



Retention of canopy lichens after partial-cut harvesting in wet-belt interior cedar–hemlock forests, British Columbia, Canada

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Received 27 April 2004; received in revised form 8 September 2004; accepted 9 September 2004

Abstract

Old-growth cedar–hemlock forests of the interior wet-belt of British Columbia are rich in abundance and diversity of canopy lichens, but are subject to forest harvesting. If these distinctive canopy lichen communities are to be conserved, it is important to learn how they are affected by forestry practices, including partial-cutting techniques designed to retain old-growth attributes. The retention of canopy lichens after 30 and 70% partial-cut harvesting (immediate post-harvest and 2-year post-harvest measurements) was examined using direct canopy access methods (tree climbing) in two old-growth interior cedar–hemlock forest stands of the upper Fraser River valley. Mean lichen loading was generally lower in all treatment areas, including control sites, 2 years after harvesting. However, three of four lichen-sampling groups (cyanolichen, foliose, and Bryoria group lichens) did not show significant treatment effects (total lichen loading) by harvesting type (30, 70 or 100% retention), when data sets were standardized against initial post-harvest lichen loading. Only in Alecatoria group lichens were treatment effects observed. Although cyanolichen loading was not significantly different in retained trees in most harvest blocks, many thalli, especially those near south-facing edges, were discolored, suggesting that future cyanolichen loading may be lower within partial-cut harvest blocks. Litterfall in general was greater during 2001/2002 than 2002/2003, even in the control units, suggesting weather-related differences between years. For Alecatoria, there appeared to be a treatment-related pulse of litterfall that was more pronounced in the 70% removal than the 30% removal treatment unit. Deposition patterns of litterfall components in relation to edges of openings indicated a heightened level of Alecatoria litterfall along edges. Treatment-related differences were absent or weak in other groups, and cyanolichen litterfall did not differ between years in any study area/treatment unit combination. These findings suggest that lichen retention in the residual stand of both partial-cut treatments was adequate to meet management goals,

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but also point to the necessity of future monitoring, as other edge effects (e.g. microclimate changes) influence future lichen growth and mortality.

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Keywords: Partial-cut harvesting; Variable retention harvesting; Old-growth lichens; Cyanolichens

1. Introduction

As Pacific storm systems sweep over the interior mountain ranges of British Columbia they create a zone of high precipitation, the so-called interior wet-belt, which favours the development of lush wet-temperate cedar–hemlock rainforests. These inland rainforest ecosystems occur at lower and mid-slope positions from Idaho and Montana north to central British Columbia. In British Columbia, they are classified into the interior cedar–hemlock (ICH) zone (Meidinger and Pojar, 1991). The wettest variants of these ICH forests, where canopy lichen cover is highest, cover an area of over 1.4 million ha in interior British Columbia (Jull et al., 1998). Historically, these forests were dominated by old-growth stands in sites that often had ecological continuity (time between major disturbance events) of 500–1000 years or more (Arsenault and Goward, 2000; Sanborn et al., 2001).

Wet ICH forests contain rich canopy lichen communities, particularly cyanolichen species (e.g. *Lobaria pulmonaria*, *L. scrobiculata*, *L. hallii*, *Nephroma helveticum*, and *Sticta fuliginosa*) belonging to the Lobarion alliance (Goward and Arsenault, 2000), a distinctive assemblage of epiphytic lichens and bryophytes that characterize nutrient rich forests in humid regions at temperate latitudes (Rose, 1998). Goward (1994) proposed that wet ICH stands with high cyanolichen diversity and long site continuity be designated as “antique” forest stands, noting that they support many lichen species not found elsewhere in regional landscapes. Antique forest stands are commonly found in toe-slope positions, where moist nutrient rich soils favour tree growth and limit their susceptibility to wildfire. These topographic positions, however, are highly vulnerable to human caused disturbances, ranging from timber extraction to road construction and hydroelectric development (Arsenault and Goward, 2000).

In the upper Fraser River watershed of central-interior British Columbia landscapes that were

historically dominated by old-growth forests (DeLong et al., 2004) have increasingly been replaced by a mosaic of even-aged forest stands after harvesting. Future harvesting in these stands is contemplated as occurring at intervals of approximately 110 years (BC Ministry of Forests, 2001). This poses significant conservation biology challenges for the retention of canopy lichens, especially in light of recent research findings showing that development of old-growth forest characteristics that support cyanolichen growth can take well in excess of 140 years, even under conditions of optimal lichen dispersal (Radies and Coxson, 2004; Campbell and Fredeen, 2004).

It has been proposed that “alternative” or so-called “new-forestry” harvesting practices, such as partial-cut harvesting (Franklin, 1989; Peck and McCune, 1997; Stevenson and Coxson, 2003), may provide a means of insuring that old-growth stand characteristics and associated canopy lichen communities are retained within forested landscapes. Yet we know little about the interaction of patch size and level of harvest intensity with the retention of canopy lichens in wet-belt forests of interior British Columbia. Clearly forest harvesting can have a major impact on canopy lichen communities, both from the immediate loss of habitat, and from the influence of edge effects on adjacent patches of unharvested forest (Esseen and Renhorn, 1998). At a landscape level the cumulative impact of managed forests on lichen retention may be quite high (Dettki and Esseen, 1998), particularly where the pattern of harvesting leaves little “interior” forest habitat (Esseen and Renhorn, 1998).

A series of replicate trials evaluating the impact of partial-cut harvesting in wet ICH forests of the upper Fraser River valley were established by Jull et al. (2002). We have now examined canopy lichen loading in these trials, comparing immediate post-harvest lichen loading within the residual stand with that found 2 years after harvesting. This provides an evaluation of changes in canopy lichen loading, particularly those resulting from physical processes such as wind-scouring along newly

created edges. Visual estimates of canopy lichen loading were conducted on marked branches within the same trees, using single-rope climbing techniques to gain access to the canopy environment. Concurrent measurements of lichen litterfall at the forest floor surface provided an independent indication of changes in the retention of canopy lichen communities within the residual stand.

2. Materials and methods

2.1. Study sites

Partial-cut harvesting sites were located near Lunate Creek and Minnow Creek along the Rocky Mountain Trench in the upper Fraser River watershed in east-central British Columbia (Fig. 1), in the very wet (Lunate) and wet (Minnow) subzones of the ICH Zone. Based on long-term climate station data for these subzones (Reynolds, 1997), mean annual precipitation ranges from 840 to 1214 mm, and mean summer (May–September) precipitation from 353 to 466 mm. Mean annual temperature ranges from 3.3 to 4.8 °C. Short-term climate stations operating at the two study areas measured summer precipitation of 445 mm in 2002 and 382 mm in 2003 at Lunate Creek, and 376 mm in 2002 and 318 mm in 2003 at Minnow Creek (R. Sagar, unpublished data).

Information about wind is relevant to the interpretation of litterfall patterns during the sampling period, 2001–2003. Wind data measured on a 30 ft (9.14 m) wind tower 4.5 km northwest of the Minnow Creek site, at a similar elevation and exposure, indicated that 2001/2002 was an unusually windy year (R. Sagar, unpublished data). Four of the 12 gust events (1 s wind speeds >20 m/s) recorded during the 8 years of tower operation occurred in 2001/2002, and those included the two gust events with the highest recorded wind speeds (23.8 and 24.1 m/s). Hourly average windspeeds >7 m/s occurred about twice as frequently during 2001/2002 as during 2002/2003.

