Lichen Colonization and Gap Structure in Wet-temperate Rainforests of Northern Interior British Columbia

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Abstract. *Abundant canopy lichen communities characterize wet-temperate rainforests on the windward slopes of interior mountain ranges in north-central British Columbia, Canada. Historically, these forests have regenerated through gap-dynamics; however, our knowledge of lichen colonization within gaps is limited. We have now compared lichen biomass on regenerating trees in naturally occurring 1–3 ha gap-disturbances (these gaps presumed to have originated from insect out-breaks in the late 1800's) with those on regenerating trees of similar age growing in the understory of the surrounding old growth forest. Only small differences were seen in total lichen biomass on regenerating trees between the two settings, however, analysis of the individual lichen groups (Alectoria, Bryoria, Foliose, and Cyanolichen) revealed striking differences. The* Bryoria *group was 35% more abundant on gap trees (632 g/tree) and was distributed vertically through a larger proportion of the tree crown. The Cyanolichen functional group was largely absent from gap trees, despite high levels of biomass loading (1,332 kg/ha) in the surrounding old-growth stand.* Alectoria *and Foliose functional groups did not differ significantly in biomass or distribution between regenerating trees of the two types. Tree size positively affected lichen loading. Total lichen biomass was 38% greater on the larger size class (31–44 cm dbh) regenerating trees, with the Alectoria functional group alone having 45% greater biomass on larger trees. Presence or absence of leaves on branch substrate had no effect on lichen loading. Stand-level projections indicate that the old growth forest had 19% more arboreal lichen biomass (2,684 kg/ha) and contained greater lichen species diversity than did the ''second-growth'' regenerating forest patches. The low cyanolichen biomass in naturally occurring gap openings poses concern for the proposed utility of ''new-forestry'' type harvesting practices to retain canopy biodiversity using current harvest rotation intervals.*

As Pacific storm systems move over the interior mountain ranges in British Columbia, they create a zone of high precipitation, allowing the development of an inland wet-temperate rainforest. Even with a continental climate, vascular and non-vascular plant communities of this inland rainforest are similar to those of coastal forests in the Pacific Northwest (i.e., Oregon, Washington, and British Columbia – Ketcheson et al. 1991).

The wettest subzones of these inland rainforests, the interior-cedar hemlock zone (ICH) of the northern Cariboo and Rocky Mountains (Ketcheson et al. 1991), are characterized by natural disturbance regimes in which fire is infrequent (Sanborn et al. 2001). More common disturbance agents are insects, pathogens, and weather, which result in stand regeneration through gap dynamics. Historically, this has produced landscapes with a high proportion of uneven-aged old-growth forests and a long continuity of forest cover (Arsenault & Goward 2000).

This has favored the development of rich canopy lichen communities (Goward & Arsenault 2000*a*) that support many ecosystem functions, for instance, providing a major winter forage source for mountain caribou populations (Stevenson et al. 2001).

The establishment of lichens within forest stands requires that several prerequisite conditions be met — lichen propagules must arrive at the site (dispersal), lichen propagules must find a suitable surface for establishment (substrate availability); and conditions must be adequate for lichens to grow (microclimate). When stand regeneration occurs primarily through gap dynamics, young trees should have more ready access to lichen propagules from the surrounding stand. Under these conditions, one would expect that limitations of substrate (physical and chemical) and growth conditions (microclimate) may play a more important role in determining the rate at which lichen communities develop.

Stevenson (1988) and Dettki (1998) noted that dispersal capability is a major factor limiting lichen

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colonization on regenerating trees in second growth forest stands and that dispersal of lichen propagules depended on distance to a mature stand, abundance of lichen in the mature stand, and the area and height of the mature stand. Tree structure is another important factor determining the success of lichen colonization. Armstrong (1990) found that lichen propagules had higher rates of survival on rough bark compared with smooth bark, while Esseen et al. (1996) reported that smaller trees provided less available substrate for lichens, therefore limiting their abundance. These factors interact with gradients of canopy microclimate to determine the composition and placement of lichens within the canopy (Campbell & Coxson 2001; Liu et al. 2000). Additionally, site specific factors, such as proximity to water bodies, presence of wolf-trees (trees with large diameter lower branches), and enrichment of throughflow precipitation by remnant deciduous trees (Goward & Arsenault 2000b; Neitlich & McCune 1997), can play an important role in enhancing lichen colonization and growth.

