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## Arboreal forage lichens in partial cuts – a synthesis of research results from British Columbia, Canada

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**Abstract:** The mountain ecotype of the woodland caribou (*Rangifer tarandus caribou*) is highly dependent on the arboreal hair lichens *Bryoria* spp. and *Alectoria sarmentosa* during winter. In parts of British Columbia, partial-cutting silvicultural systems have been used in an effort to provide continuously usable winter habitat for mountain caribou, while allowing some timber removal. We reviewed available information about the changes in hair lichens after partial cutting in Engelmann spruce (*Picea engelmannii*) – subalpine fir (*Abies lasiocarpa*) forests of British Columbia and Idaho. Generally, abundance of *Bryoria* spp. in the lower canopy of individual residual trees increases with increased exposure after partial cutting, until the new regeneration begins to shelter the lower canopy of the residuals. Heavy basal area removal, however, results in low lichen availability at the stand level for many years. Abundance of *Bryoria* on the regeneration is low, and appears to be limited largely by the structure of the young trees, not by lichen dispersal, although dispersal capability may be limiting in *Alectoria*. Both distributional and physiological data suggest that *Bryoria* is intolerant of prolonged wetting, and that increased ventilation, rather than increased light, accounts for enhanced *Bryoria* abundance in the partial cuts. *Alectoria sarmentosa* reaches its physiological optimum in the lower canopy of unharvested stands; its growth rates are somewhat reduced in the more exposed environment of partial cuts. Both genera are capable of rapid growth: over a 7-year period, individual thalli of *A. sarmentosa* and *Bryoria* spp. (excluding those with a net biomass loss due to fragmentation) in an unlogged stand more than tripled their biomass. Calculated growth rates, as well as dispersal potential, are influenced by fragmentation. *Bryoria* produces more abundant, but smaller, fragments than *Alectoria*, and fragmentation in both genera increases in partial cuts. In subalpine mountain caribou habitat, partial-cutting prescriptions that enhance exposure of residual trees while keeping basal area removal low will maintain forage best. Regeneration management should focus on maintaining ventilation in the lower canopy of the residual stand.

**Key words:** *Alectoria*, *Bryoria*, hair lichens, mountain caribou, *Rangifer tarandus caribou*, silvicultural systems.

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### Introduction

In British Columbia, Canada, the range of the mountain ecotype of the woodland caribou (*Rangifer tarandus caribou*) is closely associated with the Interior Wetbelt (Stevenson *et al.*, 2001; Apps & McLellan, 2006), an area of high precipitation located on the western slopes of the Rocky Mountains. Mountain caribou spend all or part of the winter in high-elevation subalpine fir (*Abies lasiocarpa*) – Engelmann spruce (*Picea engelmannii*) forests, where they forage almost exclusively on the arboreal hair lichens *Bryoria* spp. and *Alectoria sarmentosa*. Where both genera are available,

*Bryoria* is preferred (Rominger *et al.*, 1996). A settled snowpack of 2–4 m increases the caribou's access to the lichens on the lower branches of trees. As well, the caribou remove lichens from freshly fallen trees, and consume lichen litterfall when it is available on top of the snowpack.

Mountain caribou have been red-listed by the British Columbia Conservation Data Centre, and designated as threatened under the Canadian *Species at Risk Act*. Even before they were formally considered to be at risk, the mountain caribou were a species of management

concern because of their declining numbers and their apparent sensitivity to resource development and human activity within their range (Stevenson & Hatler, 1985). Clearcut forest harvesting was thought to be incompatible with the conservation of mountain caribou, which were known to be closely associated with old-growth forests. Recommendations for the use of partial cutting, rather than clearcutting, within the range of mountain caribou were developed (Stevenson *et al.*, 1994; 2001), and a number of experimental and operational partial cuts were implemented. These have included group retention, in which trees are removed in patches up to 1 ha, and single-tree retention, in which trees are removed in a dispersed pattern from throughout the harvest block.

Part of the rationale for using partial cutting rather than clearcutting methods in mountain caribou range is that partial-cutting prescriptions can be designed to maintain substantial numbers of lichen-bearing trees, and may provide continuously usable winter habitat for mountain caribou. Partial cutting may affect mountain caribou in many ways: by altering abundance of forage for other ungulates; by altering abundance or efficiency of predators; by increasing road access and the potential for human disturbance; by modifying snowpack characteristics; and by changing the amount of available forage for the caribou. This paper addresses only the question of how partial cutting affects the abundance and dynamics of the hair lichens *Bryoria* spp. and *Alectoria sarmentosa*.

Partial cutting results in immediate loss of the lichen substrate on felled trees. It creates growing space for new regeneration, and over time, increasing amounts of substrate on young trees become available. The residual trees are exposed to a different microclimatic regime, characterized by greater insolation, more wind exposure, lower humidity, and more exposure to precipitation. Hair lichens in subalpine spruce-fir stands exhibit a marked vertical zonation, with *Bryoria* peaking in abundance in the mid to upper canopy, and *Alectoria sarmentosa* reaching its greatest abundance in the lower canopy (Campbell & Coxson, 2001). For some time after partial cutting, the light environment in the canopy of the residual stand resembles that in the mid canopy of an unlogged stand (Coxson *et al.*, 2003), but as the regeneration develops it will begin to shade the lower branches of the residuals. As well, partial cutting, like any forest harvesting, alters the spatial relationships among trees, increasing the distance between large old residual trees and the new regeneration. These changes in spatial relationships raise the question of the effectiveness of dispersal in promoting the colonization of the new regeneration by lichens.

The objective of this paper is to synthesize what is known about the changes in hair lichens (*Bryoria* spp. and *Alectoria sarmentosa*) after partial cutting in subalpine fir-spruce forests of British Columbia and adjacent Idaho. We review studies of lichen abundance at the tree level and at the stand level in mountain caribou habitat after partial cutting, and studies of the dispersal capability of *Bryoria* spp. and *Alectoria sarmentosa*. We then draw on studies of the physiology and growth rates of these lichens to try to elucidate the mechanisms that might explain the abundance patterns that have been observed. We conclude with the implications of our findings to the management of partial cuts in mountain caribou habitat.

