichen growth rate cages were installed in the unlogged control area in fall 1997, in the group selection area in fall 1998, and in the single-tree selection area in fall 1999. We used ladders and single-rope climbing techniques (Perry 1978) for access to the 3–5 and 10–15 m zones in the canopies of scattered trees in the treatment unit, where we collected small (about 4–8 cm), discrete thalli of *A. sarmentosa* and *Bryoria fuscescens* (Gyeln.) Brodo & D. Hawksworth (s. lat.; including *Bryoria glabra*). The lichens were examined under a dissecting microscope and cleaned of bark fragments, needles, and other debris. Three apparently healthy thalli of the same species were selected for each composite sample and transferred to a laboratory that was maintained at a constant relative humidity of 60%.

After 48 h in the laboratory, the samples were weighed to the nearest 0.0001 g on a Mettler analytical balance. The relative humidity in the laboratory was monitored with an Assman psychrometer during the periods of stabilization and weighing. We used fungicide-free silicone seal to attach the lichens to glass tubes 3.6 cm long and 1.6 cm (outside dimension) in diameter. The lichen–tube assemblies were held in the laboratory for 1 week, the period of time required for the mass of a small dab of silicone seal to stabilize. Then, the assemblies were reweighed and fitted into lichen cages (Fig. 2). The cages were used to prevent other lichens from falling on the samples, to collect any fragments that might break off the samples, and to protect the samples from removal by wildlife. The cages are rectangular enclosures approximately 29 cm × 23 cm × 20 cm constructed of an acrylic frame and covered with 4-mm polypropylene landing net mesh. Each cage holds two glass tubes, one for each lichen species, that fit into snap assemblies at the tops of the cages.

Fig. 2. Lichen growth rate cage suspended from a branch in the Pinkerton Mountain study area.

Sixty composite samples of each species were located in each of the three treatment areas. Sample trees were randomly selected from a larger population of candidate trees that could be climbed safely and that had sturdy, accessible branches in the two target height zones, 3–5 and 10–15 m. In each treatment unit, 15 cages were placed in each of the following locations: the south-facing side of the upper height zone, the north-facing side of the upper height zone, the south-facing side of the lower height zone, and the north-facing side of the lower height zone. In the unlogged area and the single-tree selection area, which are relatively homo-geneous in structure, the cages were hung on five sample trees located in the vicinity of the litterfall transects. In the more heterogeneous group selection area, however, the cages were located in the most exposed environment: along the edges of the group selection openings. The 30 south-facing cages were placed in five trees along the south-facing edges of openings, and the 30 north-facing cages were placed along north-facing edges.

The cages were suspended with nylon cord about 10–20 cm below the branches of the sample trees. In June and September–October of each subsequent year, the lichens

were brought to the laboratory, allowed to stabilize for at least 48 h, reweighed, and returned to the field. Large lichen fragments found in the bottoms of the cages were weighed and discarded.

Turnover

Turnover was calculated by dividing litterfall (kilograms per hectare) (*Alectoria* and *Bryoria* biomass corrected for decomposition) for a given year by estimated canopy biomass (kilograms per hectare) for that year. The use of this method of calculating turnover allowed us to compare turnover based on litterfall losses with independent measurements of gains through growth.

Data analysis

The *Alectoria* and *Bryoria* litterfall data used in the analyses were corrected for decomposition, as described above. Relationships between mean litterfall values and distance from the nearest tree were graphed. Because the distributions of all of the litterfall components were positively skewed, the data were normalized by a logarithmic transformation. We used *t* tests with Bonferroni adjustments for multiple comparisons to test for significant differences between 1998–1999 and 1999–2000 in the biomass of each litterfall component in each of the three treatment units.

Relative growth (RG) of the lichen samples in the growth rate cages for each year was calculated as

$$[2] \qquad RG = (W_2 - W_1)/W_1 \times 100$$

where W_1 is lichen weight in October of the first year and W_2 is lichen weight in October of the next year. Lichen growth rate cages were not entirely effective at retaining lost fragments or excluding fragments from external sources. Occasionally, samples lost a large amount of mass, but no fragments were found on the bottoms of the cages. Conversely, we sometimes found fragments on the bottoms of cages that were attached to twigs and clearly had not originated from within the cage. Because our objective was to characterize the suitability of the site for lichen growth processes, rather than to measure net lichen growth in the canopy after fragmentation, samples that lost mass during a given year were removed from the data set for that year. Outliers in the remaining data set were removed using the method of Grubbs (1969) (table DD in Rohlf and Sokal 1995). The arcsine transformation was applied and nested analysis of variance performed on the data for 1999–2000, the only year in which lichen cages were in place in all three treatment units. The Bonferroni procedure was used to compare means.