The interaction of these factors is becoming increasing important to the management of inland rainforests, where the adoption of ''new forestry'' type approaches such as partial-cut or variable retention harvesting, creates small harvest openings, where regenerating trees will be surrounded by mature canopy (Franklin et al. 1997). Unresolved, at the present time, however, is whether or not this emulation of natural processes (i.e., gap dynamics) will insure that canopy lichens will be retained in managed forests. A better understanding of lichen colonization will provide forest managers with a valuable predictive and explanatory tool to aid in management decisions.

The goal of this study was therefore to investigate factors influencing lichen colonization in the canopy of trees in small to medium sized natural gaps (1–3 ha in size) within old-growth cedar-hemlock stands of north-central B.C. We have taken canopy based (using single rope climbing techniques) measurements of the composition, abundance, and distribution of lichen communities on older and regenerating trees, comparing trees in naturally occurring even-aged 1–3 ha ''gap'' stands (dating from the same originating disturbance event) with trees in adjacent old-growth cedar-hemlock forest stands.

By controlling for the structure and age of sample trees from the two stand types, we can infer the effects of dispersal capability and microclimate associated with canopy structure. The role of substrate quality was evaluated by comparing branch structural attributes (diameter, length, density) of regenerating trees. Branch substrates with and without leaves were inspected to detect habitat differ-

FIGURE 1. Location of study area within the province of British Columbia, Canada. The shaded areas show the extent of wet subzone interior cedar-hemlock forests in BC.

ences affecting colonization. The effect of tree size on lichen loading was further examined comparing a subset of regenerating trees of similar age but different diameters. This study tested four hypotheses 1) Regenerating trees in the understory of old growth forests will support more lichen biomass than regenerating trees in gap stands. 2) Lichens will be distributed differently within the crowns of regenerating trees found in old growth and gap stands. 3) Larger trees will support more lichen biomass than smaller trees of the same age. 4) Branch substrates with leaves will contain more lichen biomass than branch substrates without leaves.

METHODS

Study area.—The study area was located approximately 120 km east of Prince George, BC, Canada in the very wet cool (vk2) subzone of the interior cedar-hemlock (ICH) biogeoclimatic zone (Ketcheson et al. 1991) (Fig. 1). The forests were classified as old growth (250+ years), with western red cedar, *Thuja plicata* L. and western hemlock, *Tsuga heterophylla* (Raf.) Sarg., as the leading species. The interior, continental climate of the ICH is characterized by prevailing westerlies that produce cool wet winters and warm dry summers. Mean annual precipitation in the ICH is 840 mm (374 mm in

TABLE 1. Tree class definitions.

Tree Class	Definition	Stand Type
Matrix Old Growth (M–OG)	Late-seral (> 180 yrs old) western hemlock and western red cedar, diameter generally greater than 55 cm; dead, broken, or forked top; large, complex branch systems in lower crown. Lower canopy 0–11.9 m, midcanopy 12–23.9 m, upper canopy 24–36 m.	Old growth matrix
Matrix Regen (M–R)	Mid-seral (100 yr old) western hemlock, diameter range of 20.3–44 cm, located in the understory of older trees. Lower canopy 0–7.9 m midcanopy 8–15.9 m, upper canopy 16–24 m.	Old growth matrix
Gap Veteran (G–V)	Late-seral (> 180 yrs old) western hemlock, diameter generally greater than 55 cm; dead, broken, or forked top; large, complex branch systems in lower crown. Lower canopy 0–7.9 m, midcanopy 8–15.9 m, upper canopy 16–24 m.	Gap
Gap Large Regen (G–LR)	Mid-seral (100 yr old) western hemlock with diameter range of 30.9–44.0 cm. Lower canopy 0–7.9 m, midcanopy 8–15.9 m, upper canopy 16–24 m.	Gap
Gap Standard Regen (G–SR)	Mid-seral (100 yr old) western hemlock with diameter range of 17.3–30.9 cm. Lower canopy 0–7.9 m, midcanopy 8–15.9 m, and upper canopy 16–20 m.	Gap

summer and 465 mm in winter) with a mean summer temperature of 14.7°C and a mean winter temperature of −12.1°C (Ketcheson et al. 1991). Recorded mean annual snowfall is 306.8 cm, with snow persisting on the ground nine months of the year (Reynolds 1997). The slow-melting snow pack keeps soil moisture levels high during the summer (Ketcheson et al. 1991).

