Short-term impacts of partial cutting on lichen retention and canopy microclimate in an Engelmann spruce – subalpine fir forest in north-central British Columbia

Darwyn Coxson, Susan Stevenson, and Jocelyn Campbell

Abstract: The retention of canopy lichens (*Alectoria*, *Bryoria*, and foliose) in group selection (GS) and single-tree selection (STS) partial cuts (30% removal) was studied within a subalpine spruce–fir forest (*Picea englemannii* Parry ex Engelm. – *Abies lasiocarpa* (Hook.) Nutt.) in north-central British Columbia. Baseline canopy lichen loading (preharvest and immediate postharvest) was compared with lichen loading 2 years after harvesting, using both ground-and canopy-based sampling techniques. Additionally, canopy microclimate was compared between GS and adjacent stand areas with no harvest treatment (NT). Partial cutting did not have a significant effect on lichen loading in residual trees, although a trend of declining lichen abundance was observed in each of the GS, STS, and NT areas. Partitioning of lichen abundance data showed significant postharvest declines for upper canopy STS *Bryoria* and smaller, but significant, changes in foliose lichen abundance in the NT and STS areas. No significant changes in canopy microclimate were observed between treatments, with the exception of south-facing aspects in GS trees, which showed reduced duration of lichen hydration. Taken together, these factors suggest that although the placement of *Bryoria* in residual trees may shift towards lower canopy exposures, partial-cut harvest treatments can maintain short-term lichen loading and associated ecosystem values (e.g., caribou forage) in subalpine spruce–fir stands.

Résumé: La conservation des lichens du couvert (Alectoria, Bryoria et le lichen foliacé) dans les coupes partielles (prélèvement de 30 %) par sélection de bouquets (SB) et de réserves (SR) a été étudiée dans une forêt subalpine d'épinettes et de sapins (Picea engelmannii Parry ex Engelm. - Abies lasiocarpa (Hook.) Nutt.) au centre nord de la Colombie-Britannique. La charge de base en lichens dans le couvert (avant et immédiatement après la récolte) a été comparée avec celle observée 2 ans après la récolte, en utilisant à la fois des méthodes d'échantillonnage au sol et dans le couvert. De plus, le microclimat du couvert a été comparé entre les aires SB et des aires témoins non traitées constituées de peuplements voisins (NT). La coupe partielle n'a pas eu d'effet significatif sur la charge en lichens des arbres résiduels, même si une tendance vers une diminution de l'abondance en lichen a été observée dans toutes les aires SB, SR et NT. Un partitionnement des données d'abondance en lichen a montré un déclin significatif suite à la récolte pour Bryoria dans le haut du couvert des aires SR et des changements plus faibles mais significatifs dans l'abondance du lichen foliacé dans les aires NT et SR. Aucun changement significatif dans le microclimat du couvert n'a été observé entre les traitements, à l'exception du côté sud des arbres SB qui a montré une durée réduite dans l'hydratation des lichens. Pris ensemble, ces facteurs suggèrent que même si l'emplacement de Bryoria dans les réserves peut se déplacer vers le bas du couvert, les traitements de récolte par coupe partielle peuvent maintenir à court terme une charge en lichen et les valeurs de l'écosystème s'y rattachant (p. ex. le fourrage du caribou) dans les peuplements subalpins d'épinettes et de sapins.

doi: 10.1139/X03-006

[Traduit par la Rédaction]

Introduction

Arboreal lichens, especially *Alectoria* and *Bryoria*, are abundant in high elevation forests of interior British Colum-

Received 22 November 2001. Accepted 19 December 2002. Published on the NRC Research Press Web site at http://cjfr.nrc.ca on 11 April 2003.

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bia, where stand-level lichen loading can exceed 400 kg·ha⁻¹ (Campbell and Coxson 2001; Edwards et al. 1960). These lichens are important as forage for mountain caribou (*Rangifer tarandus caribou*) (Edwards and Ritcey 1960; Rominger and Oldemeyer 1989; Rominger et al. 1996; Stevenson et al. 2001). Additionally they provide significant other ecosystem values, such as food and shelter for small mammals and a source of readily labile nutrient capital (Pike 1978; Coxson and Curteanu 2002). Forest management practices based on clear-cut harvesting and standard rotation intervals (ca. 100–120 years) are believed to be incompatible with the production of abundant forage lichens in high elevation forests, because of the long time interval (>150 years) required for canopy lichen communities to reach their maxi-

mum development (Detrick 1985; Antifeau 1987; Stevenson et al. 2001).

Related concerns have also been raised about the impact of forestry operations on adjacent patches of retained oldgrowth forest, particularly the significance of edge effects. Esseen and Renhorn (1998) noted that the impact of harvest openings within a closed-canopy forest can extend well beyond the trees that were actually removed, because of changes in canopy microclimate and forest canopy structure in the retained forest. The loss of lichens, both in terms of biodiversity and ecosystem function, at forest edges has been raised as an important concern in boreal and montane forests, where clear-cut harvesting can increase canopy exposure and habitat fragmentation (Dettki and Esseen 1998). The reduced availability of lichen propagules in retained old-growth forest patches may significantly limit future dispersal of lichens into surrounding second-growth forest patches.

One of the major variables that mediates these changes in composition of arboreal lichen communities at forest edges is the influence of canopy microclimate, both through immediate effects such as wind scouring and photoinhibition of retained lichen thalli, and through long-term effects, such as changes in growth rates as lichens respond to new gradients of light and moisture availability (Renhorn et al. 1997). Community composition of canopy lichens (McCune et al. 1997) may shift in forest patches where interior habitats are absent or greatly reduced. Further, lichens from old-growth dependent microsites (McCune et al. 2000) may be susceptible to the proportion of edge in managed forests (Esseen and Renhorn 1998).