### Abundance of hair lichens on residual trees after partial cutting

The impact of partial cutting on the abundance and genus composition of arboreal lichens is expected to change over time. The first partial cuts in mountain caribou habitat that have been consistently monitored were established in the early 1990s. In some parts of the range of mountain caribou, however, partial cuts dating back to the late 1960s have been examined in retrospective studies. We reviewed both types of studies to evaluate long-term patterns in the abundance and genus composition of arboreal forage lichens. All studies but one used the photo guide of Armleder *et al.* (1992) to classify each tree into a lichen abundance class, using photographs of trees with known quantities of lichen below 4.5 m for reference. The study of Rominger *et al.* (1994) was based on biomass sampling in the 2- to 6-m range.

Rominger *et al.* (1994) found no difference between tree-level lichen abundance in partial cuts and unlogged stands in two study areas (Table 1). In northeastern Washington, estimated lichen abundance at the tree level declined between 7 and 15 years after partial cutting; this decline may have been due a windstorm that resulted in significant blowdown in the study area (T. Layser, Idaho Panhandle National Forests, pers. comm., 29 March 2006). All other studies (Table 1) reported an increase in forage lichen abundance in the lower canopy of individual trees after partial cutting.

The studies were consistent in reporting an increase in the proportion of total forage lichens composed of *Bryoria* spp. Based on a retrospective study of 26 partial cuts and 37 unlogged stands, Lewis (2004) reported that in partial cuts, tree-level *Bryoria* biomass increased rapidly for the first 20 years, then appeared to stabilize. The rate of *Bryoria* accumulation on residual trees was greatest in partial cuts with low levels of green tree retention (basal area <10 m<sup>2</sup>/ha).

*Alectoria* biomass increased linearly with increasing basal area of the residual stand, regardless of time since logging. The proportion of total forage lichens composed of *Alectoria* decreased with time since logging to about 20 years, then showed a slight increase in partial cuts older than about 30 years, especially the ones with higher basal area (>20 m<sup>2</sup>/ha). This shift in genus composition in the oldest partial cuts probably occurred because tree growth was begin-

ning to alter the lower canopy environment to favor development of *Alectoria*. The findings of Lewis (2004), in combination with the other studies (Table 1), strongly suggest that the increased exposure associated with partial cutting promotes the growth of *Bryoria* on the residual trees, at least for the first 30 years. *Alectoria* remains present on residual trees in the partial cuts, but does not appear to benefit from the increased exposure.

Table 1. Summary of effects of partial cutting on abundance and genus composition of arboreal forage lichens on residual trees.

Reference; local population <sup>1</sup>	Partial cuts	Unlogged comparison	Time since harvest	Tree-level effect on lichen abundance	Tree-level effect on genus composition
Delong <i>et al.</i> , 1999; South Selkirks	15 operational bark beetle salvage blocks	known caribou foraging areas in Revelstoke and N. Cariboo Mtns.	14-23 years	Significantly more trees with high lichen abundance in partial cuts	Significantly more trees dominated by <i>Bryoria</i> rather than <i>Alectoria</i> in partial cuts
Rominger <i>et al.</i> , 1994; South Selkirks and adjacent Idaho	1 high-volume removal cut (density 33% of unlogged stand and 1 low-volume removal cut (density 81% of unlogged stand)	adjacent stands	12-15 years	No difference between partial cuts and unlogged stands	Slightly higher proportion of <i>Bryoria</i> in partial cuts
Stevenson, 2001 and unpubl. data; North Cariboo Mtns.	1 block with dispersed retention ranging from 51-31% of initial basal area	adjacent stand	measured in Years 0, 4, 8, & 13	Decrease in Year 4 followed by increase	Percent <i>Bryoria</i> increased
Lewis, 2004; Wells Gray South	26 partial cuts with various levels of dispersed retention	37 unlogged stands of various ages	0-38 years	Lichen biomass increased after logging due to increased rate of <i>Bryoria</i> accumulation.	Percent <i>Bryoria</i> increased with time since logging to about 20 years, then decreased slightly in the oldest partial cuts
Waterhouse <i>et al.</i> , 2007; Wells Gray North	4 replicates; group selection harvesting w/ 3 opening sizes; 30% volume removal	adjacent stands	10 years	More trees in partial cuts than uncut stands shifted toward higher lichen classes	Slightly higher proportion of <i>Bryoria</i> in partial cuts
Layser, unpubl. data <sup>2</sup> ; NE Washington	1 block w/40% crown closure retention	adjacent stand	measured after 7 & 15 years	Apparent loss between Years 7 and 15; may have been due to major windthrow event	Percent <i>Bryoria</i> increased

<sup>1</sup> Local populations as defined by Mountain Caribou Technical Advisory Committee (2002).

<sup>2</sup> T. Layser, Idaho Panhandle National Forests, pers. comm., 29 March 2006.

Effects of partial cutting on forage lichen biomass at the stand level may differ substantially from effects at the tree level. DeLong *et al.* (1999) found that the average density of trees >12.5 cm dbh in the partial cuts they studied was 50-60% lower than the density in known mountain caribou foraging areas. They concluded that the partial cutting maintained suitable trees, but perhaps not enough of them to maintain suitable habitat. Lewis (2004) reported that stand-level lichen biomass was low (<12 kg/ha) in older partial cuts with basal area <10 m<sup>2</sup>/ha, even though tree-level lichen biomass was high. Older partial cuts with basal area >15 m<sup>2</sup>/ha supported up to 10 times as much stand-level biomass, sometimes exceeding that in unlogged stands, even though stem density was lower.

### Abundance of hair lichens on young trees after partial cutting

Most of the available forage lichen biomass in partial cuts is present on the residual trees, not on the trees that have regenerated after harvesting. Although few studies have documented lichen biomass on young trees in partial cuts, research from a variety of forest types has documented low biomass of hair lichens in young stands in general (McCune, 1993; Price & Hochachka, 2001; Campbell & Fredeen, 2004). Within mountain caribou range, Lewis (2004) reported that biomass of both *Bryoria* and *Alectoria* was low in stands younger than 50 years and the proportion of the biomass composed of *Alectoria* decreased as stand age decreased. Seventy-five years after wildfire, hair lichen biomass in a regenerating Engelmann spruce-subalpine fir stand was low compared to old-growth stands, and *A. sarmentosa* was particularly sparse (Goward & Campbell, 2005). In a western larch seed tree block, none of the 20- to 40-year-old trees sampled by Bunnell *et al.* (2007) reached Lichen Abundance Class 3 of Armleder *et al.* (1992), the threshold for potential caribou feeding sites identified by field researchers (Stevenson *et al.*, 1998).