The wet subzones of the ICH experience infrequent stand-level disturbances, with fire return intervals of 500 to 1,000 yr or more (Sanborn et al. 2001). However, small-scale disturbances (i.e., wind, snow loading, or insect attack) that result in single-tree or small (1–3 ha) gap openings are more common (BC Ministry of Forests 1995). Within the study area, small patches of even-aged regenerating hemlock, approximately 100 yr old, were scattered throughout old growth forest stands. The most likely cause of the disturbance was the western hemlock looper [*Lambdina fiscellaria lugubrosa* Hulst] (Lepidoptera: Geometridae), a defoliating insect. There have been two documented western hemlock looper outbreaks in the ICH zone since 1911, with the most recent occurring in 1994 (Parfett et al. 1995). The occasional large diameter veteran trees that survived defoliation events remain interspersed within the regenerating stands. No evidence of recent fire (charred stumps, surface charcoal) was visible within the stand.

Experimental design.—Three field sites were selected in the Viking Ridge (53°51′38″ N, 121°33′50″ W) and Hungary Creek (53°49′53″ N, 121°28′44″ W) watersheds, in the upper Fraser River Valley, ca 100 km east of Prince George (Fig. 1). The sites are referred to as Viking West, Viking East, and Hungary. Care was taken to ensure that the sites were relatively similar in elevation (900–1,000 m), slope (7–23°) and aspect (north to northwesterly) to allow for better comparisons between sites.

Each study site comprised a 1–3 ha gap stand paired with an adjacent old growth stand. The sampling area within each stand type was defined by three 11.3 m radius circular plots, evenly spaced along a 50 m transect line. The gap transect was located close to the center of the gap to minimize edge effects. The old growth transect was established at least 50 m from any edge to minimize edge effects. All trees within the circular plots greater than one cm diameter at breast height (dbh) were recorded by species, including snags. The regenerating trees used for sampling (hereafter referred to as regen trees) were restricted to a single species, western hemlock, reflecting its dominance in the gap stands.

Gap regen trees were split into two different size classes, standard regen (SR) and large regen (LR) (see Table 1 for complete listing of acronyms). The dbh range identifying standard regen sample trees was arrived at by calculating the mean dbh from stand characteristic data. The tree diameter range of standard regen trees in gaps (G–SR) was defined by the mean ± one standard deviation (24.08 ± 6.79 cm) of gap stand trees. The tree diameter range of large gap regen trees (G–LR) was categorized as trees above 30.89 cm dbh. An upper limit of 44 cm dbh was established to denote the point above which structural features characteristic of veteran/old growth trees were noticed.

The dbh range for regenerating trees in the old-growth matrix (M–R) trees was calculated in a similar fashion. The data set included early-seral stage tree dbh data from the sites with lower and upper limits set at 20.3 and 44 cm dbh respectively. The

TABLE 2. Inventory of sample trees (western hemlock) by site. Standard regen (SR), large regen (LR), veteran (VET), old growth regen (OGR), old growth (OG).

Tree class	Site						
	Hungary Gap	Viking East Gap	Viking West Gap	Hungary Old Growth	Viking East Old Growth	Viking West Old Growth	Total
M–OG[1]	—	—	—	3	3	3	9
M–R[2]	—	—	—	5	5	5	15
G–V[2]	3	0[3]	3	—	—	—	6
G–LR[2]	5	5	5	—	—	—	15
G–SR[2]	5	5	5	—	—	—	15
Total							60

[1] Western red cedar (3 trees total) and western hemlock (6 trees total).