In recent years a variety of forestry practices have been proposed to increase the retention of old-growth structures and organisms in forests managed for timber production (Franklin 1989; Franklin et al. 1997). Although most studies on lichen retention and forestry techniques based on ecosystem management have been confined to coastal forests of the Pacific Northwest, there has been widespread recognition of the importance of residual trees in enhancing lichen biodiversity in other ecosystems (Peck and McCune 1997; Rosso et al. 2000).

In British Columbia, forest managers have begun to use partial cutting systems in areas where abundant arboreal forage lichens, as well as other features characteristic of old forests, are important to the survival of wildlife. Guidelines have been developed for the use of partial cutting systems to maintain habitat for mule deer (Odocoileus hemionus hemionus) (Armleder et al. 1986) and for mountain caribou (Stevenson et al. 1994, 2001). The mountain caribou guidelines recommend a maximum of 30% removal of timber by volume, area, or basal area, through single-tree selection (STS) or group selection (GS) harvesting. GS harvest openings should be ≤ 1 ha, with a mean opening size ≤ 0.5 ha, and harvest entries should be at least 80 years apart. Some land use plans currently in effect (summarized by Stevenson et al. 2001) restrict forest harvesting to this type of partial cutting in areas zoned for the maintenance of caribou habitat.

Although the adoption of these guidelines is a useful precautionary measure on the part of forest managers, there is an urgent need to understand how the stand structural changes that result from partial cutting affect the composition and dynamics of arboreal lichen communities. We examined the retention of major groups of canopy lichens and changes in canopy microclimate in partially cut harvest blocks in a subalpine spruce—fir forest in north-central British Columbia. Our use of both ground- and canopy-based lichen sampling measures to assess postharvest changes in lichen abundance strengthened the validity of our findings and provided for a detailed assessment of within-canopy response on the part of lichen communities.

Materials and methods

Site description

The study area was in the Cariboo Mountains, approximately 90 km east, southeast of Prince George, British Columbia (53°37′38″N, 121°25′33″W), in the wet cold subzone of the Engelmann Spruce – Subalpine Fir (ESSF) zone (Meidinger and Pojar 1991). It is in an area zoned as "caribou medium" by the B.C. Ministry of Water, Land and Air Protection. "Caribou medium" is a designation applied to mid-elevation ESSF forests that are used for foraging by caribou, especially during early winter, but are not used as frequently as the higher-elevation zone designated as "caribou high." The land use plan currently in effect specifies that conservation of caribou habitat is a priority in that area, and that alternative silvicultural systems are preferred over clear-cutting (Province of British Columbia 1999, pp. 166–167).

The mesic to subhydric site is on a moderate, southwest-facing slope, between 1350 and 1450 m elevation. Vegetation in the shrub layer is dominated by *Rhododendron albiflorum* (white-flowered rhododendron) while the herb layer is largely made up of *Valeriana sitchensis* (Sitka valerian), *Veratrum viride* (Indian hellebore), *Rubus pedatus* (fiveleafed bramble), and *Gymnocarpium dryopteris* (oak fern).

The preharvest stand was uneven-aged, with trees up to approximately 350 years old (Campbell 1998). The trees were unevenly distributed and much of the stand was composed of closely associated trees forming clumps, separated by natural gaps in the canopy. These natural gaps composed about 50% of the stand area. Approximately 53% of the gaps were created by the death of a single tree, and 33% were created by the death of more than one tree (S. Stevenson, unpublished data). The absence of dead trees in some gaps and the fact that many openings appeared to be larger than could be explained by the originating mortality event(s) suggest that the site may be transitional between gap and tree-island regeneration patterns (Brett and Klinka 1998). The preharvest basal area was 36–39 m²·ha⁻¹, composed of mostly subalpine fir (Abies lasiocarpa (Hook.) Nutt.) (78%) with Engelmann spruce (Picea engelmannii Parry ex Engelm.) constituting only 22% of the canopy layer.

Epiphytic lichens in the study area were evaluated within three lichen growth-form sampling groups. These sampling groups were (i) Alectoria spp. lichens (mainly A. sarmentosa, but also including Usnea species, which were rare in the study area); (ii) Bryoria spp. lichens (including B. capillaris, B. fremontii, B. fuscescens, B. glabra, and B. pseudofuscescens, and Nodobryoria oregana); and (iii) foliose lichens (including Cetraria platyphylla, Hypogymnia imshaugii, H. metaphysodes, H. occidentalis, H. physodes, H. rugosa, H. tubulosa, Parmelia sulcata, and Platismatia glauca). The first two of these lichen

groups (Alectoria and Bryoria) can be treated, to some degree, as lichen functional groups, with dark coloured Bryoria spp. preferentially occupying drier upper canopy exposures, while the light coloured lichen A. sarmentosa is restricted to lower canopy exposures (Campbell and Coxson 2001). Usnea spp., also placed in the *Alectoria* group, prefer drier upper canopy exposures, but were largely absent from our study area. The foliose lichen group was more diverse in the ecological preferences of its members. The dominant member of the foliose lichen group, H. physodes, was found in all canopy height positions (Campbell and Coxson 2001) and appears to have a wide ecological tolerance. Three other sampling groups, commonly used in epiphyte studies, were not included in the present study. These were bryopytes and cyanolichens, which were excluded because they were rare or absent from canopies in the study area, and crustose lichens, which were excluded because of time constraints.

Silvicultural prescription

The Pinkerton Mountain installation is part of a larger, replicated set of silvicultural systems trials (Jull et al. 2001²) that comprises two sites in the ESSF zone and three at lower elevations in the Interior Cedar–Hemlock zone (Meidinger and Pojar 1991). Criteria for site selection included good road access, a willing forest licensee, and a homogeneous area large enough to accommodate a range of treatments at an operational scale. Harvesting has been completed at four of the five sites. Logging at the second ESSF site has been delayed because of unforeseen engineering problems, but is still planned.