There has been considerable discussion in the literature of the extent to which the low abundance of hair lichens in young stands is attributable to dispersal limitations, to slow growth rates, to microclimatic variables, or to structural limitations of young trees (e.g., Esseen *et al.*, 1996; Peck & McCune, 1997; Peterson & McCune, 2001; Goward & Campbell, 2005). Dispersal studies in a variety of locations have consistently shown that *Bryoria* spp. disperse more effectively than *Alectoria sarmentosa* (Stevenson, 1988; Dettki, 1998; Dettki *et al.*, 2000; Quesnel & Waters, 2001; Stevenson & Coxson, 2003). Within mountain caribou range, Goward (2003) reported that *Bryoria*

fragment densities on snow in subalpine meadows were greatest near the forest edge but still substantial at 1 and 2 km from the edge. In a larch stand in the East Kootenay region of British Columbia, abundance of *Bryoria* spp. on the regenerating trees was not associated with proximity to the larch seed trees (Bunnell *et al.*, 2007). It appears that, at least at the scale of a partial cut, dispersal does not limit the colonization of regeneration by *Bryoria* spp. in high-elevation mountain caribou range.

There is more evidence for dispersal as a limiting factor for *A. sarmentosa*. In addition to studies cited above that showed limited dispersal distances of *A. sarmentosa*, abundance of *A. sarmentosa* in managed stands has been associated with the presence of remnant old trees (Neitlich & McCune, 1997; Peterson & McCune, 2001). The limited dispersal capability of *A. sarmentosa* is probably associated with both large fragment size and, in many forest types, its characteristic location in the lower canopy that results in a low release height of fragments.

There is mounting evidence that the abundance of *Bryoria* spp. in young stands is limited primarily by the structural attributes of young trees. Goward (1998) hypothesized, based on the distributional patterns of *Bryoria* spp. in Engelmann spruce-subalpine fir forests, that *Bryoria* is intolerant of prolonged wetting, especially as a result of snowmelt. He observed that *Bryoria* biomass is invariably much greater on defoliated portions of branches than in the foliated zone, except where foliated branches are exposed to high ventilation. He ascribed the low abundance of *Bryoria* on foliated branch portions primarily to greater accumulation and retention of snow, resulting in prolonged wetting and periodic dieback of *Bryoria*. *Bryoria* does not become abundant until trees are old enough – usually 100-150 years – to develop a substantial defoliated zone. In their study of a regenerating stand 75 years after wildfire, Goward & Campbell (2005) attributed the low *Bryoria* biomass in the upper canopy to substrate limitations – the availability of defoliated branches and the stable environmental conditions that develop once crown growth has slowed. They attributed the low *Bryoria* biomass in the lower canopy (above the snow-pack) to sheltered conditions producing humidity levels that are too high for many *Bryoria* species.

### Physiology and growth rates of hair lichens

The studies of hair lichen abundance in high-elevation mountain caribou range discussed in the previous sections revealed that *Alectoria sarmentosa* is often abundant in the lower canopy of old stands, and sparse or absent in the upper canopy. It remains present on

residual trees after partial cutting, but does not exhibit a conspicuous increase in biomass. It is extremely sparse or absent on young regeneration after partial cutting.

These studies also showed that *Bryoria* spp. are present throughout the canopy in old Engelmann spruce-subalpine fir stands, but reach their highest abundance in the mid to upper canopy. After partial cutting, the abundance of *Bryoria* on residual trees increases. *Bryoria* spp. are consistently present on regenerating trees in young stands and partial cuts, but do not attain high biomass until later in stand development. The distribution pattern of *Bryoria* spp. suggests that many species do not tolerate prolonged wetting, and are excluded from locations that are poorly ventilated or subject to prolonged hydration.

Studies of the physiology and growth rates of lichens can help to elucidate the mechanisms behind observed patterns of abundance. Coxson & Coyle (2003) examined the hypothesis that height-related niche partitioning of *Alectoria* and *Bryoria* reflects differential growth responses to gradients in canopy microclimate. If that hypothesis was supported, it would also help to explain changes in abundance patterns in partial cuts, where increased exposure alters the canopy microclimate profile. Coxson & Coyle (2003) measured microclimate variables at two heights in an old Engelmann spruce-subalpine fir stand: at 4 m, in the zone where *A. sarmentosa* is abundant, and at 15 m, in the lower portion of the zone dominated by *Bryoria* spp. In the laboratory, they measured photosynthetic and respiratory activity of *A. sarmentosa* and *Bryoria* spp. at a range of temperatures, moisture levels, and light intensities. Combining the two data sets, they estimated net assimilation by month for *A. sarmentosa* and *Bryoria* spp. at the 4- and 15-m level over a 20-month period.

Both genera were capable of maintaining positive net assimilation during most of the year, experiencing negative assimilation only during early winter (Fig. 1). Lichen thalli were hydrated from snowmelt events 26-29% of the time during the winter, though 75% of the time hydration occurred in the dark. During summer, the lichens were hydrated by rainfall 16% of the time, 45% of this in the dark. During both winter and summer, the single largest limitation on net assimilation in both genera was thallus moisture content (Coxson & Coyle, 2003). *A. sarmentosa* showed consistently higher rates of net assimilation at 4 m than at 12 m. These results would predict reduced biomass accumulation in upper canopy positions, though perhaps not as abrupt a decline as is observed in the field. This may reflect the relatively small gradients in moisture availability observed with height in the canopy profile, due to the quite open

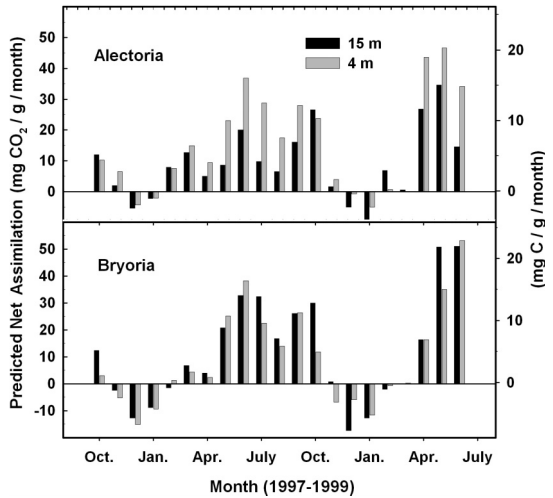


Fig. 1. Predicted net assimilation ( $\text{mg CO}_2 \cdot \text{g}^{-1} \cdot \text{month}^{-1}$  and  $\text{mg C}^{-1} \cdot \text{g}^{-1} \cdot \text{month}^{-1}$ ) in *Alectoria sarmentosa* and *Bryoria* spp. (*B. fremontii* and *B. fuscescens*) at heights of 4 and 15 m within the canopy. Measurements are for the period October 1997 to June 1999 (reproduced from Coxson & Coyle, 2003).

canopy structure in ESSF. Other factors, such as breakage of the long, relatively heavy thalli of *A. sarmentosa* when subjected to loads of ice or snow, may be more important in excluding *Alectoria* from the upper canopy positions in these high-snowfall ecosystems.