[2] Western hemlock only.

[3] Western hemlock trees present but unsafe to climb.

mean dbh was 27.61 ± 7.27 cm. The upper end of this diameter range was extended to 44 cm dbh to include the desired number of sample trees. The crowns of many early-seral stage trees less than 25 cm dbh were rejected as sample trees for safety reasons.

Large regenerating trees in gaps (G–LR) were more similar in structure to M–R trees than to G–SR trees. For the comparison of gap and matrix regen trees, only large gap regen trees were used (except for cyanolichens, see below). G–SR and G–LR were compared to evaluate the effect of tree size (amount of available substrate) on lichen colonization. The abundance of lichen growing in foliated and non-foliated regions of branches was examined in all regen tree classes to assess the effect of substrate type on lichen colonization.

Veteran trees in gap stands were assessed for lichens to evaluate their role as propagule sources for gap regen trees. Veteran sample trees were also restricted to western hemlock, to represent their dominant proportion within the gap stands. In old-growth stands, western red cedar and western hemlock were co-dominant and mature trees of both species were sampled to obtain a complete picture of lichen propagule sources.

Sample trees were randomly selected from a pool of representative candidates. In each gap stand, five G–SR, five G–LR, and three gap veteran (G–V) trees (if present) were identified as sample trees. In each old-growth stand, five M–R and three matrix old-growth (M–OG) trees (two western red cedar and one western hemlock), to represent the ratio of species occurrence within the stand) were identified as sample trees. When a sample tree of a specific tree class was not found within the sampling area defined by the three 11.3 m radius circular plots, the nearest tree within the stand meeting all specifications was selected as the sample tree. In total, 60 trees were sampled, 36 from the gap stands and 24 from old growth stands (Table 2).

Lichens were grouped based on a modified version of the functional groups described by McCune (1993). In this study, the Alectorioid group of lichens was split into an *Alectoria* functional group and a *Bryoria* functional group to investigate their ecological roles separately, despite their common function as forage for mountain caribou (Rominger et al. 1996). The Alectoria functional group consisted of *Alectoria* and *Usnea* species (*Alectoria sarmentosa*, *Usnea filipendula*, and *U. scabrata*), while the *Bryoria* functional group included *Bryoria* and *Nodobryoria* species (*Bryoria capillaris*, *B. fremontii*, *B. fuscescens*, *B. lanestris*, *B. pseudofuscescens*, and *Nodobryoria oregana*). The Cyanolichen functional group comprised all foliose lichens containing a cyanobacterium as the photobiont (including *Lobaria pulmonaria*, *L. scrobiculata*, *Nephroma helveticum*, *Sticta fuliginosa*) and the Foliose functional group included all other foliose lichen species [*Cavernularia hultenii*, *Cetraria chlorophylla*, *C. orbata*, *Hypogymnia metaphysodes*, *H. occidentalis*, *H. physodes*, *H. tubulosa*, *H. vittata*, *H. spp. nov.* (Goward), *Parmelia hygrophila*, *P. sulcata*, *Parmeliopsis ambigua*, *P. hyperopta*, *Platismatia glauca*, *P. norvegica*].

Lichen assessments were made from within the crown in order to have an unobstructed view of lichens at all levels. Stevenson (1979) reported that a clear view of lichens increased consistency of assessments. We used the single rope technique to access the canopy (Perry 1978). For all sample trees, lichen biomass was visually estimated on every branch > one cm diameter at the tree bole and > 10 cm long using the "clump method" (Campbell et al. 1999; Stevenson 1979). This method involves comparing the amount of lichen on a given branch to a lichen standard of known dimensions and reporting the biomass as a multiple of that standard (i.e., two "clumps" lichen). Lichen estimates were made separately for each functional group. We used the lichen standards developed by Campbell et al. (1999) with the addition of a Cyanolichen standard (15 × 20 cm "card").