Two uneven-aged silvicultural systems were used at Pinkerton Mountain: group selection (GS) and single-tree selection (STS) (Stevenson et al. 1999). In the 59-ha group selection area, trees were removed in discrete groupings ranging from 0.1 to 0.4 ha, 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 (Fig. 1). Area-based regulation of cut was maintained at the target 30% level by global positioning system (GPS) traverses of the marked openings.

In the STS area (40 ha), trees were removed from across the range of diameter classes to achieve a target diameter distribution. The prescription was developed by BDq regulation (Alexander and Edminster 1977; Guildin 1990), in which the residual stand is defined by setting targets for residual basal area (B), maximum residual diameter (D), and the shape of the postharvest diameter distribution (q). The residual basal area was determined by the recommended 30% limit on level of removal in mountain caribou habitat (Stevenson et al. 1994, 2001). There was no maximum residual diameter; instead, trees larger than 52.5 cm DBH were retained unless they had to be felled to clear skid trails. A q value of 1.2 was selected, because it allows relatively high retention of larger diameter classes.

In addition to these prescription areas, a similar area adjacent to the harvest block with no harvest treatment (NT) was

used for comparative measures. Both treatment units were harvested in March and April 1998, on a settled late-winter snowpack. Trees were felled with a zero-tailswing feller–buncher (Timbco 455C), and skidded to the landings and roadsides by tracked grapple skidders. The resulting post-harvest basal area was 23–27 m²·ha⁻¹ for both treatment units.

Lichen biomass estimation

We used two techniques to quantify lichen abundance, a ground-based assessment, after Armleder et al. (1992), and a canopy-based assessment, after Campbell et al. (1999).

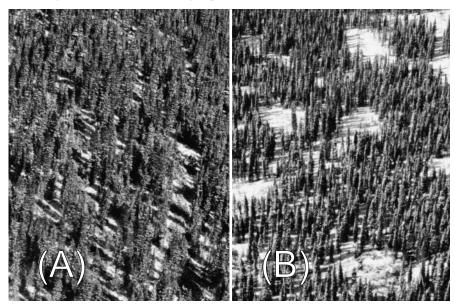
For the ground-based assessments, we used a photo guide (Armleder et al. 1992) to extensively survey the abundance of the Alectoria and Bryoria lichen groups, collectively, in the lower canopy before and after harvest. The photo guide presents a series of photos of trees with known biomass of Alectorioid lichens below 4.5 m, which is the part of the tree that is potentially within reach of caribou in high-elevation forests during winter. The user compares the tree being assessed to the photos, and classifies it into one of six lichenabundance classes (0, 1, 2, 3, 4, or 5; in which 0 indicates no lichens and 5 indicates very high lichen abundance). We used additional, unpublished photos representing the midpoints of classes 3 and 4 to further distinguish between high and low subclasses, termed 3-low, 3-high, 4-low, and 4-high. Comparisons of classifications based on the photo guide with actual biomass measurements have shown that an experienced observer can classify most trees correctly, but that when errors occur, they are more likely to be underestimates than overestimates (Stevenson et al. 1998).

In 1993, photo guide estimates were completed on all trees (both *A. lasiocarpa* and *P. engelmannii*) ≥7.5 cm DBH in 0.01-ha plots that were systematically located throughout the two treatment areas, and in the NT area. In 2001, we relocated 11 plots in each of the three areas and reclassified the trees. We refer to these two measurement sets as the preharvest and 2-year postharvest data sets, respectively.

The second lichen sampling technique was based on the use of intensive within-canopy based visual estimates of lichen abundance using single rope climbing techniques (Campbell et al. 1999). Ten sample trees were randomly selected from a population of 30 trees in each of the GS, STS, and NT treatment areas. This set of candidate trees included individuals of both Abies lasiocarpa and Picea engelmanni, in proportion to their relative abundance in the stand. These trees were co-dominant or dominant (typically >25 m in height), often at the centre of regenerating "clumps" of trees, in keeping with the nature of tree distribution at this site. Candidate trees were also judged on the basis of their suitability for climbing (Campbell et al. 1999). Of the complement of sample trees remaining after harvesting (some of the sample trees were removed during harvesting), 4 of the 10 sample trees in the NT area were P. engelmanni. Within the STS and GS areas, all of the remaining sample trees (5 in each case) were A. lasiocarpa.

²M. Jull, S. Stevenson, B. Rogers, P. Sanborn, and A. Eastham. 2001. Northern Wetbelt Silvicultural Systems Projet: establishment report. Unpublished report, University of Northern B.C., Prince George, B.C. Available from: M. Jull, Forestry Program, University of Northern British Columbia, 3333 University Way, Prince George, BC V2N 4Z9, Canada.

Fig. 1. Oblique aerial view of single-tree selection (A) and group selection (B) harvest areas at Pinkerton Mountain.



Visual estimates at a branch level were taken for three lichen sampling groups, an Alectoria sampling group (including A. sarmentosa and Usnea spp.), a Bryoria sampling group (including Bryoria spp.), and a foliose sampling group (including all green foliose lichens), using the "clump method" developed by Stevenson (1979) and validated by Campbell et al. (1999). This method is based on the visual estimation of the amount of lichen on a given branch compared with a standard "clump" of lichen of known size and mass. For lichens from the Alectoria and Bryoria sampling groups, a 2.5-g (dry mass) clump of lichen was used as a standard for comparison. A similar method was used for foliose lichens, based on a 1.5-g (dry mass) sample of foliose lichen (using the dominant canopy lichen H. physodes). Consistency was crucial and was maintained by frequently comparing our estimates with the standards. Regression models, based on the relationship between estimated and measured lichen biomass on a subsample of branches (Campbell et al. 1999; Campbell and Coxson 2001), were subsequently used to correct the visual estimates.