The Lunate Creek study area (53°49'53"N, 121°28'44"W) is located approximately 100 km east of Prince George and 110 km west of McBride on the southern flank of the Trench, just east of the Hungary Creek drainage. The study area is situated on a moderately sloped (25–45%) north-facing site, at an

elevation of 950–1200 m. Stand structure, relative tree size, and the absence of charcoal in the forest floor suggest that the pre-harvest forest stand was very old, probably >600 years. The forest stand was dominated by western redcedar (*Thuja plicata*), with smaller components of hybrid spruce (*Picea engelmannii* × *glauca*), subalpine fir (*Abies lasiocarpa*), and western hemlock (*Tsuga heterophylla*). Live basal area was 133.6 m²/ha.

The Minnow Creek study area (53°27'56"N, 120°21'02"W) is located on the northern side of the Rocky Mountain Trench, approximately 32 km northwest of McBride. It is situated at an elevation of 1050–1200 m on a moderate (15–45%) slope with a southwest aspect. The oldest trees are estimated to be 300–350 years old, and radiocarbon dating of charcoal layers in the forest floor indicates that the stand burned 360–450 years ago (P. Sanborn, unpublished data). The forest stand was dominated by western redcedar, with some hybrid spruce and subalpine fir; very little western hemlock was present. Live basal area was 93.7 m²/ha.

2.2. Site treatments

Four treatments were applied at each study area: 0% post-harvest retention or “clearcut” (CC); 30% post-harvest retention or “group retention” (GR); 70% post-harvest retention or “group selection” (GS), and 100% retention or “unlogged control” (C) (Fig. 2). Group retention patches were one to two tree heights in diameter, or approximately 0.1–0.4 ha, and group selection openings were similar in size. Wherever possible, we randomly allocated treatments among available treatment units. In one case, visual quality objectives precluded a particular treatment location, and in both cases, the unlogged control areas were placed where access roads or adjacent logging would least affect them.

All harvesting was done on a settled snowpack in January–March 2001. Ground-based methods (hand- or machine-felling with skidder yarding to a central location) were used in all treatment units.

2.3. Canopy sampling design

In each treatment unit, we flagged and numbered a set of candidate sample trees that met the following criteria:

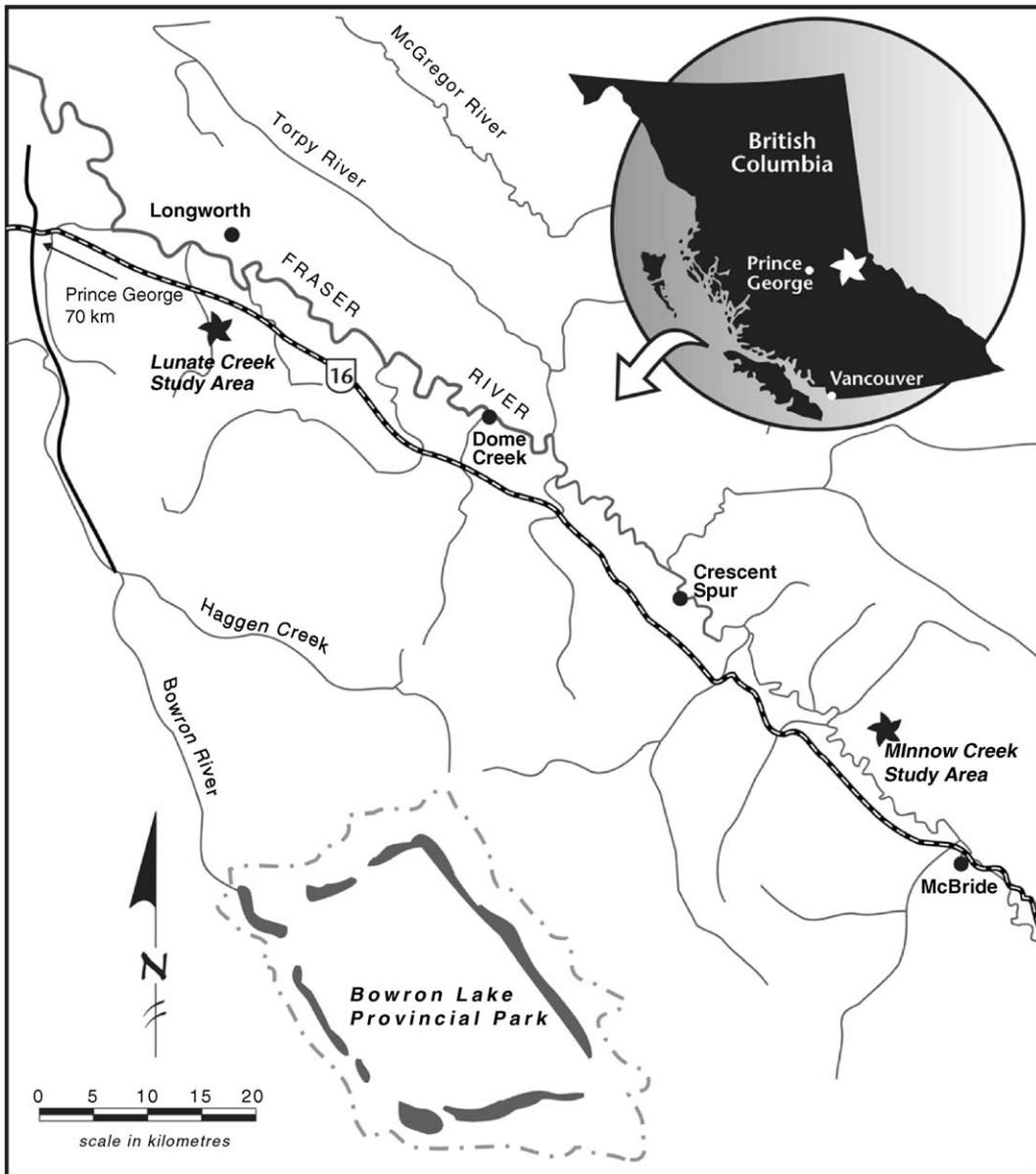


Fig. 1. Location of the Lunate Creek and Minnow Creek study areas in east-central British Columbia.

from the codominant tree layer; and apparently safe to climb. Codominant trees were selected for sampling because they support most of the canopy lichens in the stand. Dominant trees support high lichen biomass, but are uncommon; suppressed trees support only about one-sixth as much lichen biomass as codominant trees in these ecosystems (Bensen and Coxson, 2002). In the

partially cut units, candidate trees were selected from the zones in which a treatment effect was anticipated. In the group retention units, trees from any portion of the retained patches were eligible for sampling, but in the group selection units, candidate trees were selected from the edges of the openings. All openings and patches were checked for candidate trees. In the control units,