TABLE 3. Regression results for estimated and measured lichen biomass, where y equals predicted lichen biomass (destructively sampled) and x represents visual estimates of lichen biomass obtained from within the canopy.

| Functional Group | Regen Trees | | | | | | | | Old Growth/Veteran Trees | | | |
| | Foliar Region | | | | Non-Foliar Region | | | | | | | |
	a	b	R^2	n	a	b	R^2	n	a	b	R^2	n
*Alectoria***	6.916	0.602	0.73	30	4.219	0.709	0.82	22	10.526	0.912	0.90[1]	40
*Bryoria***	8.928[5]	0.969	0.52	28	9.416[1]	0.170	0.85	21	4.637	1.149	0.65	41
Foliose**	4.952[4]	0.761	0.79	18	2.761[3]	1.150	0.72	19	1.103	0.344	0.84*	13
Cyanolichen***	24.467[3]	0.155	0.76	30	—	—	—	—	12.212	−2.161	0.87	26

(n) number of outliers removed.

* $\log_{10}$ transformed data.

** Linear regression ($y = ax + b$).

*** Regen Trees use an Exponential regression ($y = a(1-b^x)$) with pooled data for foliar and non-foliar regions; Old Growth trees use a Linear regression ($y = ax + b$).

For regen trees, lichen biomass estimates were made separately in the foliar and non-foliar region to assess the effect of substrate type on colonization. The foliar region included all foliated sections of the branch. The non-foliar region was defined as any segment of branch not covered directly by foliage or any area of dead/defoliated branch among the foliar region. Separate foliar/non-foliar region estimates were not performed on old growth or veteran trees because the long, complex branch systems common in older trees made it difficult to accurately estimate lichens in the two regions. In addition to estimating lichen biomass, we also recorded the following for each branch sampled on all sample trees: branch height and diameter, branch length class (Class 1, 0.1–0.2 m; Class 2, 0.2–1 m; Class 3, 1–3 m; Class 4, < 3 m), and proportion of the branch containing foliage as a foliar index (1, no foliage/dead; 2, < 1/3 foliated; 3, 1/3–2/3 foliated; 4, > 2/3 foliated). The dbh, age, and height of each tree were also measured.

A subsample of branches was selected for destructive sampling, to verify the visual lichen biomass estimates for all functional groups, using Probability Proportional to Prediction (3P) sampling (Campbell & Coxson 2001; Cochran 1977). In 3P sampling, the subsampled units (branches) are selected with a frequency proportional to their predicted (estimated) biomass. Thus, branches with greater biomass were selected with greater frequency than branches with lower biomass. Destructively sampled branches were cut from the tree, taking care not to lose any lichen. Branches were brought back to the laboratory where they were air dried and stripped of lichen. The lichens were sorted by functional group and then placed under a constant humidity of 60% for 48 hr to equilibrate before weighing under the same conditions.

All lichen mass data reported here are based on lichens equilibrated at 60% humidity. Stevenson and Jull (1996) provided equations to convert from mass at 60% humidity to oven-dried mass. These show that an equivalent oven-dried mass of Alectorioid lichens (*Alectoria* and *Bryoria* functional groups) would be 8.6% below that from lichens weighed at a 60% R.H. equilibrium, while that of cyano- and foliose lichens would be 6.0% less.

This verification of visual estimate sampling was conducted separately for regen and old growth/veteran trees because of their differences in canopy structure and attendant visual sight lines. Estimates in the foliated and non-foliated regions of regen trees were also verified separately, except for the cyanolichen group, where very low abundances led us to pool the physically sampled lichen fragments from each branch (foliar and non-foliar regions). Linear regression analysis was run using the estimated and weighed lichen biomass data for each lichen functional group to generate correction factors for converting ''clump'' based estimates to grams, with the exception of the cyanolichen regen group, where an exponential equation was used (Table 3). The use of regressions on log transformed data (foliose functional group only) can potentially introduce a bias on back-transformation of results. However, trial corrections to our data adding a constant to the regression equation (after Campbell & Coxson 2001) had no discernable impact, hence this additional step has not been included in the present data set.

For comparisons of lichen loading between different tree classes, data from the three sites were pooled if ANOVA results showed no effect for differences within stand type. Tukey's post-hoc tests were used for comparisons of significant ANOVA results, including analysis of lichen abundance, distribution, and tree structure. A $\log_{10}$ transformation was used where needed to improve the normality of skewed data.