A significance level of $p < 0.05$ was used in all tests.

Results

Correction of litterfall data for decomposition under snowpack (Appendix A) increased the estimate of *Alectoria* litterfall by 43.5% in winter 1998–1999 and 58.7% in winter 1999–2000. *Bryoria* estimates were increased by 50.4% in winter 1998–1999 and 64.6% in winter 1999–2000.

Quantities of all litterfall components were noticeably lower in the group selection area than in either the single-tree selection area or the unlogged control area, which were

Table 1. Annual biomass (g·m^{-2}) of litterfall components in unlogged (UN), group selection (GS), and single-tree selection (ST) treatment units at Pinkerton Mountain during the first 2 years after forest harvesting and results of *t* tests comparing the 1998–1999 and 1999–2000 data.

Litter component	1998–1999		1999–2000		*t* test	
	Mean	SE	Mean	SE	df	*p*
Alectoria[†]						
UN	1.55	0.55	0.85	0.28	33	1.000
GS	0.45	0.15	0.42	0.13	35	1.000
ST	1.77	0.5	0.88	0.21	32	0.334
Bryoria[†]						
UN	6.09	0.7	1.84	0.19	33	0.000*
GS	3.78	0.7	0.71	0.14	35	0.000*
ST	7.66	1.02	1.97	0.32	32	0.000*
Foliose						
UN	0.95	0.22	0.44	0.11	33	0.009*
GS	0.36	0.08	0.08	0.02	35	0.000*
ST	1.92	0.45	0.28	0.06	32	0.000*
Other						
UN	140.12	23.6	129.2	8.12	33	1.000
GS	47.66	5.92	49.5	5.34	35	1.000
ST	161.93	30.18	98.42	12.15	32	0.051

*Significant values ($p \leq 0.05$).
[†]Data adjusted to include decomposition under snowpack.

generally similar (Table 1). Biomass of two litterfall components, *Bryoria* and foliose lichens, declined significantly from 1998–1999 to 1999–2000 in the unlogged control area as well as in the two treatment areas. Biomass of *Alectoria* and other material did not differ between years in any treatment unit. In the single-tree selection area, however, the decline in biomass of other material approached statistical significance.

Biomass of lichen litterfall decreased rapidly with distance from the nearest tree (Fig. 3). Biomass of *Alectoria* and of foliose lichens tapered off more rapidly than that of *Bryoria*. At distances greater than 15 m from the nearest tree, litterfall biomass of *Alectoria* and foliose lichens was only 1% of that in the 0–3 m distance class, whereas litterfall biomass of *Bryoria* was about 5% of that in the 0–3 m class.
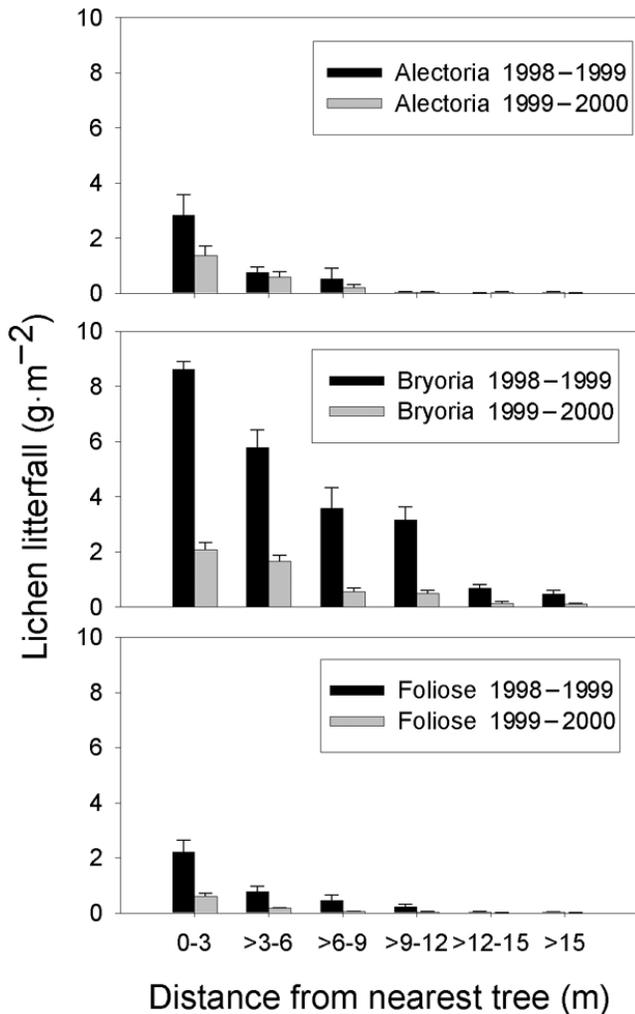
Estimated standing crop of the three functional groups of canopy lichens along each of the three litterfall transects in 1998–1999 and 1999–2000 is given in Table 2. In all treatments and years, biomass of *Bryoria* > biomass of foliose lichens > biomass of *Alectoria*. Standing crop of all three lichen groups was lower in the group selection area than in the single-tree selection area, even though the same level of harvest was prescribed in the two treatment units. By chance, harvest openings were overrepresented on the group selection transect line, occupying more than 50% of its length. Thus, both the litterfall and the standing crop data for the group selection area represent a higher level of volume removal than was characteristic of the treatment unit as a whole.