In contrast, Coxson & Coyle (2003) found no consistent relationship between canopy position and net assimilation for *Bryoria* spp. Their results predict that *Bryoria* would occur with equal abundance in upper and lower canopy positions. As that is not the case, Coxson & Coyle (2003) also examined the possibility that some *Bryoria* spp. are excluded from the lower canopy by their response to prolonged wetting. They measured rates of gas exchange of thalli of *Bryoria* spp. and *A. sarmentosa* that were kept fully saturated for 12 days. Although rates of net photosynthesis of saturated thalli declined over time in both genera (Fig. 2), *Bryoria* spp. showed a more abrupt decline after six days of continuous hydration, whereas *A. sarmentosa* declined more gradually. It should be noted that this decline appears mainly to be one of the algal biont's physiological response, as rates of dark respiration (predominantly from the fungal biont) show little change over this time period. These results, though not conclusive, tend to support Goward's (1998) hypothesis that some *Bryoria* species do not persist in canopy positions where they experience prolonged wetting, either from summer rainfall events or from wet snowpack held on branches within the canopy. Although a more open stand structure will

most immediately reduce the duration of periods when lichens can grow, with evaporation rates increasing as exposure to wind and solar insolation increase, these same trends will limit respiratory loss of lichen biomass during extended wetting events (and subsequent dieback events). Further, the sloughing of accumulated snow from canopy branches during high wind gusts may reduce *in-situ* decomposition of thalli within lower canopy positions.

It is reasonable to expect that differences in net assimilation will be reflected in the growth rates of individual lichen thalli. On the basis of physiological studies, we would predict higher growth rates for *Alectoria* in sheltered locations, such as the lower canopy or a more closed stand, than in exposed locations, such as the upper canopy or a more open stand. Physiological studies do not suggest any difference in *Bryoria* growth rates between more sheltered and more exposed locations, although there does appear to be a physiological basis for the exclusion of *Bryoria* from sheltered locations. The lichen abundance studies, however, suggest that individual thalli of *Bryoria* might grow faster in more exposed locations.

### Growth rates of individual lichen thalli

At three silvicultural systems study areas in Engelmann spruce-subalpine fir stands (Table 2), we have measured growth rates of arboreal lichens by repeatedly weighing lichen thalli that were attached to an artificial substrate and grown in the field.

Although methods varied slightly among study areas, the general approach was the same: we weighed composite samples of 2-4 individual specimens of either *Alectoria sarmentosa* or *Bryoria* spp. in a laboratory in which temperature and humidity were controlled, and then attached the samples to glass tubes with silicone seal. After the silicone seal dried, we reweighed the lichen/tube assemblies, fitted them into mesh-covered enclosures, and suspended them from the branches of trees. In spring and fall of each year, we reweighed the lichen/tube assemblies and returned them to the field. Lichen fragments found on the floor of the enclosure were weighed and discarded, but some loss of sample fragments as well as gain of non-sample fragments occurred. These methods were described in more detail by Stevenson (2001) and Stevenson & Coxson (2003).

In all treatments except the Group Selection treatment (Table 2), the enclosures were placed on randomly selected trees located along transects. In the Group Selection treatment at Pinkerton CP377, enclosures were placed on randomly selected trees along the edges of the openings (Stevenson & Coxson 2003).

We expressed the results of these three studies as relative growth (RG) over the entire measurement period (Fig. 3), or

$$RG = (W_2 - W_1) / W_1 * 100$$

where  $W_1$  is lichen weight at the beginning of the study and  $W_2$  is lichen weight at the end of the study. Thus, relative growth of 100% indicates that the

**Table 2.** Summary of lichen growth rate study areas

Study area	References	Monitoring period	Treatments	Treatment description	Number of growth rate samples
Pinkerton CP 376	Stevenson <i>et al.</i> , 2001; S. Stevenson, unpubl. data	1992-1994	Single-tree selection (STS)	61% basal area removal with dispersed retention	17 <i>Bryoria</i> 16 <i>Alectoria</i>
			Unlogged control (UN)		19 <i>Bryoria</i> 19 <i>Alectoria</i>
Lucille Mountain	Stevenson, 2001; S. Stevenson, unpubl. data	1993-2000	Irregular shelterwood (ISW)	50% basal area removal with dispersed retention	11 <i>Bryoria</i> 12 <i>Alectoria</i>
			Group retention (GR)	69% basal area removal with clumped retention	13 <i>Bryoria</i> 14 <i>Alectoria</i>
			Unlogged control (UN)		17 <i>Bryoria</i> 16 <i>Alectoria</i>
Pinkerton CP 377	Stevenson & Coxson, 2003	1999-2000	Single-tree selection (STS)	30% basal area removal with dispersed retention	39 <i>Bryoria</i> 46 <i>Alectoria</i>
			Group selection (GS)	30% basal area removal in openings of 0.1-0.4 ha	36 <i>Bryoria</i> 32 <i>Alectoria</i>
			Unlogged control (UN)		41 <i>Bryoria</i> 39 <i>Alectoria</i>