For the analysis of tree structure, the canopies of each tree class were subdivided into low, mid, and upper regions to make more detailed comparisons.
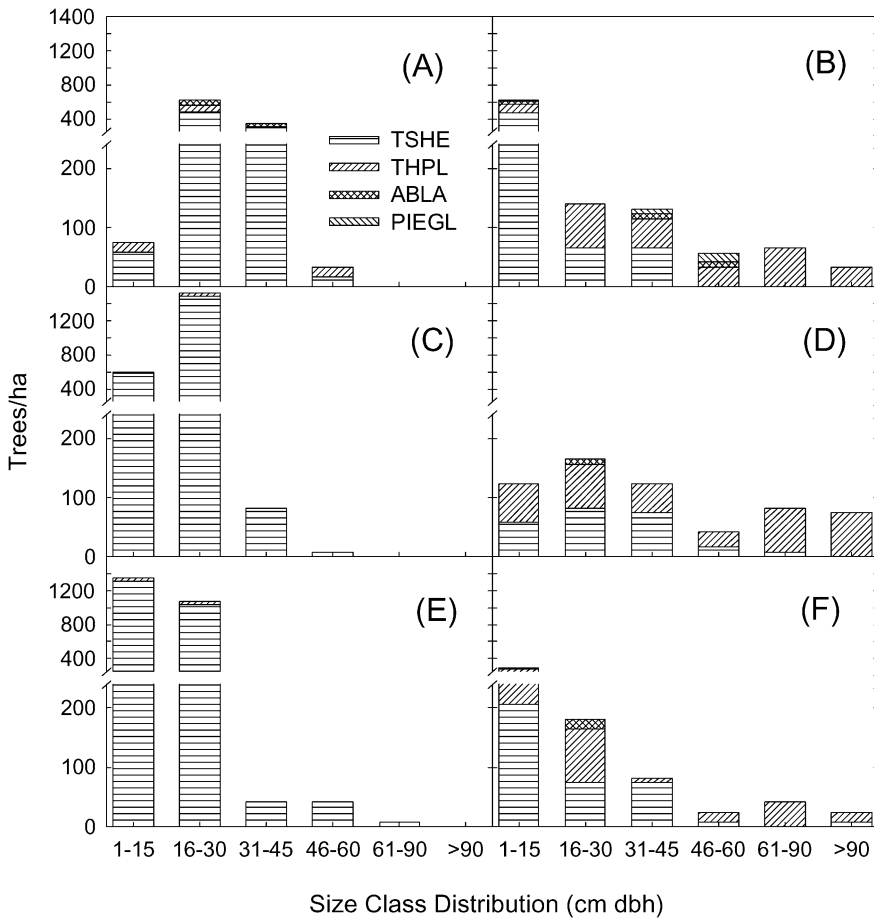
FIGURE 2.   Diameter size class distribution for mean number of trees/ha.: — A. Hungary Gap. — B. Hungary Matrix. — C. Viking East Gap. — D. Viking East Matrix. — E. Viking West Gap. — F. Viking West Matrix. TSHE–*Tsuga heterophylla*, THPL–*Thuja plicata*, ABLA–*Abies lasiocarpa*, PIEGL–*Picea engelmanii x glauca*.

These regions were arbitrarily set using the maximum tree height interval (tree height marked by four m increments) and equally dividing the tree into thirds (see Table 1 for height class ranges). An ANOVA was used to test for differences in tree structural variables across canopy strata within a given tree class. The structural variable of summed branch length was used to represent the amount of available substrate for lichen colonization. This was calculated by converting branch length classes to meters using mid-point values. These lengths were then summed for a specific canopy region or for the entire tree.

A conservative approach was taken in estimating stand-level arboreal lichen loading. Projections were based only on tree classes and species restrictions described previously in the methodology. Therefore, trees present in the stand that were outside the diameter range set for sample trees (e.g., < 17.31 cm dbh and between 44 and 55 cm dbh in gap stands) were not considered in stand-level projections. Also, the projections did not include tree species other than those defined as sample trees (i.e., western hemlock for all regen classes and the veteran class, and western hemlock and western red cedar for the old growth class). Stand-level lichen loading (g of lichen/ha) was calculated by multiplying the mean density of each tree class by its mean lichen biomass. All statistical analyses were performed using the Statistica statistics package (1997 by StatSoft Inc.).