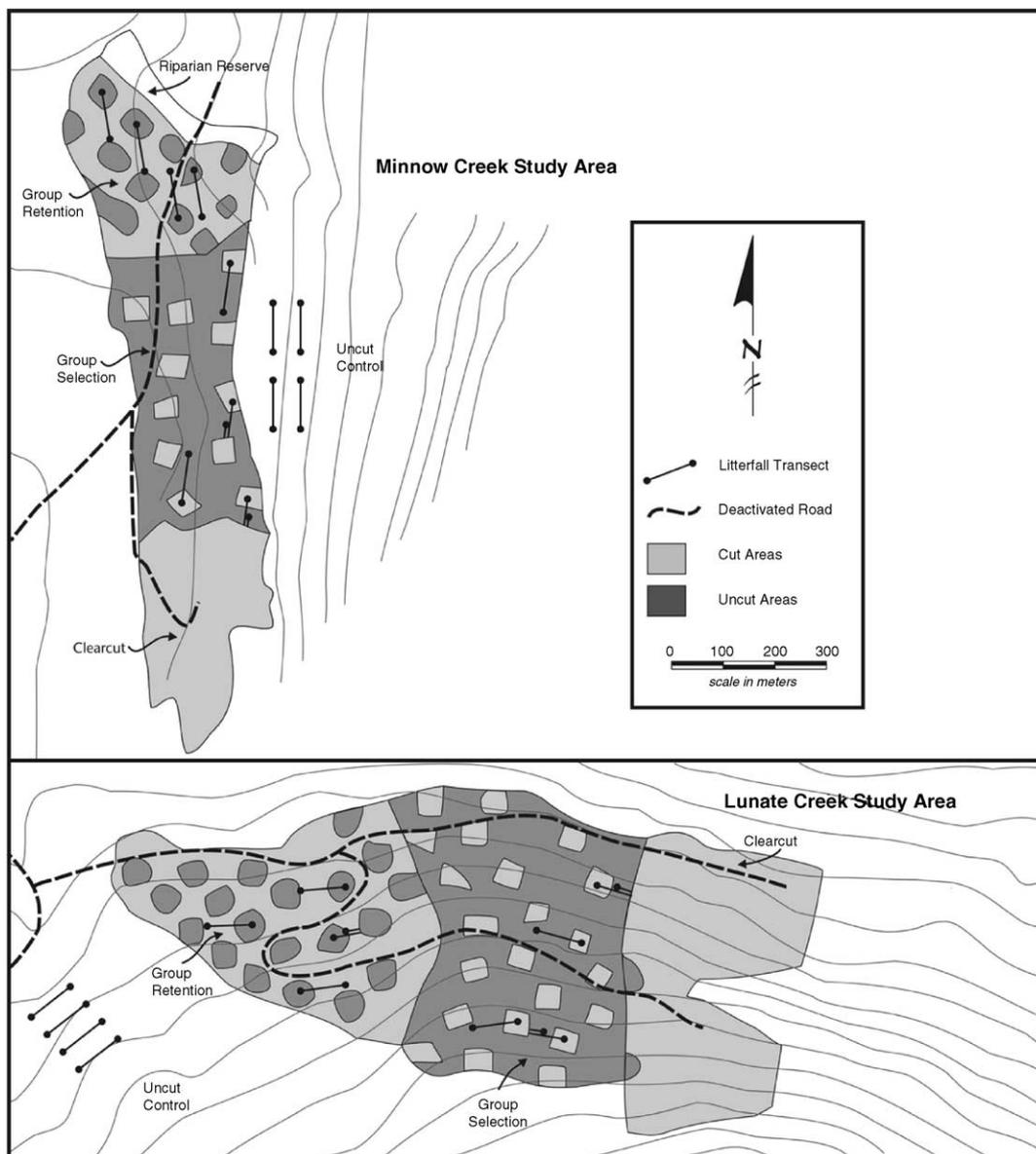


Fig. 2. Layout of the Lunate Creek and Minnow Creek silvicultural systems trials. Contour interval = 25 m.

candidate trees were selected from the vicinity of the litterfall transects.

Nine trees were randomly selected for sampling from each list of candidate trees. Because of the high level of tree damage and internal decay in these old stands, safety was a major constraint on the selection of sample trees. Our initial plan to sample the canopy trees in proportion to their occurrence by species was

abandoned after the first week of sampling, because very few codominant hemlocks met our safety criteria. Thereafter, sampling was restricted to western redcedar, the most common species in the codominant tree layer. Some trees that had been randomly selected from the candidate list were later rejected by our climbing supervisor, and other trees from the candidate list were substituted.

Single-rope climbing techniques (Campbell et al., 1999) were used to access the canopy. Beginning at the highest accessible point, all branches >1 cm diameter at the base and longer than 10 cm were counted. Every fifth branch was systematically selected as a sample branch, and permanently tagged. Lichen loading on each sample branch was evaluated using visual estimation techniques, in which the amount of lichen on the branch was compared to clumps of known biomass mounted on cards. Regression equations of Bensen and Coxson (2002) were used to provide a standardization of visual estimates against a subset of previously (destructively) sampled branches within old-growth ICH forest canopies. Lichens were grouped using sampling categories of Bensen and Coxson (2002). The Alectoria sampling group consisted of *Alectoria sarmentosa* and small amounts of *Usnea* spp. The Bryoria sampling group included *Bryoria* and *Nodobryoria* species. The cyanolichen sampling group comprised all foliose lichens containing a cyanobacterium as the photobiont, though visual estimates were strongly influenced by the most abundant species in this category, *Lobaria pulmonaria*. The foliose sampling group included all other foliose lichen species, including *Platismatia glauca*, *Hypogymnia physodes*, *Hypogymnia tubulosa*, *Parmeliopsis ambigua*, *Parmeliopsis hyperopta*, *Hypogymnia occidentalis*, and *Tuckermannopsis chlorophylla*. A more detailed listing of foliose macrolichens present at the Lunate study site is provided by Radies and Coxson (2004).

Biomass of canopy lichens was assessed first in summer 2001. The assessments were repeated in summer 2003.

2.4. Litterfall sampling design

Layout of the litterfall traps was designed to sample the harvested and unharvested portions of each treatment unit approximately in proportion to their occurrence. Four litterfall transects were established in each treatment unit. In the group retention unit, each litterfall transect began in the center of a retention patch, randomly selected from a list of all retention patches in that unit, and ran along the contours in a randomly selected direction (either left or right). The distance from the center to the edge of the patch was

measured, and the transect was continued beyond the patch into the logged area for a distance equal to twice the distance from the center of the patch to the edge. If the transect line ran into another patch, or the treatment unit boundary, it bounced back along the same path toward its origin. Thus, one-third of each transect was located in the retention patch, and one-third in the logged area. We used a random number table to select 10 distances in meters from the origin of each transect, and placed a litterfall trap at each randomly-selected distance.

Transects in the group selection area were laid out in a similar fashion, except that the starting point for each transect was the center of a group selection opening. In each control area, four 100 m transects were laid out systematically. Ten litterfall trap locations were randomly selected along each transect in the group selection and control areas.

The litterfall traps had a collection surface area of 1 m × 1 m. The traps were constructed of nylon screen attached with glue and automotive tie-down straps to a frame of 12 mm PVC pipe. Shrubs were clipped at ground level from the area where the trap was to be placed, and where necessary, the forest floor was leveled so that the traps could be placed horizontally. Landscape fabric was placed under the traps to prevent new shoots from growing through the screen. Overhanging shrubs were clipped at the point where they intercepted the vertical projection of the traps. In the partial-cut treatment units, litterfall traps were classified as either under the forest canopy, in a harvested opening, or within 3 m of the edge of an opening.