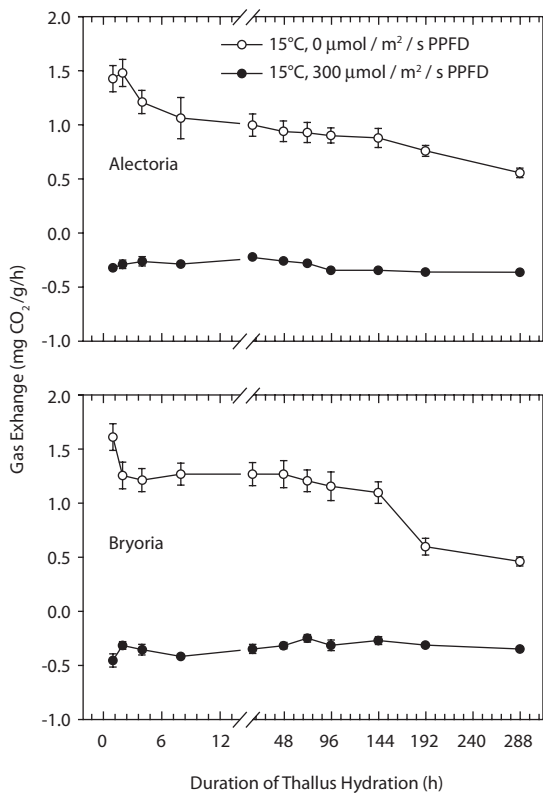


Fig. 2. Mean rates of gas exchange ( $\text{mg CO}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$ ) in summer-collected thalli of *Alectoria sarmentosa* and *Bryoria* spp. held at full thallus saturation for up to 288 h. Gas exchange measurements took place at 15°C, and each of 0 and 300  $\mu\text{mol} \cdot \text{g}^{-1} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$  photosynthetic photon flux density (PPFD) (reproduced from Coxson & Coyle, 2003).

thalli doubled their mass; the relative growth rates of approximately 250% observed in the unlogged treatment unit at Lucille Mountain indicate that the thalli more than tripled their mass over a 7-year period. Thalli that failed to gain mass during the study period – generally because of mortality, loss of large fragments, or damage to the enclosures – are excluded; the resulting sample sizes are shown in Table 2. Data were arcsine transformed for statistical analysis. Significant differences shown in Figure 3 are based on *t*-tests (Pinkerton CP376) and analysis of variance with Bonferroni adjustments for multiple comparisons (Lucille Mountain; Pinkerton CP377).

In general, growth rates of *Alectoria* were lower in the partially cut areas than in the unlogged control areas. At Lucille Mountain, *Alectoria* growth rates appeared to be lower in the more evenly dispersed retention of the irregular shelterwood treatment than in the clumpier retention of the group retention treat-

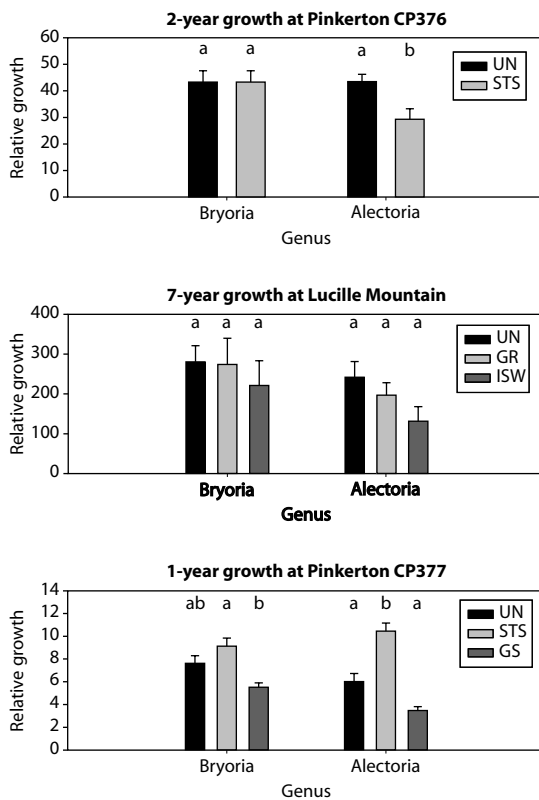


Fig. 3. Relative growth (per cent) and standard error of *Bryoria* spp. and *Alectoria sarmentosa* thalli at three silvicultural systems study areas: Pinkerton CP376 (adapted from Stevenson *et al.*, 2001), Lucille Mountain (S. Stevenson, unpubl. data; methods in Stevenson, 2001), and Pinkerton CP377 (adapted from Stevenson & Coxson, 2003). Within species, means sharing the same letter were not significantly different ( $P > 0.05$ ; Bonferroni adjustment for multiple comparisons).

ment, even though basal area removal was higher in the group retention treatment (Table 2). These trends were not statistically significant at the 0.05 level, perhaps because attrition over the seven-year study period resulted in small sample sizes. The single exception to this pattern occurred in the single-tree selection treatment unit at Pinkerton CP377, which represented the smallest increase in canopy exposure of any of the treatments studied. Thus, the *Alectoria* growth rates observed in the growth rate studies are generally consistent with the physiological studies and with the abundance patterns observed in partial cuts.

On the basis of the lichen abundance studies reviewed above, we would expect that growth rates of individual *Bryoria* thalli would be elevated in partial cuts. Physiology studies, which found no relationship