Growth rates of both species in the unlogged area were relatively consistent during the 3 years for which we have

Table 2. Estimated biomass (kg·ha^{-1}) of canopy lichens along litterfall transects in the unlogged, group selection, and single-tree selection treatment units at Pinkerton Mountain.

Year	Treatment unit	Alectoria		Bryoria		Foliose	
		Mean	SE	Mean	SE	Mean	SE
1998–1999	Unlogged	165.2	17.7	1115.7	119.9	508.4	54.9
	Group selection	42.6	11.9	267.6	79.4	135.7	35.8
	Single-tree selection	105.7	28.1	703.7	188.4	338.6	89.2
1999–2000	Unlogged	155.0	16.7	949.2	102.0	492.7	53.2
	Group selection	35.6	9.9	226.9	67.3	119.0	31.3
	Single-tree selection	79.1	21.0	438.0	117.2	323.9	85.2

Fig. 3. Relationship between *Alectoria*, *Bryoria*, and foliose lichen litterfall (mean ± SE) and distance from the nearest tree in all treatment units at Pinkerton Mountain, 1998–1999 and 1999–2000. *Alectoria* and *Bryoria* litterfall was corrected for decomposition under snowpack.

Table 3. Nested analysis of variance of annual relative growth by species, 1999–2000, in the unlogged, group selection, and single-tree selection treatment units at Pinkerton Mountain.

Source	Sum of squares	df	Mean square	F ratio	p
Alectoria sarmentosa					
Treatment	1175.401	2	587.700	39.27	0.000*
Aspect	21.273	1	21.273	0.841	0.362
Height	93.165	1	93.165	3.684	0.059
Tree(treatment)	254.416	17	14.966	0.592	0.887
Cage(tree)	471.813	25	18.873	0.746	0.791
Error	1770.377	70	25.291		
Bryoria fuscescens					
Treatment	193.918	2	96.959	3.534	0.052
Aspect	31.892	1	31.892	1.752	0.190
Height	39.759	1	39.759	2.184	0.144
Tree(treatment)	466.432	17	27.437	1.507	0.117
Cage(tree)	279.875	23	12.168	0.668	0.860
Error	1292.584	71	18.205		

Note: Data were arcsine transformed.
*Significant value ($p \leq 0.05$).

enced fragmentation, and usually, that assumption was confirmed by the presence of a fragment on the bottom of the cage. The number of samples of both species that lost fragments was noticeably elevated in the group selection area during 1998–1999.

Five outliers were removed from the data set. These may have represented specimens that grew substantially more than the others, but because the mesh on a few cages was damaged, we cannot preclude the possibility of contamination from outside sources.