The 240 litterfall traps were initially laid out in September/October 2001. Litter was collected in June 2002, September/October 2002, June 2003, and October 2003, placed in labeled paper bags, and air-dried for storage. Litter was sorted into five categories: fruticose lichens (*Alectoria* and *Bryoria* groups), foliose lichens, cyanolichens, non-canopy material (e.g. shrub leaves, insects, rodent droppings), and other (e.g. wood, needles, bark, cones). The proportion of the fruticose lichens composed of *Alectoria* was estimated, using photos of Armleder et al. (1992) for reference; the remainder was *Bryoria*.

The litter was equilibrated and weighed in a laboratory in which the relative humidity was held

constant at 40%. The lichens were weighed to the nearest 0.0001 g, and the other material to the nearest 0.01 g.

2.5. Statistical analysis – canopy lichen loading

Paired comparisons between mean lichen loading in 2001 and in 2003 were made for each lichen functional group in all treatment by site combinations using Bonferroni *t*-tests, a more conservative test that accounts for multiple comparisons (Wilkinson, 1990). Overall harvesting treatment effects were examined within each lichen functional group using analysis of variance (ANOVA) on standardized data sets, where the 2001 (immediate post-harvest) whole tree lichen loading (sum of individual branch measurements) values for each tree were set equal to 100%. This minimized the influence of tree-to-tree variation within treatment areas, while retaining year-to-year changes in the data set. Bonferroni multiple comparison tests were subsequently conducted between treatment areas within lichen sampling groups. The Kolmogorov–Smirnov test was used to check for normal distributions. ANOVA's were subsequently repeated on a subset of experimental data, including only the GS and GR trees that were within 5 m of the newly created stand edges. This provides a more narrowly focused test for treatment effects on edge trees. In each case, data from Minnow and Lunate sites were pooled, after Bonferroni tests showed no significant site differences between standardized sampling group treatment means.

Each of the two study sites (harvest blocks) had a defined spatial area within which individual harvesting treatments (group selection and group retention) were applied, and hence might be regarded as single units of replication in the experimental design. However, we do not believe that lichens on individual trees necessarily perceive this harvest treatment in the same (uniform) manner as that of the prescribing forester. The magnitude of changes due to direct disturbance (such as branch loss or physical damage to thalli) and indirect disturbance (such as changes in exposure to wind and sun) experienced by lichens on individual trees can be highly variable, even on trees that are only meters apart. Given similar concerns about the scale at which lichen and bryophyte communities perceive their environment, Fenton

and Frego (2003) noted that individual permanently marked sampling plots were a more appropriate unit of replication than treatment units when evaluating harvest treatments on lichen and moss communities within individual stands. We have adopted this usage and treat lichen samples from permanently marked trees as our basic unit of replication.

2.6. Statistical analysis – lichen litterfall

Because the distributions of all the litterfall components were skewed right, statistical tests were performed on log-transformed data. *t*-Tests with Bonferroni adjustments for multiple comparisons were used to test for significant differences between 2001/2002 and 2002/2003 in the biomass of each litterfall component. Because the sample size of edge traps was small, edge effects were examined by pooling the data from both study areas and both years and testing the hypothesis that there was no difference between traps along edges and traps located under the canopy.

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

3. Results

3.1. Canopy lichen loading

Changes in mean canopy lichen loading during the 2-year post-harvest period were greatest in the Alectoria sampling group, with 2003 lichen loadings below those observed in 2001 in all treatment groups. This decline was greatest in the GS treatment, followed by GR and C treatment plots. These differences were significant at the Lunate site in each of the harvest treatments, and in the Minnow site in the GS treatment (Fig. 3). In Bryoria, there were slight declines in mean lichen loading in all site by treatment combinations, these significant in the Lunate GS and Minnow GR treatments. Foliose lichens declined in abundance in each of the Minnow treatment areas (significantly so in the GR and GS areas), and increased in abundance (not significant) in each of the Lunate treatment areas. Cyanolichen abundance declined slightly in all site by treatment combinations, though significantly so only in the Lunate GS site.

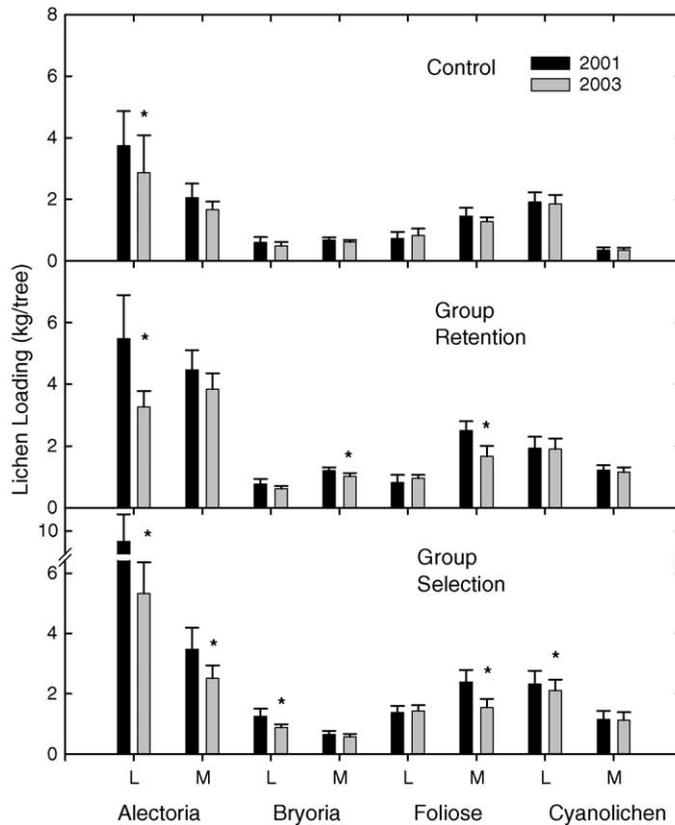


Fig. 3. Mean lichen loading (kg/tree) (+1 standard error) by lichen sampling group (Alectoria, Bryoria, foliose, and cyanolichen) in each of the control, group retention, and group-selection treatment areas of the Lunate (L) and Minnow (M) study sites. Asterisks, where present, indicate significant differences ($P < 0.05$) between 2001 and 2003 mean values in each paired comparison.

Mean lichen loading (all groups combined) was 7.2 kg/tree at the Minnow site and 10.1 kg/tree at the Lunate site, representing 763 and 848 kg/ha respectively for cedars within these two stands. Stand loading for the cyanolichen component was 76 and 174 kg/ha respectively, for the Minnow and Lunate sites (again calculated only for cedars within the stand).

Reductions in post-harvest canopy lichen loading in Alectoria were greatest near stand edges (Fig. 4). In contrast, Bryoria showed little or no trend in abundance near edges, whereas foliose group lichens showed a trend towards increasing abundance at the edge of GS and GR patches.

Analysis of variance on standardized data sets (2001 lichen loading in each tree assigned a value of 100%), pooled for both Lunate and Minnow sites,

found significant treatment effects (harvest type) for the Alectoria sampling group (Table 1). Post-hoc tests showed significant differences between the C and GS values for mean lichen loading in Alectoria. When analysis of variance was confined to edge trees, treatment effects were also seen for the foliose lichen sampling group, with C lichen loadings being significantly different from GR lichen loadings. No treatment effects were seen in the Bryoria or cyanolichen groups.