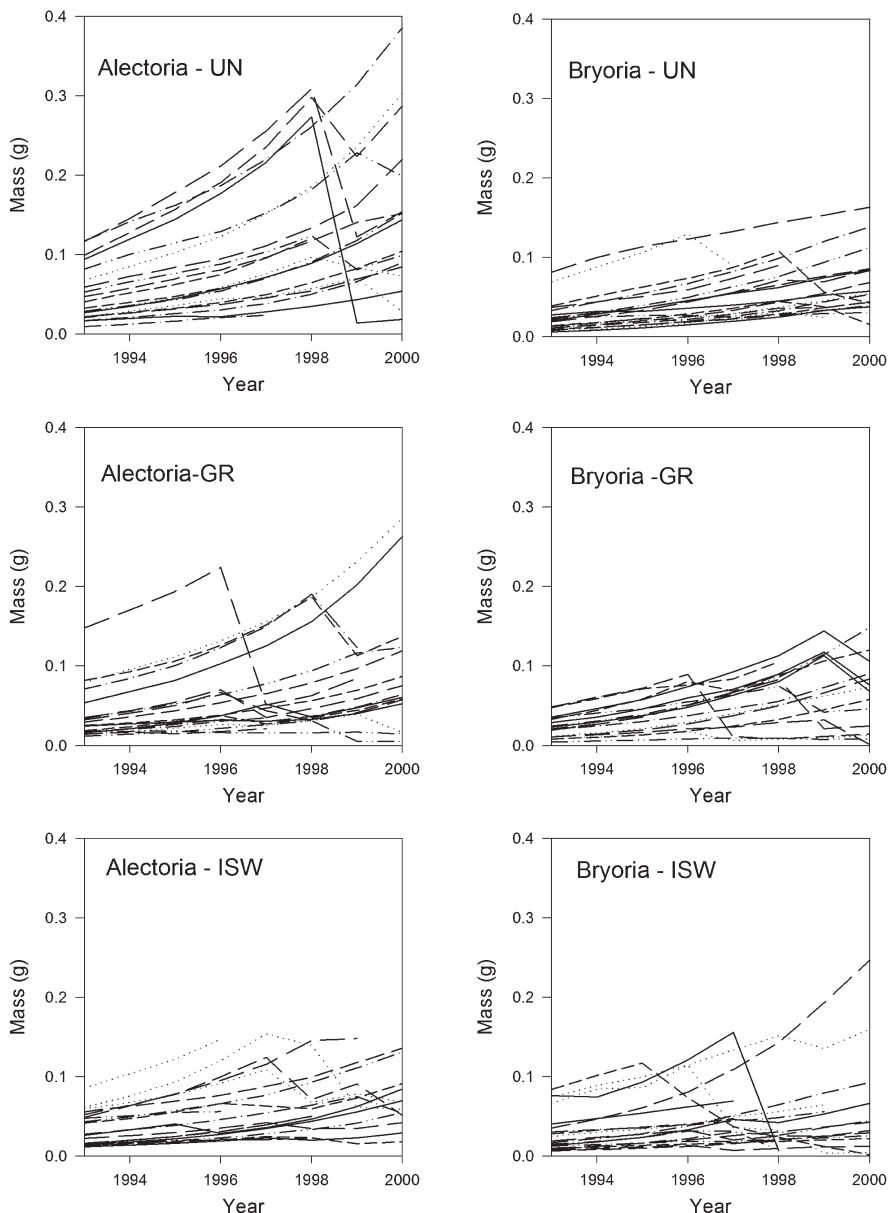


Fig. 4. Mass (g) of individual growth-rate replicates of *Alectoria sarmentosa* and *Bryoria* spp. in the unlogged control area (UN), group retention area (GR), and irregular shelterwood area (ISW) at Lucille Mountain, fall 1993-fall 2000 (S. Stevenson, unpubl. data; methods and site description in Jull & Stevenson, 2001).

between net assimilation in *Bryoria* and canopy position, would predict that growth rates of *Bryoria* in partial cuts would not differ from those in an unlogged stand. Our results (Fig. 3) show few significant differences in *Bryoria* growth rates between the unlogged control areas and the partial cuts. Only on trees at the edges of group selection openings at Pinkerton CP377 were growth rates of *Bryoria* spp. significantly lower than growth rates in the unlogged control area. Stevenson & Coxson (2003) suggested

that the reduced growth rates reflected reduced duration of lichen hydration at the edge of the group selection openings, as described by Coxson *et al.* (2003). As well, substantial fragmentation of both *Alectoria* and *Bryoria* growth rate samples was documented at Pinkerton CP377 (Stevenson & Coxson 2003). Although samples that lost biomass were not included in the growth-rate analysis (Fig. 3), calculated growth rates may still have been affected by the loss of smaller fragments.



## The role of fragmentation

Changes in the biomass (standing crop) of canopy lichens depend on their net carbon assimilation (growth), but also on several other factors: losses through consumption by herbivores, losses through in situ decomposition, losses through fragmentation, and gains through colonization. Consumption by caribou in these ecosystems is relatively low because there are few caribou, and most of the lichens in the forest canopy are out of their reach. In situ decomposition probably is a significant factor in subalpine forests (Goward, 1998; Stevenson & Coxson, 2003), but it tends to differentially affect lichens in low-exposure habitats. As the growth-rate samples were small clumps isolated within mesh enclosures, they were well ventilated and unlikely to be subject to the dieback described by Goward (1998). Fragmentation, however, is an important factor in the ecology of hair lichens, and is the major source of the propagules that are responsible for colonization.

The seven-year growth rate data set from Lucille Mountain described above (Table 2) allows us to examine biomass accumulation of individual lichen thalli from fall 1993 until fall 2000, or until samples were lost due to enclosure damage or breakage of the entire specimen (Fig. 4). The data reveal a pattern of exponential growth, interrupted by deviations from the pattern. About half of the thalli that experienced a precipitous decline in biomass resumed exponential growth, while the remainder continued to decline. Thalli such as these, which lost large fragments, would have been excluded from the results shown in Fig. 3, because of their net loss of biomass over the 7-year period. Other thalli leveled off or declined slightly in biomass, and then resumed exponential growth. These individuals, which presumably lost smaller fragments, would have been included in the data summarized in Fig. 3. Overall, the results reveal a dynamic system in which fragmentation has a major influence on calculated growth rates.

Fragmentation does not affect calculated growth rates equally, however, in all lichen groups. The tendency of *Alectoria sarmentosa* to produce fewer but larger fragments than *Bryoria* spp. has been documented in several studies (Stevenson, 1988; Renhorn & Esseen, 1995; Dettki, 1998). Using the Lucille Mountain growth rate data set, we calculated the mass of each fragment found on the floor of the enclosure as a percent of the mass of the growth rate sample at the beginning of the measurement period, and graphed the results by 10% intervals. More small fragments of *Bryoria* spp. than *Alectoria* were found in the bottoms of cages (Fig. 5). These results actually understate the effect because the smallest fragments (< about 1% of the mass of the growth rate sample),

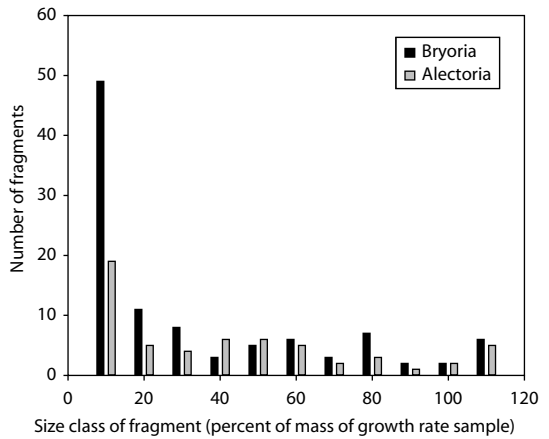


Fig. 5. Size-class distribution of *Bryoria* and *Alectoria* fragments collected from the bottoms of enclosures at Lucille Mountain, 1993–2000. Size classes represent the mass of the fragment as a percentage of the mass of the sample at the beginning of the measurement period (S. Stevenson, unpubl. data; methods in Stevenson, 2001).

which were overwhelmingly *Bryoria* spp., were not collected and weighed. As well, fragmentation occurs more commonly in partial cuts than in unlogged stands. Over the course of the Lucille Mountain study, the occurrence of fragments at the bottoms of cages in the partial cuts was about twice that in the unlogged control area (unpublished data).