Analysis of variance of the 1999–2000 data indicated a highly significant treatment effect on *A. sarmentosa* and a treatment effect that approached statistical significance ($p = 0.052$) for *B. fuscescens* (Table 3). Both species exhibited the same response pattern, with highest growth rates in the single-tree selection area, intermediate growth rates in the unlogged control, and lowest growth rates in the group selection area, but not all pairs were significantly different from one another (Appendix B). Neither the aspect of the branches on which the cages were located (north-facing or south-facing side of the tree) nor the height at which the cages were placed (3–5 or 10–15 m) had significant effects on growth rate for either *A. sarmentosa* or *B. fuscescens*.

data, except that *B. fuscescens* growth was somewhat lower during the first year (Appendix B). During the second year, growth rates of both species were markedly lower in the group selection area than in the unlogged area. The number of samples that lost biomass during each year of the study is given in Appendix B. These are assumed to have experi-

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Fig. 4. Annual relative growth (mean ± SE) and estimated annual turnover (litterfall as a percentage of standing crop) of *Alectoria*, *Bryoria*, and foliose lichens in the unlogged area (UN), the group selection area (GS), and the single-tree selection area (ST) at Pinkerton Mountain, 1998–1999 and 1999–2000. In the group selection area, growth rate and turnover data are not directly comparable (see text). Turnover rates of *Alectoria* and *Bryoria* are based on litterfall values corrected for decomposition under snowpack.
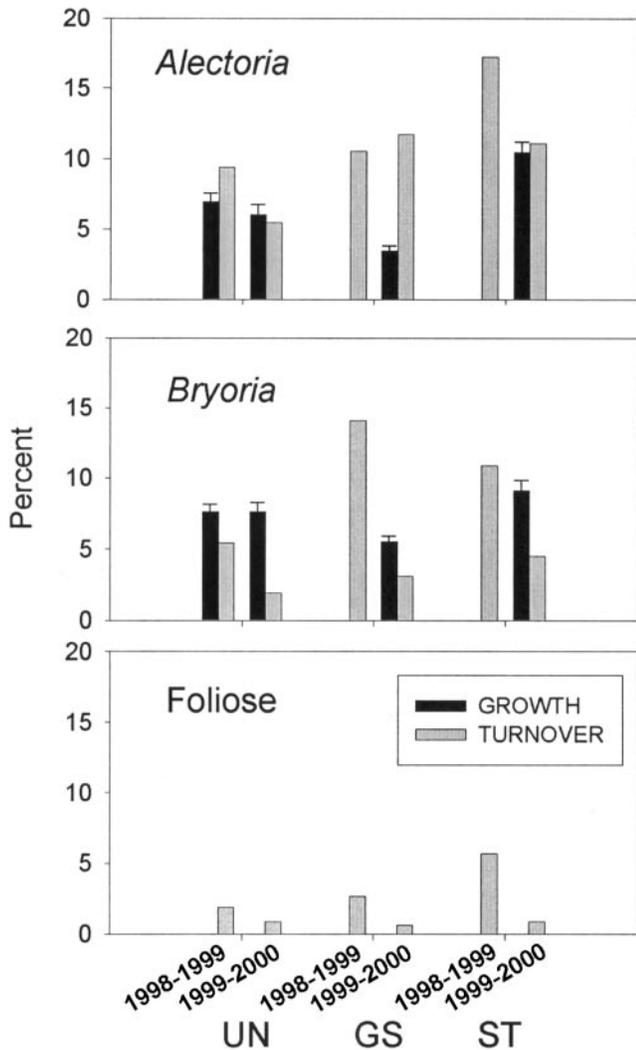

Figure 4 shows annual turnover of the three lichen groups during the 2-year period after partial cutting and lichen growth rates for the corresponding areas where those are available. Growth rates for the group selection area are not comparable with turnover rates because the growth rate cages were located along opening edges rather than along the litterfall transects. Growth rates of foliose lichens were not studied. In the unlogged area, mean growth of *Alectoria* over the 2-year period (6.47%) was approximately in balance with mean turnover (7.43%). Growth of *Bryoria* exceeded turnover in the unlogged area in both years. In the single-tree selection area, turnover of all three functional groups was higher during 1998–1999 than during 1999–2000. In 1999–2000, *Alectoria* growth and turnover were in balance in the single-tree selection area, but *Bryoria* growth

exceeded turnover. Turnover of foliose lichens was consistently lower than turnover of the two fruticose lichen groups.