3.2. Lichen litterfall

Alectoria litterfall ranged from 1.7 to 18.9 kg/ha, Bryoria from 3.8 to 13.6 kg/ha, foliose lichens from 4.3 to 30.6 kg/ha, and cyanolichens from 0.5 to 23.1 kg/ha (Table 2). Non-lichen litterfall ranged from

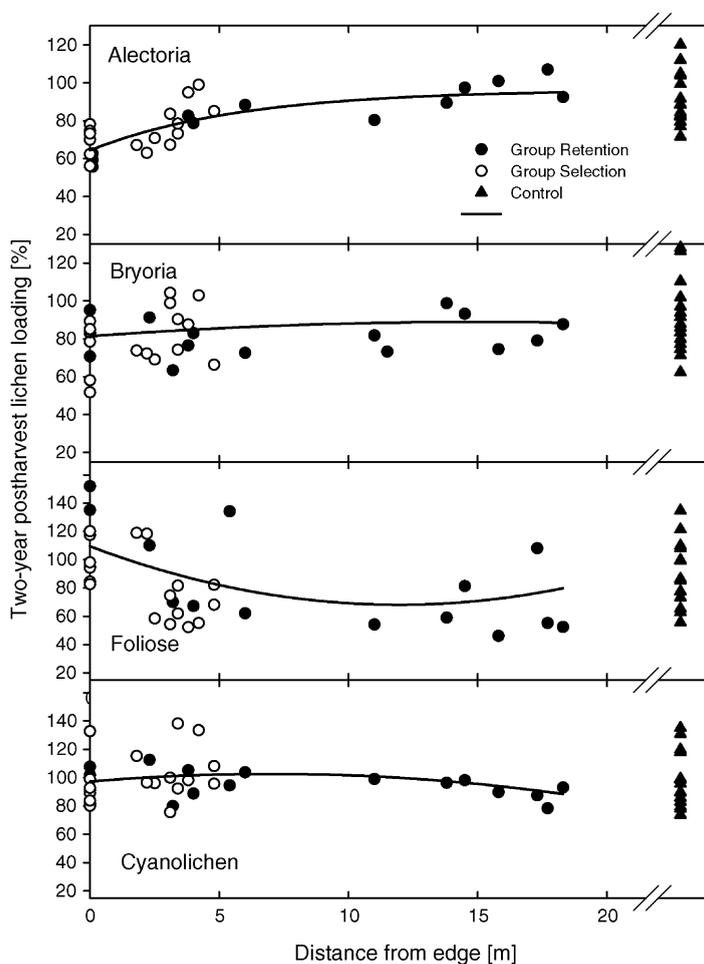


Fig. 4. Two year post-harvest lichen loading (% relative change from 2001 to 2003) by lichen sampling group (Alectoria, Bryoria, foliose, and cyanolichen) in control, group retention, and group-selection treatment areas (pooled site data). Data trends indicated by quadratic polynomial regression lines ($r^2 = 0.869, 0.605, 0.153$ and 0.161 for Alectoria, Bryoria, foliose and cyanolichen groups, respectively).

Table 1

Analysis of variance and post-hoc tests (Bonferroni) for harvest treatment by lichen functional group

| Lichen functional group | Source of variation | Degrees of freedom | Sum of squares | Mean square | F-ratio | P | Bonferroni comparisons | t | P |
|-------------------------|---------------------|--------------------|----------------|-------------|---------|---------------|------------------------|--------|---------------|
| Alectoria (all trees) | Treatments | 2 | 2104 | 1052 | 5.466 | 0.0080 | C vs. GR | 1.565 | >0.05 |
| | Residuals | 40 | 5624 | 192 | | | C vs. GS | 3.306 | < 0.01 |
| Bryoria (all trees) | Treatments | 2 | 1177 | 588 | 1.481 | 0.2376 | C vs. GR | 1.688 | >0.05 |
| | Residuals | 48 | 19079 | 397 | | | C vs. GS | 1.168 | >0.05 |
| Foliose (all trees) | Treatments | 2 | 611 | 305 | 0.2958 | 0.7454 | C vs. GR | 0.2619 | >0.05 |
| | Residuals | 45 | 46526 | 1039 | | | C vs. GS | 0.4421 | >0.05 |
| Cyanolichen (all trees) | Treatments | 2 | 366 | 183 | 0.4591 | 0.6346 | C vs. GR | 0.8921 | >0.05 |
| | Residuals | 48 | 19162 | 399 | | | C vs. GS | 0.1677 | >0.05 |

Significant treatment effects (probability $[P] < 0.05$) indicated in boldface.

Table 2

Annual biomass (kg/ha) of litterfall components in unlogged control (C), group retention (GR), and group selection (GS) treatment units at Lunate Creek and Minnow Creek during the first 2 years after forest harvesting and results of *t*-tests comparing log-transformed data from 2001/2002 and 2002/2003

| Litter component | 2001/2002 | | 2002/2003 | | <i>t</i> -Test | |
|---------------------|-----------|--------|-----------|--------|----------------|----------------|
| | Mean | S.E. | Mean | S.E. | d.f. | <i>P</i> |
| Alectoria | | | | | | |
| Lunate GR | 13.79 | 3.09 | 6.39 | 1.57 | 36 | < 0.001 |
| Lunate GS | 18.92 | 2.29 | 16.57 | 2.99 | 38 | 0.204 |
| Lunate C | 9.18 | 1.65 | 5.66 | 1.02 | 39 | 0.004 |
| Minnow GR | 5.47 | 1.47 | 1.66 | 0.63 | 37 | < 0.001 |
| Minnow GS | 4.63 | 1.04 | 4.07 | 1.02 | 38 | 0.004 |
| Minnow C | 2.47 | 0.38 | 3.74 | 0.96 | 38 | 1.000 |
| Bryoria | | | | | | |
| Lunate GR | 4.64 | 0.82 | 4.88 | 3.15 | 36 | < 0.001 |
| Lunate GS | 9.39 | 1.25 | 4.12 | 0.98 | 38 | < 0.001 |
| Lunate C | 7.65 | 0.98 | 5.26 | 0.75 | 39 | 0.003 |
| Minnow GR | 13.59 | 1.97 | 3.80 | 0.80 | 37 | < 0.001 |
| Minnow GS | 13.54 | 2.27 | 6.03 | 0.74 | 38 | < 0.001 |
| Minnow C | 11.93 | 1.38 | 6.48 | 0.99 | 38 | < 0.001 |
| Foliose | | | | | | |
| Lunate GR | 13.58 | 2.58 | 7.53 | 1.85 | 36 | < 0.001 |
| Lunate GS | 20.99 | 3.30 | 13.10 | 2.41 | 38 | 0.003 |
| Lunate C | 30.58 | 3.77 | 19.31 | 2.42 | 39 | < 0.001 |
| Minnow GR | 18.02 | 4.14 | 4.30 | 1.76 | 37 | < 0.001 |
| Minnow GS | 10.63 | 1.48 | 7.03 | 1.07 | 38 | 0.017 |
| Minnow C | 16.62 | 2.09 | 14.08 | 1.89 | 38 | 0.220 |
| Cyanolichens | | | | | | |
| Lunate GR | 23.13 | 6.44 | 9.20 | 1.99 | 36 | 0.951 |
| Lunate GS | 10.84 | 1.97 | 7.64 | 2.03 | 38 | 0.467 |
| Lunate C | 22.25 | 4.12 | 18.86 | 6.04 | 39 | 0.224 |
| Minnow GR | 4.30 | 1.76 | 0.53 | 0.21 | 37 | 0.062 |
| Minnow GS | 3.35 | 0.98 | 2.75 | 0.76 | 38 | 1.000 |
| Minnow C | 2.53 | 0.85 | 1.72 | 0.56 | 38 | 1.000 |
| Non-lichen | | | | | | |
| Lunate GR | 2305.10 | 439.93 | 1095.71 | 196.94 | 36 | < 0.001 |
| Lunate GS | 3946.60 | 362.36 | 2247.83 | 252.12 | 38 | < 0.001 |
| Lunate C | 4099.93 | 223.02 | 2240.89 | 128.60 | 39 | < 0.001 |
| Minnow GR | 2813.31 | 601.31 | 1081.69 | 170.22 | 36 | < 0.001 |
| Minnow GS | 2890.88 | 285.82 | 1734.63 | 199.10 | 38 | < 0.001 |
| Minnow C | 4921.15 | 263.78 | 3043.6 | 192.02 | 38 | < 0.001 |