RESULTS

Gap stands were more dense than old growth stands at all sites, with the largest concentration of trees falling into the smaller dbh size classes (Fig. 2). Trees were more evenly distributed through the full range of size classes in old growth stands. Mean stand density in old growth and gap stands was 766 and 1,930 trees/ha respectively. Gap stands had a greater density of snags than old growth

TABLE 4. Mean results for structural analysis of sample trees in matrix old growth (M–OG), matrix regen (M–R), gap veteran (G–V), gap large regen (G–LR), and gap standard regen (G–SR) tree classes. Standard deviations are in parentheses.

Structural Attribute	Tree Class				
	M–OG $n = 9$	M–R $n = 15$	G–V $n = 6$	G–LR $n = 15$	G–SR $n = 15$
Tree height (m)	32.2(4.3)	19.4(3.5)	22.5(3.4)	20.2(3.5)	17.0(3.6)
Tree dbh (cm)[a]	80.5(14.0)	33.1(7.2)	61.2(13.2)	35.3(3.7)	23.4(3.5)
Age	—	83.7(11.9)	269.0(30.0)	90.2(8.0)	96.5(9.7)
No. of branches	246.6(74.4)	98.0(39.9)	98.5(54.8)	130.9(45.3)	63.2(29.6)
Branch density (branches/m)					
Lower canopy		3.7(2.0)	—	2.8(1.4)	1.2(1.1)
Midcanopy		5.6(1.8)	—	7.4(1.7)	5.2(1.8)
Upper canopy[b]		7.1(2.6)	—	13.6(6.2)	9.0(2.3)
Total	7.8(2.7)	5.0(1.7)	4.2(1.8)	6.4(1.5)	3.7(1.2)
Branch diameter (cm)					
Lower canopy	—	2.8(0.5)	—	1.9(0.3)	1.9(0.4)
Midcanopy	—	2.9(0.5)	—	2.5(0.4)	2.1(0.3)
Upper canopy[b]	—	3.1(1.1)	—	2.4(0.2)	2.1(0.6)
Total	4.3(1.6)	2.9(0.6)	5.2(1.4)	2.4(0.3)	2.1(0.3)
Σ branch length (m)[c]					
Lower canopy	—	57.9(39.0)	—	19.1(11.4)	7.2(8.3)
Midcanopy	—	93.1(35.1)	—	92.4(34.1)	47.5(17.5)
Upper canopy[b]	—	52.1(54.1)	—	82.7(59.1)	48.7(34.5)
Total	523.8(118.8)	199.6 (86.9)	276.1(110.0)	188.7(58.7)	83.9(33.4)

[a] $n = 6$ for M–OG; $n = 4$ for G–V.
[b] $n = 14$ for M–R and G–LR; $n = 9$ for G–SR.
[c] $n = 6$ for M–OG, $n = 3$ for G–V.

stands (1,260 and 211 snags/ha respectively), and snags in both stand types were largely in the 1–15 and 16–30 dbh size classes. Stand density for the Hungary old growth stand was high in comparison to the other old growth stands because the sampling area contained a single-tree opening, thick with small regenerating trees. Old growth and gap stands did not differ greatly in mean basal area, 95 and 74 m^2/ha respectively.

Matrix old growth vs. matrix regen.—Matrix old growth trees differed significantly from matrix regen trees in all structural variables considered (Tables 4–5). M–OG trees supported more total lichen biomass than M–R trees (Table 5, Fig. 3). All functional groups considered were more abundant in M–OG trees, up to ten times more for the *Alectoria* functional group.