Discussion

Litterfall rates

Based on their data on *Alectoria* biomass and thallus size in relation to stand edge, Esseen and Renhorn (1998) postulated that a pulse of litterfall of pendulous lichens occurs along clearcut edges during the first winter after logging. At Pinkerton Mountain, *Bryoria* and foliose lichen litterfall was significantly greater in 1998–1999 than in 1999–2000. The differences cannot be attributed to treatment, as they occurred in the control area as well as in the partial cuts. The higher litterfall observed during the first year after logging was probably the result of weather events. Winter 1998–1999 was snowier and windier than winter 1999–2000 and resulted in more top breakage along permanent treefall transects (M. Jull, unpublished data). Weather events in 1998–1999 may also have stripped arboreal lichens, frozen in clumps of snow or ice, from foliage and branches.

The elevated levels of lichen litterfall that we observed in 1998–1999 were consistent with changes in standing biomass of canopy lichens in the study area. From 1998 to 2000, lichen biomass on permanent sample trees declined by 10%–20% in the unlogged and group selection areas and somewhat more in the single-tree selection area, although the differences among treatment units were not statistically significant (Coxson et al. 2003). The decline in lichen abundance was most pronounced in the upper canopy, especially in the single-tree selection area, where the decline in *Bryoria* abundance was statistically significant.

Litterfall of *Alectoria* and other material did not exhibit the same pattern of interyear variation as that of *Bryoria* and foliose lichens, except perhaps in the single-tree selection area. As *Alectoria* is largely confined to the lower canopy at Pinkerton Mountain (Campbell and Coxson 2001), these results are consistent with the observation (Coxson et al. 2003) that disturbance to the lichens was greatest in upper canopy positions. "Other" litterfall, composed mainly of woody material, was not elevated in 1998–1999, perhaps because the predominantly short, living branches of the upper canopy are resistant to breakage, except when an entire top is dislodged.

In the single-tree selection area, the trend of decline in "other" litterfall from 1998–1999 to 1999–2000 suggests that the partial cutting treatment may have brought about an additional increase in litterfall during 1998–1999 and that the effect may not have been confined to the upper canopy. This is consistent with the observations of Coxson et al. (2003) of greater decline in standing crop of canopy lichens in the single-tree selection area. We conclude that there may have been a modest postharvest pulse of litterfall at Pinkerton Mountain but that it was restricted to the single-tree selection area and that it was largely masked by natural variation in litterfall among years.

Growth rates

Although the absence of geographic replication limits extrapolation of our results outside the study area, analysis of variance of the growth rate data is a valuable tool for examining the dynamics of the lichens within the study area. In

1999–2000, growth rates of both *A. sarmentosa* and *B. fuscescens* were highest in the single-tree selection area, intermediate in the unlogged control, and lowest in the group selection area. Apparently, the lichen growth environments offered at the cage locations in the single-tree selection area were as good, if not better, for lichen growth than the equivalent environments in the unlogged control area.

Changes in biomass of canopy lichens are a function of net carbon gain and biomass losses through fragmentation, in situ decomposition, and consumption. The lichen growth rate samples in the group selection area, but not in the other treatment units, showed elevated levels of apparent fragmentation during 1998–1999, probably because of the exposed position of the cages along the edges of openings. Reduced growth rates in samples that were retained in the data set (i.e., did not experience major fragmentation or dieback) likely reflect reduced duration of lichen hydration at the edge of the group selection patches, as described by Coxson et al. (2003).

Adverse effects of exposure on pendulous lichens have been reported previously. In Oregon, *A. sarmentosa* was four to five times more abundant in litterfall in the forest interior than along a 20-year-old edge (Sillett 1995). In northwestern Sweden, both biomass and maximum thallus length of *A. sarmentosa* were markedly lower along clearcut edges than in the forest interior at 9 of 10 study sites (Esseen and Renhorn 1998). Hilmo and Holien (2002) did not find a clear edge effect on *A. sarmentosa* in a Norwegian *Picea abies* (L.) Karst. stand but found significantly fewer thalli of *Bryoria* spp. at the exposed forest edge.

We conclude that in the short term, the moderate increase in exposure that occurred in the single-tree selection area at Pinkerton Mountain had no adverse effect on the growth rates of *Alectoria* and *Bryoria*. The increase in exposure along the edges of the group selection openings appears to have been sufficient to inhibit growth but not to reduce standing biomass per tree in the residual stand as a whole (Coxson et al. 2003).