Branch level within-canopy lichen visual assessments were conducted in the summer of 1998, immediately after harvesting, and again in the summer of 2000, 2 years after harvesting. We have referred to the 1998 within-canopy lichen assessments as immediate postharvest measurements and the year 2000 measurements as 2-year postharvest measurements. The collection of our within-canopy data in the period immediately after harvesting insured that any differences between the 1998 and 2000 assessments were due to changes in the postharvest environment, and not to branch breakage or other damage sustained during logging.

Canopy microclimate

Lichen growth environments were assessed by canopy microclimate measurements from September 1999 to August 2000, after Campbell and Coxson (2001). Three replicate trees were instrumented within each of the NT and GS treatment areas. In the NT stand area, these trees were selected

on the same basis as the lichen biomass sample trees. In the GS area, trees were randomly selected from a pool of candidate trees using the same criteria, but also selecting trees that had a southerly exposure on the edge of retained groupselection patches. No microclimate measurements were taken in the STS area. Instrumentation was installed on north- and south-facing branches at 4- and 15-m heights above ground, typically at the midpoint of each branch, between the trunk and branch tip. Two to three replicate thalli of each of Alectoria sarmentosa and Bryoria spp. (mainly B. pseudofuscescens) were instrumented on each branch. No canopy climatology measurements were taken on thalli from the foliose lichen group.

Lichen temperature was measured using fine-wire thermocouples (Omega Engineering, Stanford, Conn.) held appressed against lichen thallus surfaces. The hydration of lichen thalli was measured using an impedance technique (Coxson 1991), adapted for Alectorioid lichens (Campbell and Coxson 2001), in which small clips were used to measure electrical conductivity across lichen thalli.

Light intensity was measured using LI-COR quantum sensors (LI-COR, Lincoln, Nebr.), held level in gimbel mounts at the upper branch surface at each height location. Precipitation was measured using a 1-mm tipping-bucket rain gauge (model 1000-20, Sierra Misco, Richmond, Calif.). Wind speed was measured using Met-One cup-anemometers (Met-One Instruments, Grant Pass, Oreg.), placed at 4 and 15 m on an instrumentation mast within an adjacent canopy gap at the group-selection area. Instrumentation signals were recorded using Campbell Scientific (Logan, Utah) CR-7 and CR-10 dataloggers. Sampling rates were based on a variable-rate trigger, recording data at 3-h intervals when lichen thalli were dry, and at 10-min intervals when lichen thalli were wet under daylight conditions.

Data analysis

For each tree that had been assessed before and after harvest using the photo guide, we determined the direction and

magnitude of the change in lichen-abundance class. The log-likelihood ratio G, which is more robust than the χ^2 test when expected frequencies are small (Sokal and Rohlf 1995), was used as a test statistic to compare the frequency distributions of changes in class in the three treatment areas. As the frequency distributions of lichen-abundance classes on A. lasiocarpa and P. engelmannii did not differ significantly either before harvest (G = 4.398; df = 3; P = 0.222) or after harvest (G = 2.931; df = 3; P = 0.402), the data for the two tree species were pooled for analysis.

Comparisons of total lichen loading on intensively (within-canopy) sampled trees of *A. lasiocarpa* and *P. engelmanni* in the NT treatment area indicated no significant differences by tree species (Bonferroni adjusted probabilities) for either of the *Bryoria* (*P* values of 0.114 and 0.335 for 1998 and 2000 sampling, respectively), *Alectoria* (*P* values of 0.317 and 0.727 for 1998 and 2000 sampling, respectively), or foliose (*P* values of 0.927 and 0.408 for 1998 and 2000 sampling, respectively) lichen functional groups. Consequently, we have not differentiated between host tree species in our analysis of preharvest and postharvest NT treatment area data. This was not an issue in the GS and STS treatment areas, where all sampled trees were *A. lasiocarpa*.

Treatment effects on intensively sampled trees (canopy based) were subsequently examined using analysis of variance on standardized data sets, where the 1998 (immediate postharvest) whole tree lichen loading (sum of individual branch measurements) values for each tree were set equal to 100%. Transformed data were tested for normality of distribution and homogeneity of variance prior to analysis. Tukey multiple comparison post-hoc tests were subsequently used to test comparisons between treatment areas by lichen sampling group.

t tests for paired comparisons (Bonferroni adjusted probabilities) were used to test for significant differences between immediate postharvest and 2-year postharvest branch-level lichen loading estimates within individual treatment areas, stratified by height in canopy (lower canopy, 0–5 m; middle canopy, >5–15 m; and upper canopy, >15 m in height above ground) and lichen sampling group.

Replicate measurements of lichen thallus temperature and hydration for *Alectoria* and *Bryoria* were pooled, based on our previous observation that very small differences in thallus microclimate occur between the finely dissected pendulous thalli of these two lichen groups at Pinkerton Mountain (Campbell and Coxson 2001). Total number of hours of lichen hydration was taken as the cumulative number of hours that thalli were recorded as having a relative water content greater than 20% thallus hydration. This threshold corresponds with the point below which physiological activity (gas exchange) ceases in these species (D.S. Coxson, unpublished data).

Results

In all three treatment units, most trees were given the same ground-based lichen-abundance class rating before and after the harvest (Fig. 2). A smaller number of trees, in each treatment unit, shifted up or down by one class. The frequency distributions of changes in lichen-abundance class

Fig. 2. Percent frequency distribution of changes in lichenabundance class by tree in stand areas with no harvest treatment (NT), and stand areas with group selection (GS) and single-tree selection (STS) harvest treatments at Pinkerton Mountain. The sample size (number of trees) for each group is indicated in brackets.