We agree with the contention of Goward (1998) that ventilation has an important role in the ecology of *Bryoria* spp. Although a more exposed microclimate does not appear to enhance the capacity of *Bryoria* spp. for net assimilation (at least within the microclimatic range we studied), it probably helps to prevent the dieback phenomenon described by Goward (1998) in less open stands. As well, it increases the amount of substrate available for colonization by *Bryoria*, because increased ventilation enables *Bryoria* to survive on the foliated portions of branches. Finally, we suggest that a windier environment increases fragmentation rates. Although continuous production of small fragments in *Bryoria* may have somewhat reduced calculated growth rates, the dispersal and colonization of copious amounts of small fragments probably enhanced the overall levels of biomass accumulation in partial cuts.

The evaluation of lower canopy environments and their ability to support lichen growth after harvesting can be assessed using measurements of light availability and/or canopy openness from a fish-eye lens or canopy densiometer (see Coxson & Stevenson 2007 for an outline of relevant methodologies). Although it is unlikely that light availability by itself is an important parameter controlling net assimilation in *Alectoria*

or *Bryoria* (Coxson & Coyle, 2003), it provides a valuable surrogate for the assessment of convective exchange and associated ventilation of lichen thalli. Vertical profiling of convective exchange within forest stands, using cup- or hot-wire anemometers, provides a more direct assessment of canopy ventilation, though installation costs can be high. Direct measurements of lichen hydration status using impedance measurements may provide the most cost-effective approach for assessing lichen growth environments (Coxson, 1991), though care must be taken to ensure sufficient replication to capture what can be quite high levels of variability between adjacent branches.

## Management implications

The development of partial-cutting prescriptions that will maintain adequate availability of forage lichens for mountain caribou in Engelmann spruce-subalpine fir forests requires a balance between increasing the level of exposure of retained trees to enhance tree-level *Bryoria* accumulation, and retaining enough trees that stand-level lichen biomass is adequate. It is now clear that over time, partial cutting not only increases the relative proportion of *Bryoria* to *Alectoria*, but also increases the total amount of forage lichen available on individual trees. Prescriptions that enhance exposure while keeping basal area removal low will maintain forage best. Naturally clumped groups of trees in old stands have been found to support significantly more forage lichens per branch than solitary trees (Campbell & Coxson, 2001), and are prime candidates for retention in partial cutting prescriptions.

Maintaining a continuous supply of forage lichen at the stand level is critical to meet the objective of maintaining large, unfragmented areas of habitat for mountain caribou. Because lichen colonization on regenerating trees is slow – despite abundant propagules for colonization – prescriptions should be designed to maintain adequate lichen biomass at the stand level on residual trees. Stands with high basal area removal may show continued low lichen availability at the stand level over much of the rotation age of the stand. We recommend that managers continue to restrict basal area removal to 30% or less in partial cuts planned to maintain habitat for mountain caribou, as recommended by Stevenson *et al.* (2001).

As the regeneration develops after partial cutting, it begins to reduce ventilation in the lower canopy of residual trees, and if the regeneration is dense, it may trigger dieback of *Bryoria* spp. At this stage, spacing of the regeneration may help maintain lichen availability on the residuals. Planting or spacing prescriptions that encourage a clumped distribution of the regeneration may help maintain ventilation, and also enhance the

future ability of the young trees to support forage lichens. Nevertheless, managers who seek to maintain a continuous source of lichen using selection-harvesting systems in mountain caribou range should not expect a second harvest entry in less than 80 years.

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## Literature cited

- Apps, C. D. & McLellan, B. N. 2006. Factors influencing the dispersion and fragmentation of endangered mountain caribou populations. – *Biological Conservation* 130: 84-87.
- Armleder, H. M., Stevenson, S. K. & Walker, S. D. 1992. *Estimating the abundance of arboreal forage lichens*. BC Min. For. Land Manage. Handb. Field Guide Insert 7, Victoria, B.C. 22pp.
- Bunnell, F. L., Goward, T. Houde, I. & Björk, C. 2007. Larch seed trees sustain arboreal lichens and encourage recolonization of regenerating stands. – *West. J. Appl. For.* 22: 94-98.
- Campbell, J., & Coxson, D. S. 2001. Canopy microclimate and arboreal lichen loading in subalpine spruce-fir forest. – *Can. J. Bot.* 79: 537-555.
- Campbell, J & Fredeen, A. L. 2004. *Lobaria pulmonaria* abundance as an indicator of macrolichen diversity in Interior Cedar-Hemlock forests of east-central British Columbia. – *Can. J. Bot.* 82: 970-982.
- Coxson, D. S., 1991. Impedance measurement of thallus moisture content in lichens. – *Lichenologist* 23: 77-84.
- Coxson, D. S., & Coyle, M., 2003. Niche partitioning and photosynthetic response of Alectorioid lichens from subalpine spruce-fir forest in north-central British Columbia, Canada: the role of canopy microclimate gradients. – *Lichenologist* 35: 157-175.
- Coxson, D. S. & Stevenson, S. K. 2007. Growth rate responses of *Lobaria pulmonaria* to canopy structure in even-aged and old-growth cedar-hemlock forests. – *For. Ecol. and Manage.* 242: 5-16.
- Coxson, D. S., Stevenson, S. K. & Campbell, J. 2003. Short-term impacts of partial cutting on lichen retention and canopy microclimate in an Engelmann Spruce-Subalpine Fir forest in north-central British Columbia. – *Can. J. For. Res.* 33: 830-841.
- DeLong, D., Miller, J. McLellan, B. & Terry, E. 1999. Partial cutting prescriptions for mountain caribou in the