Turnover

A new component of our methodology was the use of correction factors to compensate for in situ decomposition under snowpack (Coxson and Curteanu 2002). Decomposition corrections were substantial, increasing estimates of annual litterfall of *Alectoria* and *Bryoria* by approximately 50%. We were not able to provide a similar correction for foliose lichens, as we have no data from which to derive correction factors. That may be one reason for our consistently low estimates of foliose lichen turnover compared with those of *Alectoria* and *Bryoria*. It is also possible that growth rates of foliose lichens are intrinsically lower than those of alectorioid lichens, as suggested by the data of Renhorn (1997).

Comparisons of lichen growth rates and lichen turnover are only valid if movement of lichens into or out of the study area is negligible. Although fragments of *Bryoria* and, to a lesser degree, *Alectoria*, are capable of dispersing several hundred metres from mature timber stands into clearcuts (Stevenson 1988; Dettki 1998; Quesnel and Waters 2000), 90% of lichen litterfall at Pinkerton Mountain was deposited within 10 m of the nearest trees. We therefore conclude that the movement of lichen fragments into and out of the treat-

ment units did not substantially affect our turnover estimates, although it is important to the understanding of dispersal.

Growth and turnover of *Alectoria* were approximately in balance in the unlogged area during the 2 years of the study and in the single-tree selection area in 1999–2000, the only year for which we have data. In contrast, *Bryoria* growth appeared to exceed turnover in both the unlogged and the single-tree selection areas. Our data suggest differences between the dynamics of *Alectoria* and *Bryoria* in the canopy. There appear to be losses of *Bryoria* from the system not explained by litterfall. Consumption of *Bryoria* by caribou is probably a minor factor because of the small number of animals and their irregular use of the area. We suspect that in situ decomposition may have a more important role in the dynamics of *Bryoria* than was previously thought. Periodic dieback of *Bryoria*, likely in response to prolonged wetting, has been documented in similar stands (Goward 1998), and we have observed substantial amounts of necrotic *Bryoria* in our study area.

The turnover rates that we observed in our study area are lower than many that have been reported elsewhere, which range from 5% to 29% (Table 4). Given the difficulty in accurately measuring the components of turnover, there is uncertainty around all of the estimates in Table 4. Litterfall in general is variable from year to year. In eight north temperate coniferous stands where total litter was measured for 4 years or longer, the ratio of maximum/minimum values ranged from 1.3 to 5.1 (Bray and Gorham 1964). A similar range is found in multiyear studies of lichen litterfall (Table 5). Unless repeated measurements of lichen litterfall are accompanied by repeated assessments of lichen biomass in the canopy, turnover estimates calculated from litterfall can be substantially in error. We addressed this problem by repeating our estimates of lichen abundance on the sample trees. Monitoring of both standing crop and litterfall over longer time periods is needed to clarify variation in turnover rates in managed and unmanaged stands.

Management implications

The long-term prospects for the production of canopy lichens in partially cut stands are a matter of practical interest. The partial-cut treatments that we tested at Pinkerton Mountain appeared to maintain a satisfactory environment for continued lichen growth. Until these results have been replicated, they should not be generalized. However, other researchers have also found that partial cutting had little effect on abundance of forage lichens in residual trees in similar forest types (Rominger et al. 1994; Stevenson 2001; H. Armleder, personal communication). Overall, existing data seem to indicate that residual trees in partially cut spruce–fir stands are able to retain, or recover, preharvest levels of forage lichen abundance.

It is less clear how well forage lichen biomass will be retained in partially cut stands after successive harvest entries. In Sweden, stands aged 100–130 years that had been managed by selective removal of large trees supported much lower arboreal lichen abundance than unmanaged stands (Esseen et al. 1996). However, there are important differences between that management regime and current partial cutting recommendations for mountain caribou range (Stev-

Table 4. Standing crop, litterfall rates, and annual turnover of arboreal lichens.