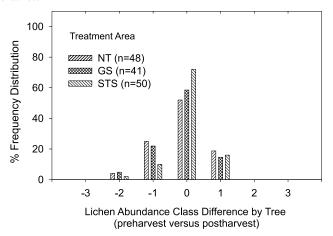
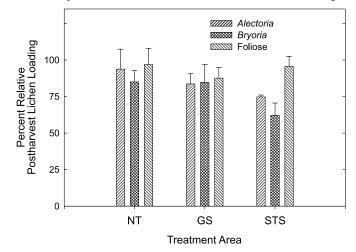


Fig. 3. Two-year postharvest (2000) lichen loading (standardized measures) by lichen sampling group (*Alectoria*, *Bryoria*, Foliose) in stand areas with no harvest treatment (NT; n = 10 trees) and stand areas with group selection (GS; n = 5 trees) or single-tree selection (STS; n = 5 trees) harvest treatments at Pinkerton Mountain study area. Immediate postharvest (1998) lichen loading assessments provided baseline values (100% relative lichen loading).



did not differ among the three treatment units (G = 6.088; df = 6; P = 0.413).

Canopy-based postharvest lichen-abundance estimates showed that 80–90% of immediate postharvest loading remained for each of the lichen sampling groups in the NT and GS areas (Fig. 3). The *Alectoria* and *Bryoria* lichen sampling groups showed a greater postharvest decline within the STS harvest area (below 70% for *Bryoria*).

Analysis of variance indicated that there were no treatment effects of harvest type on lichen loading for any of the three lichen groups (Table 1).

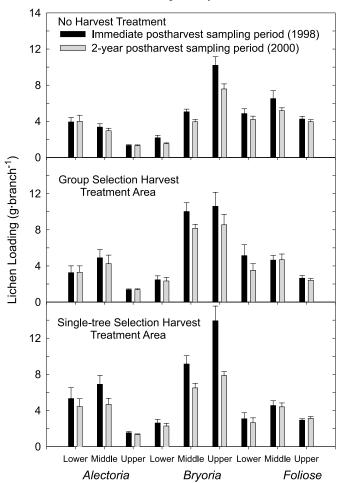
A detailed examination of immediate postharvest and 2-year postharvest lichen loading by height (Fig. 4) showed

Table 1. Analysis of variance for whole tree postharvest (year 2000) canopy lichen loading (percent relative measures, 1998 = 100) by lichen group.

	Analysis of variance								
Lichen sampling	Sum of	df	Mean						
group	squares	(n - 1)	square	F ratio	P				
Alectoria	2291.3	2	1145.6	0.968	0.4				
Bryoria	1937.1	2	968.5	1.665	0.219				
Foliose	189.3	2	94.6	0.14	0.87				

Note: Treatment effects were examined between unharvested (no treatment), single-tree selection, and group selection areas at Pinkerton Mountain. B.C.

Fig. 4. Comparison of immediate postharvest (1998) lichen loading (g·branch⁻¹) with 2-year postharvest (2000) lichen loading by lichen sampling group (*Alectoria, Bryoria*, and foliose) and canopy position (lower canopy, 0–5 m; middle canopy, >5–15 m; and upper canopy, >15 m in height above ground) for (from top) unharvested stand area, group selection stand area, and singletree selection stand area at Pinkerton Mountain. The sample sizes (number of branches) in the upper, middle, and lower canopy of the no harvest treatment area were 686, 1136, and 466, respectively. In the group selection treatment area, sample sizes by canopy position were 116, 485, and 330, respectively. In the single-tree selection treatment area, sample sizes by canopy position were 153, 507, and 228, respectively.



that the decline in lichen abundance was greatest in upper canopy STS area branches (compared with upper canopy NT area or GS branches). The *Bryoria* sampling group, in particular, showed significantly lower postharvest lichen loading in the STS area and in the NT stand at mid-canopy heights (Table 2). Foliose lichen loading declined significantly in all height positions in the NT site (Table 2). Remaining paired comparisons were not significant, except for foliose lichens in the lower canopy of the GS area and mid-canopy *Alectoria* (GS and STS) (Table 2).

Lichen microclimate measurements taken under latewinter snow-melt conditions showed greater incident photosynthetically active radiation (PAR) exposure on branches in the GS area, accompanied by a slight increase in lichen thallus temperature (Fig. 5). The duration of lichen hydration on snow-melt was reduced on GS branches. In the lower canopy these differences were less pronounced. Under midsummer conditions differences in insolation exposure persist under diffuse overcast conditions, although differences in lichen wetting were small in both canopy heights (Fig. 6). The cumulative duration of thallus hydration for lichens during the winter period was consistently greater for lichen thalli in the NT site, compared with lichen thalli in GS treatment areas (Fig. 7, top), although these differences were only significant for lichens on south aspect branches. Differences in the duration of lichen hydration between the NT and GS area lichens were less apparent in summer period precipitation events (Fig. 7, bottom). Only lower canopy south aspect lichens showed significant differences in total hydration duration.

Discussion

The responses of arboreal lichen communities to edges created by forest harvesting are complex and vary as a function of distance from edge and time since initial disturbance. Esseen and Renhorn (1998), in studies on *Picea abies* dominated Scandinavian boreal forests, found that changes in abundance of *Alectoria sarmentosa* showed an initial lag period after harvesting, until major storm events of the following winter brought about wind scouring of lichens from newly exposed branches. Lichen loading at edges declined precipitously within their study sites, falling to only 14% of that measured in forest interior sites. These effects were apparent up to two tree lengths from newly created edges. At older edges (8–16 years), lichen loading was still only 55% of that in forest interior sites.