Significant differences indicated in boldface.

1082 to 4921 kg/ha. Litterfall quantities were generally higher in 2001/2002 than in 2002/2003, even in the control area, but this effect was more pronounced in the partially cut areas.

For both Alectoria and foliose lichens, differences between the 2 years appeared to be greatest in the group retention unit (Fig. 5). Differences in Bryoria

quantities were more uniform among the three treatment units. Cyanolichen biomass tended to be more variable than the other litterfall components; no differences between years in cyanolichen abundance were statistically significant. Cyanolichen abundance in litterfall was conspicuously lower at Minnow Creek than at Lunate Creek.

Most litterfall components were most abundant under the forest canopy, intermediate in abundance along edges, and least abundant in openings (Fig. 6). Litterfall quantities were significantly lower in edge traps than in traps located under the forest canopy for Bryoria ($P = 0.031$), foliose lichens ($P = 0.013$), and non-lichen litterfall ($P = 0.022$). Quantities of Alectoria and cyanolichens did not differ between edge traps and canopy traps ($P = 0.791$ and 0.078 , respectively).

4. Discussion

4.1. Canopy lichen loading

Although group-selection and group-retention harvest patterns represent mirror images of each other in the landscape, GS creating small openings (30% removal) in a matrix of undisturbed forest, and GR leaving small patches of retained trees (70% removal) in a clearcut matrix, immediate post-harvest response of lichens to each disturbance pattern was remarkably similar. Stand edges in each treatment type showed a significant decline in retained thalli of the Alectoria sampling group, whereas thalli of Bryoria and cyanolichen sampling groups differed little in abundance along gradients from edge to interior. Previous research on edge effects predicts that changes in lichen community composition will occur over distances of several tree-lengths from newly created patch edges (Hilmo and Holien, 2002). However, on older edges, lichen response may incorporate both immediate physical restructuring due to wind-scouring and changes in substrate availability, and long-term growth (or dieback) responses (Esseen and Renhorn, 1998).

In contrast, the edge effects observed in the present study seem to reflect, for the most part, the greater susceptibility of pendulous thalli in the Alectoria sampling group to increased wind exposure and/or

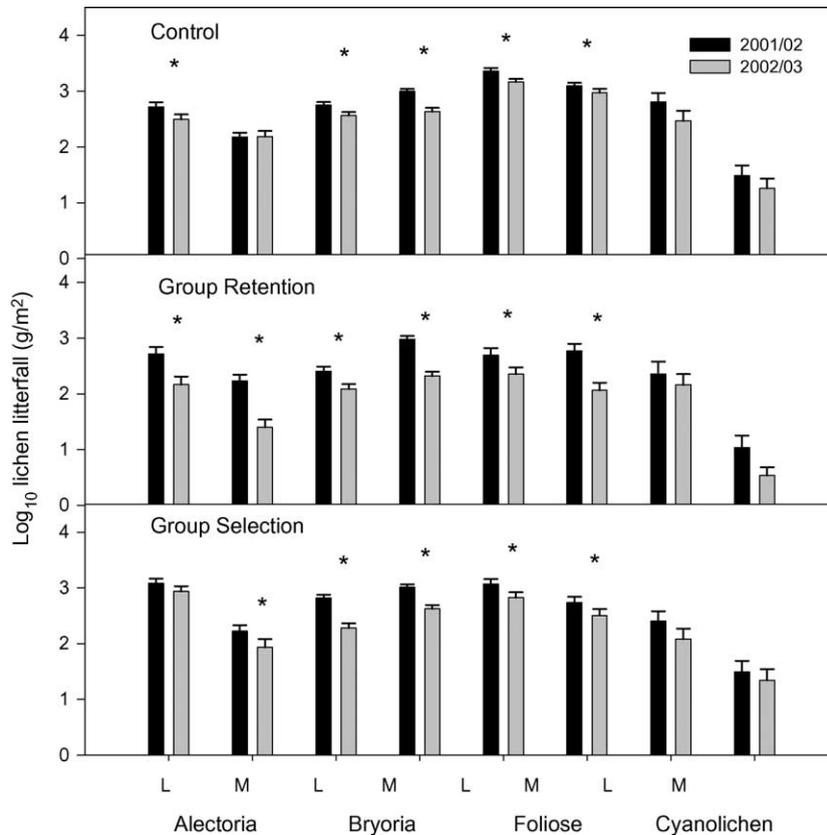


Fig. 5. Mean biomass (g/m^2) (+1 standard error) of lichen litterfall components (Alectoria, Bryoria, foliose, and cyanolichen) in 2001/2002 and 2002/2003 in each of the control, group retention, and group-selection treatment units of the Lunate (L) and Minnow (M) study areas. Statistically significant differences ($P < 0.05$) between years are indicated by asterisks.

intensity in post-harvest stands. Even within intact old-growth forest stands *Alectoria sarmentosa* is disproportionately excluded from upper canopy environments (relative to its growth potential), presumably by fragmentation of thalli (Coxson and Coyle, 2003). Thus, although Alectoria group lichens may be relatively tolerant of greater desiccation within the ICH forest canopies after harvesting, their growth form may set important limitations on their long-term accumulation of biomass in retained patches in a managed landscape matrix, at least compared to biomass levels that are possible in continuous undisturbed forest canopies. Esseen and Renhorn (1998) similarly observed that abundance of *A. sarmentosa* was significantly reduced at distances of up to 25–50 m into the forest at moderately exposed sites. This severity of edge effect was stronger than that seen in our own study

sites, however, the adjacent cutblock openings were larger in the study of Renhorn and Esseen. Harvested areas at the Lunate and Minnow partial cuts, in contrast, did not exceed three tree lengths in width at any given point across the openings.

Initial (pre-harvest) canopy biomass loading of Alectoria group lichens was higher in the GS and GR areas, compared to control plots, especially at Lunate treatment site. Although this may have resulted in a disproportionate susceptibility to wind-scouring by large thallus segments in the harvest treatment areas, when data sets were standardized (i.e. pre-harvest lichen loading on individual tree was taken at equal to 100%), the trend towards greater loss of Alectoria from harvest treatment areas was still present, lending confidence to this interpretation of experimental results.