Stand type	Location	Stand age (years)	Species group	Standing crop (kg·ha⁻¹)	Litterfall (kg·ha⁻¹·year⁻¹)	Turnover (%)	Study period	Source(s)
Quercus garryana	Western Oregon, U.S.A.	120	Epiphytes	1 775	320	18	1 year	Pike 1971
Abies alba	Massif Central, France	120	All arboreal lichens	1 040	87	8.4	31 months	André et al. 1975
Abies amabilis – Tsuga mertensiana	Western Washington, U.S.A.	>175	All arboreal lichens	1 900	170	8.9	13 months	Turner and Singer 1976
Pseudotsuga menziesii – Tsuga heterophylla	Vancouver Island, B.C.	>300	*Alectoria* and *Bryoria*	303–942	23–265	7.8–17.6*	2 winters	Stevenson 1978; S.K. Stevenson, unpublished data
Pseudotsuga menziesii – Tsuga heterophylla	Vancouver Island, B.C.	>300	*Alectoria* and *Bryoria*	140–1516	13–115†	7.6–9.4†	1 winter	Rochelle 1980; Stevenson 1978
Abies balsamea	New Hampshire, U.S.A.	22	All arboreal lichens	204	31	15.2	1 year	Lang et al. 1980
		25		133	23	17.3		
		31		120	90	75.0‡		
		35		125	27	21.6		
		44		932	50	5.4		
		52		591	32	5.4		
		61		1 283	91	7.1		
		67		635	65	10.2		
		78		1 603	94	5.9		
		79		676	68	10.1		
Picea abies	Central Sweden	164	*Usnea longissima*	2 320§	162§	7	32 months	Esseen 1985
		260		19 600§	1958§	10		
Quercus douglasii	California, U.S.A.	not given	*Ramalina menziesii*	706	203	28.8	15 months	Boucher and Nash 1990a, 1990b
Abies lasiocarpa – Picea engelmannii	North-central B.C.	350	*Alectoria*	155–165	8.5–15.5,‖ 5.9–10.9¶	5.5–9.4,‖ 3.8–6.6¶	2 years	This study (unlogged area)
			Bryoria	949–1116	18.4–60.9,‖ 12.1–40.8¶	1.9–5.5,‖ 1.3–3.7¶		
			Foliose	493–508	4.4–9.5	0.9–1.9		

*Based on 180-day winter period. Plots protected from foraging by deer.
†Based on 180-day winter period. Plots unprotected from foraging by deer.
‡Most of the litterfall originated from an older generation of veteran trees that were rapidly losing epiphytes through sloughing bark, broken branches, and treefall.
§Units are metres of thallus per hectare.
‖Litterfall rates adjusted to include decomposition under snowpack.
¶Litterfall rates not corrected for decomposition.

Table 5. Variation in litterfall of arboreal lichens in mature forests sampled for 2 or more years.

Stand type	Location	Species group	Years sampled	Litterfall (kg·ha⁻¹)			Source(s)
				Max.	Min.	Ratio	
Pseudotsuga menziesii –	Vancouver Island, B.C.		2				Stevenson 1978;
Tsuga heterophylla	Site 3	*Alectoria* and *Bryoria*		162	70	2.31	S.K. Stevenson,
	Site 4			180	151	1.19	unpublished data
	Site 5			32	15	2.13	
	Site 3	Other lichens (mostly foliose)		73	41	1.78	
	Site 4			49	46	1.07	
	Site 5			40	36	1.11	
Picea abies	Central Sweden	All lichens					Esseen 1985
	Site 1		3	188	132	1.42	
	Site 2		2	140	90	1.56	
Pseudotsuga menziesii	South-central B.C.	All lichens (mostly *Bryoria*)	3	14*	4*	3.37	Waterhouse et al. 1991
Thuja plicata – Tsuga	Southeastern B.C.	*Alectoria*	3	25	14	1.79	Quesnel and Waters
heterophylla		*Bryoria*		4	2	1.75	2000
Thuja plicata – Tsuga	East-central B.C.	*Alectoria* and *Bryoria*	3	41	8	5	S.K. Stevenson,
heterophylla							unpublished data
Abies lasiocarpa –	North-central B.C.	*Alectoria*	2	11	6	1.85	This study†
Picea engelmannii		*Bryoria*		41	12	3.37	
		Foliose lichens		9	4	2.16	

*Units are kg·ha⁻¹·month⁻¹ during winter.
†Litterfall values not corrected for decomposition.

enson et al. 2001), which were designed to maintain forage lichens. As these partially cut stands develop, the colonization and growth of lichens on the young trees should be monitored.

Our results suggest that partial cutting with low volume removal has met short-term management goals for the retention of forage lichens at Pinkerton Mountain. They do not indicate that either single-tree selection or group selection was superior to the other at this site, with respect to the retention of forage lichens. We recommend that managers continue to experiment with both approaches to partial cutting and that long-term studies of lichen dynamics continue as new regeneration develops.