The other major finding of Esseen and Renhorn (1998) was that *Alectoria* abundance at intermediate distances (e.g., 20–30 m) from newly created edges through time can show a rebound effect, ultimately reaching levels of abundance higher than those of forest interior sites. This long-term increase in lichen abundance on branches near, but not at, the new edges, was postulated to result from greater postharvest light exposure on branches that were still relatively sheltered from wind scouring. Similarly Renhorn et al. (1997) found that growth of lichen transplants was highest just inside forest edges, again in microsites that were relatively sheltered from wind scouring and dessication, but had increased light exposure from the new forest edge.

Table 2. Pairwise *t* test comparisons (Bonferroni method) stratified by canopy position for comparisons of immediate postharvest and 2-year postharvest lichen loading in each of unharvested (no treatment), single-tree selection, and group selection areas at Pinkerton Mountain, B.C.

		Canopy position								
		Upper canopy		Mid-canopy			Lower canopy			
Harvest unit	Lichen sampling group	t	n	P	t	n	P	t	n	P
No treatment (unharvested)	Alectoria	0.422	39	0.676	2.523	35	0.098	-1.124	21	0.274
	Bryoria	1.005	39	0.321	2.258	38	0.03*	1.037	18	0.314
	Foliose	3.442	39	0.001*	3.745	38	0.001*	2.3	18	0.034*
Group selection	Alectoria	-0.265	14	0.795	2.381	15	0.031*	-0.66	10	0.524
	Bryoria	1.732	14	0.105	1.932	15	0.074	-0.201	10	0.845
	Foliose	1.024	14	0.323	0.224	15	0.826	3.462	10	0.01*
Single-tree selection	Alectoria	1.304	19	0.208	3.603	19	0.001*	2.186	9	0.057
	Bryoria	5.04	19	0.001*	3.857	19	0.001*	2.269	9	0.049*
	Foliose	-0.845	19	0.408	0.123	19	0.903	2.115	9	0.064

*Significant t values ($P \le 0.05$).

In contrast, Rominger et al. (1994) found no significant changes in arboreal lichen loading in the lower canopy of subalpine spruce—fir forests of northern Idaho and southeastern British Columbia, 8–10 years after partial cutting. Similarly, edge effects on arboreal lichen communities were not pronounced in wet coastal forests of western Oregon, assessed two decades after harvesting (Sillett 1995). These contrasting findings between boreal and wet-temperate forests suggest that regional climate may influence the severity of changes in canopy microclimate at coniferous forest edges and attendant impacts on lichens.

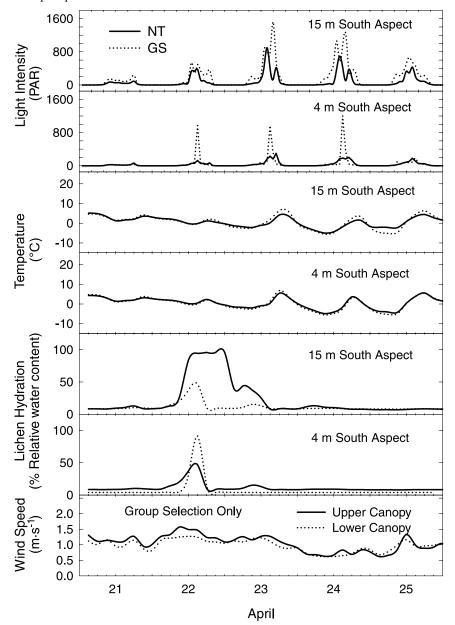
Based on prior findings of Esseen and Renhorn in boreal forest systems, we thought there was a risk that lichen loading per tree might decline significantly in the ESSF stand at Pinkerton Mountain after partial cutting. Although our sampling sites were randomly located throughout the residual stand and included both edge and interior trees, even the most sheltered trees were typically less than two tree lengths from newly created edges (and less in the STS area). Our concern about a possible decline in lichen loading was not borne out by our study results. Although branch-level measurements in the GS and STS sites did show a slight decline in postharvest lichen loading, this decline was of similar magnitude to that found in the adjacent NT site. Neither the extensive ground-based assessments of the lower canopy nor the intensive assessments of whole trees showed significant overall declines in postharvest lichen loading. Only in selected height-aspect combinations (e.g., Bryoria upper canopy in the STS) was there a significant decline in postharvest lichen loading. Thus, there did not appear to be a phase of wind scouring of lichens from the canopy at Pinkerton Mountain attributable to partial cutting.

The general decline in lichen loading throughout the study area, including the unharvested area, was evidently the result of a widespread natural phenomenon. In spring 1999 we noticed large numbers of broken tops of trees on the ground throughout the study area. In mature trees, top breakage is usually attributable to the action of ice and snow (Allen et al. 1996, p. 144). We suggest that the same weather events that resulted in top breakage may also have stripped some of the lichens from the trees.

The extreme response of A. sarmentosa to increased exposure observed by Esseen and Renhorn (1998) was not duplicated in our results for the Alectoria group (composed mainly of A. sarmentosa) during the 2-year postharvest period of our study. In addition to temporal differences between the studies, several aspects of stand structure at Pinkerton Mountain may contribute to the difference between our results and theirs. The canopy structure at Pinkerton Mountain is highly aggregated (Campbell and Coxson 2001), almost to the point of meeting definitions of tree-island type regeneration patterns (Brett and Klinka 1998). This creates a quite open canopy structure, one where lichen communities may already be adapted to significant insolation and convective exposure (Campbell and Coxson 2001). Thus, the relatively small patch opening sizes (<0.4 ha) created by harvesting at Pinkerton Mountain may have little additional effect on lichen retention within the canopy. This environment differs from the closed-canopy boreal forests studied by Esseen and Renhorn (1998), where harvest openings were much larger and the contrasts between edge and interior may have been stronger.