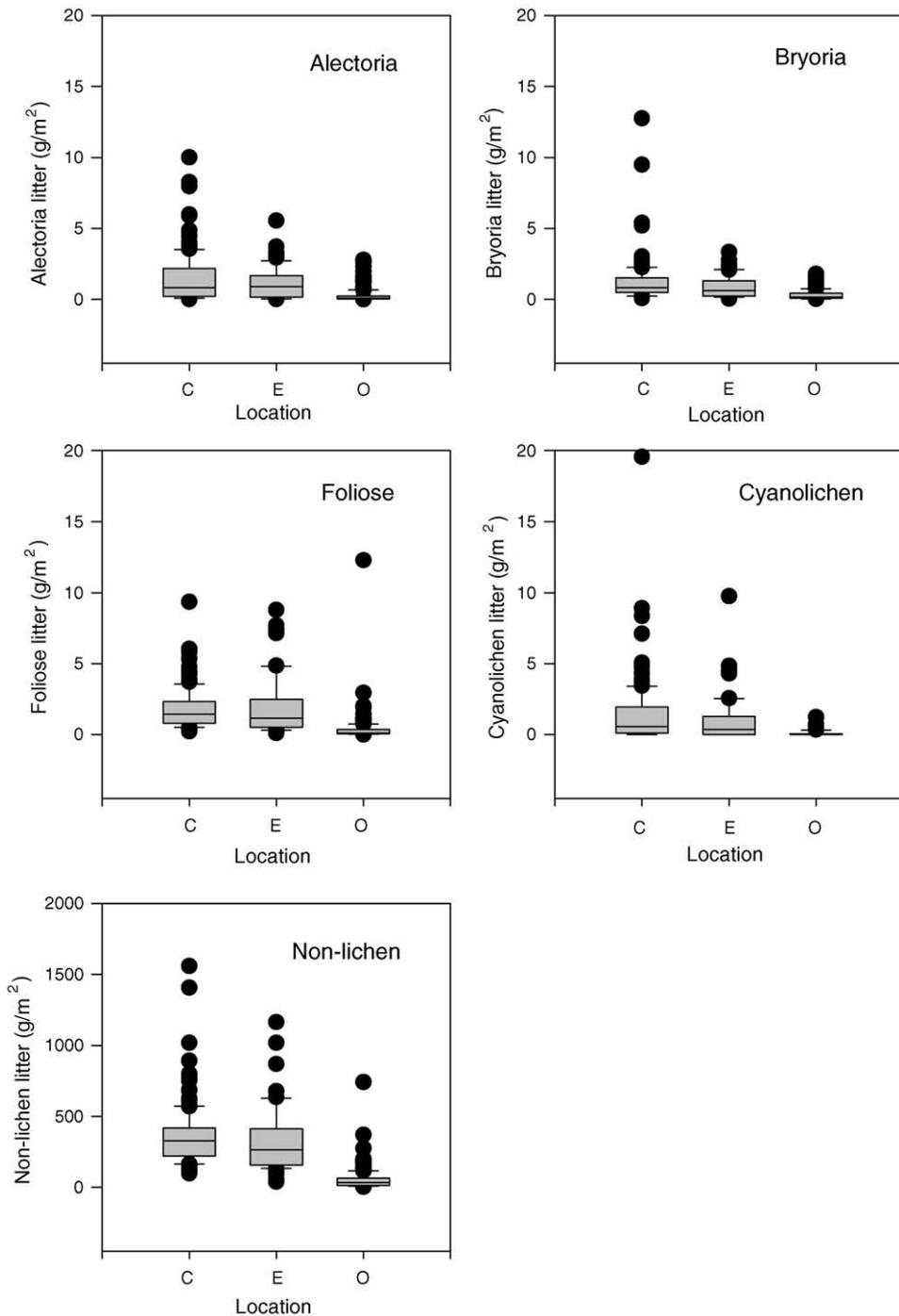


Fig. 6. Box plots showing distributions of litterfall biomass data (g/m^2) from traps located under the forest canopy (C), within 3 m of opening edges (E), and within openings (O). Note difference in scale between lichen and non-lichen litterfall components. The center horizontal line indicates the median, the box indicates the range of the central 50% of the values, or “H-spread”, and the whiskers show the range of values that fall within 1.5 H-spreads of the box. Circles indicate outliers.

Foliose lichens, particularly members of the family *Parmeliaceae* are known to be tolerant of (or even prefer) growth under early seral stand conditions (Bensen and Coxson, 2002) and are highly resistant to light stress (Gauslaa and Solhaug, 1996). Given their relative wind firmness (due to the firm attachment of thalli to small diameter branches) the observed changes in foliose lichen abundance near stand edges may in fact represent a growth response, indicative of early restructuring of canopy lichen communities. Renhorn et al. (1997) observed similar increases in the growth rates of *Platismatia glauca*, a generalist foliose species, within 12 m of edges in Norwegian *Picea abies* forests. This contrasts to findings of Hilmo and Holien (2002) who observed reduced cover of even pioneer foliose lichen communities at forest canopy edges, possibility indicative of the more harsh environment in their boreal *Picea abies* forests.

We anticipated that foliose cyanolichens would be among the most sensitive to changes in stand structure, given their seeming exclusion from naturally regenerated younger stands (Radies and Coxson, 2004). Our results showed no trends in total cyanolichen loading at stand edges, at least 2 years after harvesting. However, our observation that many of the cyanolichens on trees near exposed south-facing edges in the retained forest patches, though still firmly attached to branches, were starting to discolor, may presage future loss of cyanolichens from these managed forests. Kivisto and Kuusinen (2000) also observed major differences in lichen diversity along north- versus south-facing edges in boreal Finland.

Although the lack of cyanolichens in young coniferous forests may, in part, be due to poor growth environments, an emerging consensus would suggest that dispersal limitations also play a major role in cyanolichen scarcity in younger stands (Dettki et al., 2000; Hilmo and Sastad, 2001; Rosso et al., 2000). Transplant of old-growth associated lichens into younger stands (or on wooden racks in clearcuts) by Sillett and McCune (1998) showed that mortality rates were generally low (< 10%), although this may also reflect the wetter regional climate in the Oregon Cascades (with a mean annual rainfall of 1.5–2.2 m, compared to mean summer precipitation under 0.5 m in the wettest subzones of the ICH). However, many physiological studies show degradation of photosynthetic systems when thalli of *Lobaria pulmonaria* are

exposed to changes in ambient light environments (Gauslaa et al., 2001).

Although canopy sampling was replicated in two different stands in the upper Fraser River valley, the scale at which individual canopy lichens perceive their environment may be quite different from the scale at which prescribed harvest treatments are applied. Changes in canopy structure near individual branches, e.g. falling snags, removal of adjacent (commercial and non-commercial) trees, may have disproportionate impact on the growth and survival of individual lichen thalli. Even within our unharvested control sites, we observed changes in lichen loading. Canopy communities in old-growth stands are dynamic, subject to natural fluctuations due to weather events (Goward, 1998; Stevenson and Coxson, 2003) as well as gap-dynamics processes. Our use of permanently marked trees (and branches) upon which repeated assessments were taken provides a more accurate assessment of community changes at a scale relevant to lichens, a point emphasized by Fenton and Frego (2003) in studies on the response of forest floor bryophytes to logging practices. The use of low-impact single-rope climbing approaches (Perry, 1978; see also Campbell et al., 1999) further minimizes our disturbance within canopy environments.