Acknowledgements

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Appendix A

Appendix appears on the following page.

Table A1. Decomposition corrections for *Alectoria* and *Bryoria* in litter at Pinkerton Mountain, winters of 1998–1999 and 1999–2000, based on the decomposition data of Coxson and Curteanu (2002).

Winter	Genus	Treatment unit	L_w (g·m⁻²)	Hours of average windspeed >5.5 m·s⁻¹				Proportion of litter remaining			L_c (g·m⁻²)
				Total	P_E	P_M	P_L	R_E	R_M	R_L	
1998–1999	*Alectoria*	Unlogged	1.035	1213	0.38	0.389	0.231	0.332	0.914	0.932	1.485
1998–1999	*Alectoria*	Group selection	0.516	1213	0.38	0.389	0.231	0.332	0.914	0.932	0.740
1998–1999	*Alectoria*	Single-tree selection	1.076	1213	0.38	0.389	0.231	0.332	0.914	0.932	1.544
1998–1999	*Bryoria*	Unlogged	3.973	1213	0.38	0.389	0.231	0.348	0.851	0.872	5.977
1998–1999	*Bryoria*	Group selection	2.582	1213	0.38	0.389	0.231	0.348	0.851	0.872	3.884
1998–1999	*Bryoria*	Single-tree selection	4.529	1213	0.38	0.389	0.231	0.348	0.851	0.872	6.813
1999–2000	*Alectoria*	Unlogged	0.443	989	0.496	0.218	0.286	0.332	0.914	0.932	0.703
1999–2000	*Alectoria*	Group selection	0.239	989	0.496	0.218	0.286	0.332	0.914	0.932	0.379
1999–2000	*Alectoria*	Single-tree selection	0.414	989	0.496	0.218	0.286	0.332	0.914	0.932	0.657
1999–2000	*Bryoria*	Unlogged	0.975	989	0.496	0.218	0.286	0.348	0.851	0.872	1.605
1999–2000	*Bryoria*	Group selection	0.364	989	0.496	0.218	0.286	0.348	0.851	0.872	0.599
1999–2000	*Bryoria*	Single-tree selection	1.038	989	0.496	0.218	0.286	0.348	0.851	0.872	1.709

Note: Litter was allocated to time periods in proportion to the hours in which average windspeed exceeded 5.55 m·s⁻¹. L_w, weighed litterfall biomass; P, proportion of litterfall allocated to a time period, where subscripts E, M, and L indicate early, mid-, and late winter, respectively; R, proportion of litter fallen during a time period remaining at the end of winter (Coxson and Curteanu 2002), where subscripts E, M, and L indicate early, mid-, and late winter, respectively; L_c, calculated litterfall biomass.

References

Coxson, D.S., and Curteanu, M. 2002. Decomposition of hair lichens (*Alectoria sarmentosa* and *Bryoria* spp.) under snowpack in montane forest, Cariboo Mountains, British Columbia. Lichenologist, **34**: 395–402.

Appendix B

Appendix appears on the following page.

Table B1. Summary of biomass loss and annual relative growth of *Alectoria sarmentosa* and *Bryoria fuscescens* growth rate samples in unlogged (UN), group selection (GS), and single-tree selection (ST) treatment units at Pinkerton Mountain, 1997–1998 to 1999–2000.

| Year | Treatment unit | Samples removed from data set | | | Samples in final data set | Relative growth (mean ± SE)* |
		Samples missing or damaged	Samples that lost mass	Outliers		
Alectoria sarmentosa						
1997–1998	UN	1	5	—	54	6.41±0.30
1998–1999	UN	2	10	—	48	6.92±0.61
	GS		45	—	15	2.68±0.45
1999–2000	UN	4	17	—	39	6.01±0.72a
	GS	—	27	1	32	3.47±0.35a
	ST	7	7	—	46	10.45±0.71b
Bryoria fuscescens						
1997–1998	UN	1	8	1	50	4.62±0.38
1998–1999	UN	2	11	—	47	7.65±0.50
	GS	—	51	1	8	2.40±0.64
1999–2000	UN	4	15	—	41	7.62±0.67cd
	GS	3	20	1	36	5.52±0.38c
	ST	1	19	1	39	9.13±0.71d

*Within species, means sharing the same letter were not significantly different ($p > 0.05$; Bonferroni adjustment for multiple comparisons).