At 2 years after harvesting, we would not expect our findings to provide evidence of changes in lichen loading that might result from adaptations to altered growth conditions within the canopy. Nonetheless, microclimate data from Pinkerton Mountain show trends that may ultimately result in changes to the community structure of arboreal lichens in this partially cut stand. Our microclimate stations contrasted lichen microclimate on forest interior trees (in the unharvested site) with those on edge trees (on the southwestfacing edge of an opening in the GS area). We deliberately chose the most severe aspect contrast in the stand, recognizing that other postharvest locations may be closer to forest interior conditions (e.g., trees that are farther from openings, or along north-facing edges). Even at this exposed location lichens were not scoured from branches. However, measures of total lichen hydration duration show a significantly more xeric environment on these south-facing edge branches, especially during the winter period, when wind gusts reduce snow loading (and subsequent snow-melt periods) on exposed branches.

Fig. 5. Comparison of arboreal lichen canopy microclimate between stand areas with no harvest treatment (NT) and stand areas with group selection harvest treatment (GS) at Pinkerton Mountain under late-winter (April 21–25, 2000) snow-melt conditions. From top: incident light intensity (µmol·m⁻²·s⁻¹, PAR) at 15 and 4 m south aspects; thallus temperature (°C) at 15 and 4 m south aspects; lichen hydration (% relative water content) at 15 and 4 m south aspects; wind speed (m·s⁻¹) at 15 and 4 m south aspects (group selection only). Plotted values represent the mean of nine replicate measures for temperature and hydration, three replicate measures for light, and unreplicated measures for precipitation and wind.



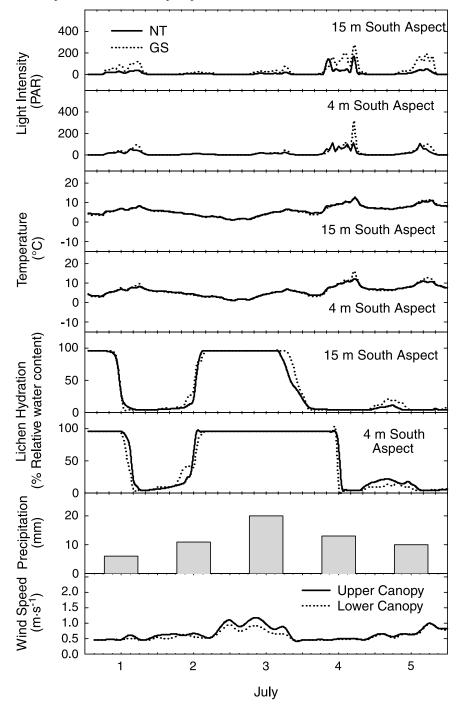
This may ultimately result in an increase in *Bryoria* loading at these locations, accompanied by a displacement or loss of *Alectoria* from lower canopy positions, in keeping with our understanding of the importance of canopy ventilation for *Bryoria* establishment in ESSF stands (Goward 1998) and the distribution of epiphyte communities along vertical gradients within coniferous forest canopies (McCune 1993). This trend has already been noticed in earlier partial-cutting trials in north-central British Columbia (Stevenson 2001). Rominger et al. (1994) also reported a higher proportion of *Bryoria* in partially cut stands than in adjacent unharvested stands. Kivisto and Kuusinen (2000) noted similar aspect-

related edge effects, where epiphytic lichen communities on *Picea abies* shifted significantly on south-facing edges, while remaining unchanged on north-facing edges.

Our data suggest that at Pinkerton Mountain the winter period may be considerably more important than summer in driving this restructuring of lichen communities. During summer precipitation events, diffuse overcast conditions would appear to limit differences in lichen hydration between sites with edge versus interior attributes (i.e., NT versus GS sites). Further, the small water storage capability in the Alectorioid lichens results in rapid drying on cessation of rainfall events in all treatment sites.

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Fig. 6. Comparison of arboreal lichen canopy microclimate between stand areas with no harvest treatment (NT) and stand areas with group selection harvest treatment (GS) at Pinkerton Mountain under mid-summer (July 1–5) precipitation conditions. From top: incident light intensity (μmol·m⁻²·s⁻¹, PAR) at 15 and 4 m south aspects; thallus temperature (°C) at 15 and 4 m south aspects; lichen hydration (% relative water content) at 15 and 4 m south aspects; precipitation (mm); and wind speed (m·s⁻¹) at 15 and 4 m south aspects (group selection only). Plotted values represent the mean of nine replicate measures for temperature and hydration, three replicate measures for light, and unreplicated measures for precipitation and wind.

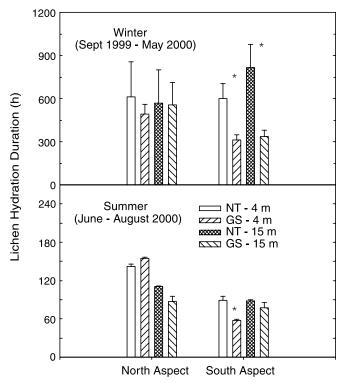


Our lichen loading and canopy microclimate assessment techniques primarily examined major lichen groups (*Alectoria*, *Bryoria*, and foliose lichens) within the canopy, in particular Alectorioid lichens, which provide forage for mountain caribou. Goward and Arsenault (1997) described techniques for examining lichen biodiversity in ESSF forests. We would ex-

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pect that assessments of lichen diversity would show that ESSF forests in central-interior British Columbia contain old-growth dependent species that may be sensitive to partial cutting. Further, the observation that lichen biomass did not change significantly on retained trees in the harvest plots at Pinkerton Mountain does not preclude the possibility that

Fig. 7. Comparison of mean lichen hydration duration between stand areas with no harvest treatment (NT) and stand areas with group selection harvest treatment (GS), stratified by height in canopy (4 and 15 m) and winter (September 1999 – May 2000) and summer (June–August) seasonal periods. Lichen hydration means are based on nine replicate measures per height or treatment combination. Asterisks denote significant differences (P < 0.05) in mean duration of lichen hydration between NT and GS areas (Bonferroni t test).



minor species within the lichen sampling groups may decline in abundance after harvesting. At the present time, however, old-growth dependent lichen species that have been described for montane forests of central-interior British Columbia have been confined mainly to cyanolichen species from lower elevation cedar–hemlock forests (Goward 1994; Goward and Arsenault 2000).