4.2. Lichen litterfall

The biomass of canopy material falling to the forest floor each year is a function of various factors, including the standing crop in the canopy, weather events, and natural and human-caused disturbances in the forest. In this study, biomass of all litterfall components was greater during 2001/2002 than 2002/2003, independent of any treatment effects. This may have been caused by regional weather differences during the 2 years, particularly the more frequent occurrence of high winds during 2001/2002 than 2002/2003. However, some litterfall components exhibited greater differences between 2001/2002 and 2002/2003 values in one or both of the treatment units than in the unlogged control area; these probably indicate immediate post-harvest treatment-related effects, especially when they correspond to changes observed through canopy sampling.

Both Bryoria and the foliose group showed statistically significant differences between the 2

years in all six study area/treatment unit combinations, suggesting that these differences were primarily weather-related. However, the noticeably greater differences between years in foliose lichens in the group retention area, especially at Minnow Creek, suggests an additional treatment-related effect in this most extreme harvesting treatment.

For *Alectoria*, there appeared to be a treatment-related pulse of litterfall that was more pronounced in the GR and the GS treatment, and more pronounced at Minnow than at Lunate. Unlike the *Bryoria*, foliose, and non-lichen litterfall components, *Alectoria* litterfall was just as abundant in traps along edges as in traps located under the forest canopy. This suggests heightened levels of *Alectoria* litterfall along opening edges, mirroring the findings of a decline in *Alectoria* in the canopy of edge trees.

A key question is whether this initial loss of *Alectoria* along edges will persist over time. Several studies suggest that where edge effects on fruticose lichen biomass occur, they tend to persist. In black spruce forests of Quebec, biomass of the fruticose lichens *Evernia mesomorpha* and *Usnea* spp. on edge trees was only 55 and 49%, respectively, of that on interior trees, and the extent of edge influence was constant over time, up to 23-year-old edges (Rheault et al., 2003). In the Swedish boreal forest, biomass of *A. sarmentosa* on trees along 0.5–2.5-year-old edges was 22% of that on interior trees, but increased to 55% of interior values along older edges (8–16 years) (Esseen and Renhorn, 1998). In a 700-year-old Douglas-fir stand adjacent to a 20-year-old clearcut, biomass and species richness of lichen litterfall in general did not differ between the forest edge and interior, but *A. sarmentosa* was 4.5 times more abundant in interior litterfall traps than in edge traps (Sillett, 1995). Here, the reduced representation of *A. sarmentosa* in litterfall probably reflected a long-term reduction in *A. sarmentosa* biomass in the canopy along the edge.

Cyanolichen biomass in litterfall, like that in the canopy, showed no evidence of a treatment-related response, and only a weak suggestion of a weather-related response. The firm attachment of the cyanolichens to branches, as well as their lower-canopy position (Bensen and Coxson, 2002) may make them relatively insensitive to wind-scouring due either to weather events or to increased exposure. Similarly, in a partial cut in an Englemann spruce (*Picea*

engelmannii)–subalpine fir (*Abies lasiocarpa*) stand, both treatment-related and weather-related effects on lichen biomass were greatest in the upper canopy (Coxson et al., 2003; Stevenson and Coxson, 2003).

The non-significant difference between cyanolichen abundance in traps under the canopy and traps along edges cannot confidently be ascribed to edge effects, as there was no corresponding decline in cyanolichen biomass in the canopy of edge trees. Cyanolichen quantities in litterfall traps located within openings were low compared to other lichen groups. The large size of most cyanolichen thalli, as well as their lower-canopy position, probably limits their dispersal range. These results are consistent with those of Sillett and Goslin (1999), who reported that biomass of *Lobaria oregana* litterfall in a 100-year-old Douglas-fir stand decreased rapidly with distance from remnant older trees.

The biomass values shown in Table 2 underestimate true quantities of lichen litterfall, because lichens decompose in the snowpack during winter. We did not correct litterfall biomass for decomposition in this study, because we had no basis on which to correct biomass of foliose lichens or cyanolichens for decomposition. Decomposition rates for *Alectoria sarmentosa* and *Bryoria* spp. are known (Coxson and Curteanu, 2002). Had we corrected for decomposition using methods described by Stevenson and Coxson (2003), our estimate of annual *Alectoria* litterfall would have increased by an average factor of 1.29 in 2001/2002 and 1.26 in 2002/2003, and our estimate of annual *Bryoria* litterfall by an average factor of 1.39 in 2001/2002 and 1.32 in 2002/2003.

In this study, total lichen litterfall biomass ranged from 26.0 to 69.7 kg/ha/year in the unlogged areas. This range was similar to that measured at a nearby subalpine stand (22.4–61.2 kg/ha/year) (Stevenson and Coxson, 2003), but no cyanolichens were present at the high-elevation site. Cyanolichen litterfall ranged from 1.7 to 2.5 kg/ha/year at Minnow Creek, and from 18.9 to 22.3 kg/ha/year at Lunate Creek. Cyanolichens fix atmospheric nitrogen into forms available to plant uptake, and release it through leaching, in situ decomposition, and decomposition of litterfall (Pike, 1978; Antoine, 2004). Given the importance of cyanolichens in forest nutrient cycling, it is surprising that little information is available on the magnitude of cyanolichen litterfall on an annual basis. Estimates of

the standing crop of cyanolichen litter on the forest floor include 0–7.9 kg/ha in the Coastal Western Hemlock Zone of Vancouver Island (Price and Hochachka, 2001), 0 to approximately 65 kg/ha in Douglas-fir stands in the western Oregon Cascades (Sillett and Neitlich, 1996), and 97 kg/ha in the interior of a 700-year-old forest in western Oregon (Sillett, 1995). Standing crop estimates are valuable for comparisons among or within stands (Sillett and Goslin, 1999), but they are not comparable to annual litterfall estimates.

5. Conclusion

Our study indicates that partial-cutting can result in the retention of canopy lichens in the residual stand, even after harvest levels as high as 70%, during the first few years after logging. The exception to this pattern was seen for thalli of *Alectoria* lichens, whose longer pendulous growth forms predisposed them more to wind-scouring at the edge of retained patches.

Several questions are raised that cannot be answered at this time. Will the observed decline in biomass of *Alectoria* along edges persist? Will the short-term increase in the biomass of foliose lichens in edge trees continue, eventually resulting in a higher proportion of foliose lichens in litterfall? Will the observed discoloration of some of the cyanolichens be followed by mortality and a decline in biomass, or will these lichens adjust to the modified environment created by the edges? The last question is of particular importance, because of the high conservation value of the cyanolichen community. However, over longer time periods (10–50 years) there clearly is a potential for shifts in canopy lichen community composition, if presently observed trends continue.

Acknowledgements

We would like to thank Kevin Jordan (Arbonaut Access), Jocelyn Campbell, Andrea Barker, Anna Hallam, and Becky L'Hirondelle for assistance with canopy assessments, Mike Jull for support of silvicultural systems design and implementation, and Bob Sagar for the use of unpublished climate data. We are also grateful to our crew of technicians

who recorded field data and collected, sorted, and weighed the litterfall. Funding support was provided by the University of Northern British Columbia and the Province of British Columbia (Forest Renewal BC and Forestry Innovation Investment).

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