- ESSF of southeastern BC – a retrospective investigation. Unpubl. FRBC rep. KB 97 194, Nelson, B.C. 28pp.
- Dettki, H. 1998. Dispersal of fragments of two pendulous lichen species. – *Sauteria* 9:123-132.
- Dettki, H., Klintberg, P. & Esseen, P. A. 2000. Are epiphytic lichens in young forests limited by local dispersal? – *Ecoscience* 7: 317-325.
- Esseen, P.-A., Renhorn, K.-E. & Pettersson, R. B. 1996. Epiphytic lichen biomass in managed and old-growth boreal forests: effect of branch quality. – *Ecol. Appl.* 6: 228-238.
- Goward, T. 1998. Observation on the ecology of the lichen genus *Bryoria* in high elevation conifer forests. – *Can. Field-Nat* 112: 496-501.
- Goward, T. 2003. On the dispersal of hair lichens (*Bryoria*) in high-elevation oldgrowth conifer forests. – *Can. Field-Nat.* 117: 44-48.
- Goward, T. & Campbell, J. 2005. Arboreal hair lichens in a young, mid-elevation conifer stand, with implications for the management of mountain caribou. – *Bryologist* 108: 427-434.
- Jull, M. J. & Stevenson, S. K. (eds.). 2001. *The Lucille Mountain Study: 8-year results of a silvicultural systems trial in the Engelmann Spruce-Subalpine Fir Zone*. BC Min. For. Working Paper 59, Victoria, B.C. 93pp.
- Lewis, D. W. 2004. *Arboreal lichens in natural and managed high elevation spruce-fir forests of the North Thompson Valley, British Columbia*. M.R.M. thesis. Simon Fraser University, Burnaby, B.C. 97pp.
- McCune, B. 1993. Gradients in epiphyte biomass in three *Pseudotsuga-Tsuga* forests of different ages in western Oregon and Washington. – *Bryologist* 96: 405-411
- Mountain Caribou Technical Advisory Committee. 2002. *A strategy for the recovery of mountain caribou in British Columbia*. BC Min. Water, Land and Air Protection, Victoria, B.C. 73pp.
- Neitlich, P. N. & McCune, B. 1997. Hotspots of epiphytic lichen diversity in two young managed forests. – *Conservation Biology* 11: 172-182.
- Peck, J. E. & McCune, B. 1997. Remnant trees and canopy lichen communities in western Oregon: a retrospective approach. – *Ecol. Appl.* 7: 1181-1187.
- Peterson, E. B. & McCune, B. 2001. Diversity and succession of epiphytic macrolichen communities in low-elevation managed conifer forests in Western Oregon. – *J. Vegetation Sci.* 12: 511-524.
- Price, K. & Hochachka, G. 2001. Epiphytic lichen abundance: effects of stand age and composition in coastal British Columbia. – *Ecol. Appl.* 11: 904-913.
- Quesnel, H. J. & Waters, L. 2001. Integrating mountain caribou requirements and forest management in the Interior Cedar Hemlock: lichen retrospective and dispersal study. Final report prepared for BC Min. For., Research Branch. 40pp.
- Renhorn, K.-E. & Esseen, P.-A. 1995. Biomass growth in five alectoroid lichen epiphytes. – In: C. Scheidegger, P. A. Wolseley & G. Thor (eds.). *Conservation Biology of Lichenised Fungi*. Mitteilungen der Eidgenossischen Forschungsanstalt für Wald, Schnee und Landschaft 70(1), Birmensdorf, Switzerland, pp. 133-140.
- Rominger, E. M., Allen-Johnson, L. & Oldemeyer, J. L. 1994. Arboreal lichen in uncut and partially cut sub-alpine fir stands in woodland caribou habitat, northern Idaho and southeastern British Columbia. – *For. Ecol. and Manage.* 70: 195-202.
- Rominger, E. M., Robbins, C. T. & Evans, M. A. 1996. Winter foraging ecology of woodland caribou in northeastern Washington. – *J. Wildl. Manage.* 60: 719-728.
- Stevenson, S. K. 1988. *Dispersal and colonization of arboreal forage lichens in young forests*. BC Min. Environ. and BC Min. For., IWIFR-38, Victoria, B.C. 58pp.
- Stevenson, S. K. 2001. Arboreal lichens. – In: Jull, M. J. & Stevenson, S. K. (eds.). 2001. *The Lucille Mountain Study: 8-year results of a silvicultural systems trial in the Engelmann Spruce-Subalpine Fir Zone*. BC Min. For. Working Paper 59, Victoria, B.C., pp. 60-65.
- Stevenson, S. K. & Coxson, D. S. 2003. Litterfall, growth, and turnover of arboreal lichens after partial cutting in an Engelmann spruce-subalpine fir forest in north-central British Columbia. – *Can. J. For. Res.* 33: 2306-2320.
- Stevenson, S. K. & Hatler, D. F. 1985. *Woodland caribou and their habitat in southern and central British Columbia*. BC Min. For. Land Manage. Rep. No. 23. Vol. 1. Victoria, B.C. 355pp.
- Stevenson, S. K., Armleder, H. M., Jull, M. J., King, D. G., Terry, E. L., Watts, G. S., McLellan, B. N. & Child, K. N. 1994. *Mountain caribou in managed forests: preliminary recommendations for managers*. BC Min. For. and B.C. Min. Environ., Lands and Parks. Victoria, B.C. 33pp.
- Stevenson, S. K., Armleder, H. M., Jull, M. J., King, D. G., McLellan, B. N. & Coxson, D. S. 2001. *Mountain caribou in managed forests: recommendations for managers*. Second Edition. BC Min. Environ., Lands, and Parks, Wildlife Rep. No. R-26, Victoria, B.C. 58pp.
- Stevenson, S. K., Lance, A. N., & Armleder, H. M. 1998. *Estimating the abundance of arboreal forage lichens: user's guide*. BC Min. For. Land Manage. Handb. 43. Victoria, B.C. 35pp.
- Waterhouse, M. J., Armleder, H. M. & Nemeč, A. F. L. 2007. *Arboreal forage lichen response to partial cutting of high elevation mountain caribou range in the Quesnel Highland of east-central British Columbia*. This volume.