The long-term retention of lichens within the harvest blocks at Pinkerton Mountain will ultimately require successful colonization of the regenerating trees. At the moment, and likely for the next several decades, these patches of regenerating trees will be in close proximity to "old-growth" trees with high lichen loading, and should have ready access to dispersal sources. After second-pass harvesting, however, when a further 30% of trees will be removed, the distance from lichen inoculum sources (especially for larger wind-borne fragments) will be increased. Dettki et al. (2000) noted a rapid decline (by over 50%) in the dispersal of *Bryoria* lichen fragments at 100 m from stand edges. The effects of distance from an inoculum source on the development of lichen communities on regenerating trees in ESSF partial cuts should be investigated.

A related issue is that after second-pass harvesting, large trees will constitute a smaller proportion of the stand than they do today. Campbell and Coxson (2001) noted that large trees bear a disproportionate amount of the total lichen loading at Pinkerton Mountain. Similarly, Arseneau et al. (1997) found a strong correlation between diameter and lichen loading in subalpine forest stands. Large trees are disproportionately important as dispersal sources because of their height as well as their well-developed lichen communities. At Pinkerton Mountain, we observed some loss of *Bryoria* from the upper canopy between 1998 and 2000. It will be important to continue monitoring these sample trees to find out whether Bryoria abundance in the upper canopy recovers, and to confirm our hypothesis that the observed reduction in Bryoria abundance was unrelated to harvest treatment. These changes in stand structure may result in greater diversity in lichen loading, from one tree to the next, even if stand-level lichen loading were to remain constant. Full evaluation of this question will require future evaluation of changes in lichen loading between stands (stand level replication) as well as within stands (as in the present study).

A third issue regarding the colonization of young trees by lichens is the time required for regenerating trees to achieve the structural characteristics required for the development of abundant canopy lichens. Esseen et al. (1996) suggested that poorer substrate quality (smaller and younger branches) may be a major factor limiting arboreal lichen abundance in managed forests. Goward (1998) described a specific instance of this limitation, suggesting that Bryoria spp. do not become abundant on conifers until the branches are old enough to have developed an inner defoliated zone. Better information on how lichen communities develop through time on growing trees would help silviculturists design prescriptions that would encourage early development of the most important structural features, and would allow managers to anticipate how much time is required between harvest entries in areas managed under selection silvicultural systems.

We would anticipate that lichen loading at Pinkerton Mountain will continue to be influenced by the species composition of retained and regenerating trees in the stand. Our ground-based survey methods (assessments below 4.5 m) did not show significant differences in lichen loading between A. lasiocarpa and P. engelmannii. Comparisons based on whole-canopy individual branch assessments (Campbell and Coxson 2001) found that both Alectoria and Bryoria were more abundant on A. lasiocarpa in the unharvested stand, although large individuals of P. engelmannii did show disproportionate Bryoria loading in the upper canopy. Comparable individual branch assessments (whole canopy) in the present study (NT trees only) did not show significant differences in lichen loading by tree species. This may be due to the larger sample size of Campbell and Coxson (2001) (40 assessed trees, compared with 10 in the NT study area). It is clear, however, that maintaining both A. lasiocarpa and P. engelmannii as stand components will be important to future lichen loading at this site.

In summary, partial-cutting silvicultural systems, as evaluated in the present study, will lead to a reduction in stand-level lichen biomass; this effect will not be as severe as it would be under a clear-cutting regime. Retention strategies for lichens and the organisms that depend on them must therefore consider cumulative landscape-level effects, as well as stand-level harvesting design (Dettki and Esseen 1998). The ecosystem management model is a useful starting point

for planning forest management, at both the stand and landscape level, that will maintain habitat for a wide range of species. The management approach that is currently being developed for caribou in British Columbia, which has driven the prescription used at Pinkerton Mountain, is generally consistent with the principles of ecosystem management (Seip 1998). However, even ecosystem-based management may depart too much from natural conditions for some highly sensitive species. Mountain caribou are currently red-listed in British Columbia, which means that they are considered candidates for designation as threatened or endangered species (B.C. Ministry of Sustainable Resource Management 2002). Their survival depends on other factors in addition to the maintenance of their winter forage supply. Long-term research on the responses of mountain caribou habitat and populations will be required to determine whether or not these animals can be maintained through fine-tuning of ecosystem management principles.

One caveat on our present findings is that, although we have clear trends in our data, they represent information from only one site, and thus do not provide for stand-level replication. We anticipate that as future harvest blocks with similar prescriptions become available as part of a planned network of partial-cutting silvicultural systems trials (Jull et al. 2001²), we will have the ability to determine whether our currently monitored plots fall within or outside the normal range of variation in subalpine spruce-fir stands of northcentral British Columbia. Nonetheless, our findings demonstrate that partial-cutting harvesting designs within the ESSF of interior British Columbia (at least after a 30% removal first-pass harvest entry) can result in a high level of lichen retention within the residual forest. Some shifts in the distribution of lichen groups are anticipated as a result of changes to canopy microclimate. These are important first steps towards designing forest harvesting practices that will insure future lichen availability.

Acknowledgements

We thank Kevin Jordan, of Arbornaut Access, for assistance with canopy access and canopy sampling measurements, and Mike Jull for discussions on silvicultural systems design. We also acknowledge the cooperation of Northwood Inc. (now Canadian Forest Products Ltd.) in developing and implementing the partial cut at Pinkerton Mountain. Funding support was provided by Forest Renewal British Columbia.

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