The *Bryoria* and Foliose functional groups had different vertical distributions in M–OG and M–R trees. The Foliose functional group was more abundant in the mid canopy of both tree classes, however, the distribution was skewed towards the upper canopy in M–OG trees and towards the lower canopy in M–R trees (Fig. 3). The *Bryoria* functional group reached greatest abundance in the upper canopy of M–R trees and the mid canopy for M–OG trees (Fig. 3), although abundance was nearly as high in the upper M–OG canopy. The vertical distribution of the *Alectoria* functional group was sim-

ilar for both tree classes, with a pattern of more biomass towards the mid canopy (Fig. 4).

Matrix old growth vs. gap veteran.—All matrix old growth trees assessed had interior rot and accurate age estimates were therefore not obtained. Individual cores of the intact outer shell showed some M–OG trees > 450 yr in age. The mean age for veteran trees was 269 ($\pm$ 30) years. Matrix old growth trees were taller than veteran trees, but there was no difference in dbh (Table 4). M–OG trees had more branches, greater branch density, and a longer summed branch length than G–V trees. Branch diameter did not differ between the two tree classes.

Branch density was compared across canopy strata for G–V trees; the lower canopy was less dense than the mid and upper regions (Table 4). For summed branch length, the lower canopy had less branch length than the upper canopy. There was no difference in branch diameter across canopy strata. A similar pattern was seen in M–OG trees with the exception of summed branch length; the lower canopy had less branch length than the mid canopy region.

The *Alectoria*, *Bryoria*, and Foliose functional groups were present on all veteran and matrix old growth trees sampled. The frequency of the Cyanolichen functional group in the veteran trees was 100% in the Hungary gap stand and 67% in the

TABLE 5. Tukey's post-hoc comparisons (*t* values and probability) for canopy structural variables between stand types [Matrix old growth (M–OG), matrix regen (M–R), gap veteran (G–V), gap large regen (G–LR), gap standard regen (G–SR)]. Significant values are indicated in bold.

| | Tree Class | | | | | | | | | |
| Tree Structural Attribute | M–OG vs M–R | | M–OG vs G–V | | G–V vs G–LR | | M–R vs G–LR | | G–LR vs G–SR | |
	t	*p*	*t*	*p*	*t*	*p*	*t*	*p*	*t*	*p*
Tree height (m)	8.001	**< 0.001**	−4.672	**< 0.001**	1.404	0.176	0.607	0.548	2.401	**0.023**
Tree dbh (cm)[a]	7.863	**< 0.001**	−2.175	0.061	3.895	**0.028**	1.044	0.306	8.979	**< 0.001**
Age	—	—	—	—	14.205	**< 0.001**	−1.767	**0.088**	−1.928	0.064
No. of branches	6.414	**< 0.001**	−4.160	**0.001**	−1.397	0.179	2.111	**0.044**	4.843	**< 0.001**
Branch density (branches/m)										
Low canopy	—	—	—	—	—	—	−1.432	0.163	3.533	**0.001**
Midcanopy	—	—	—	—	—	—	2.838	**0.008**	3.535	**0.001**
Upper canopy[b]	—	—	—	—	—	—	3.621	**0.001**	2.117	**0.046**
Total	3.153	**0.006**	−2.887	**0.013**	−2.892	**0.009**	2.334	**0.027**	5.446	**< 0.001**
Branch diameter (cm)										
Low canopy	—	—	—	—	—	—	−5.804	**< 0.001**	0.538	0.595
Midcanopy	—	—	—	—	—	—	−2.512	**0.018**	3.098	**0.004**
Upper canopy[b]	—	—	—	—	—	—	−2.372	**0.025**	1.326	0.216
Total	3.083	**0.005**	1.077	0.301	4.611	**0.005**	−3.112	**0.004**	3.183	**0.004**
Σ branch length (m)[a]										
Low canopy	—	—	—	—	—	—	−3.697	**0.001**	3.27	**0.003**
Midcanopy	—	—	—	—	—	—	−0.055	0.957	4.539	**< 0.001**
Upper canopy[c]	—	—	—	—	—	—	1.430	0.165	1.557	0.134
Total	6.972	**< 0.001**	−3.010	**0.020**	2.054	0.057	−0.403	0.690	6.011	**< 0.001**

[a] n = 6 for M–OG; n = 4 for G–V.
[b] n = 14 for M–R and G–LR; n = 9 for G–SR.
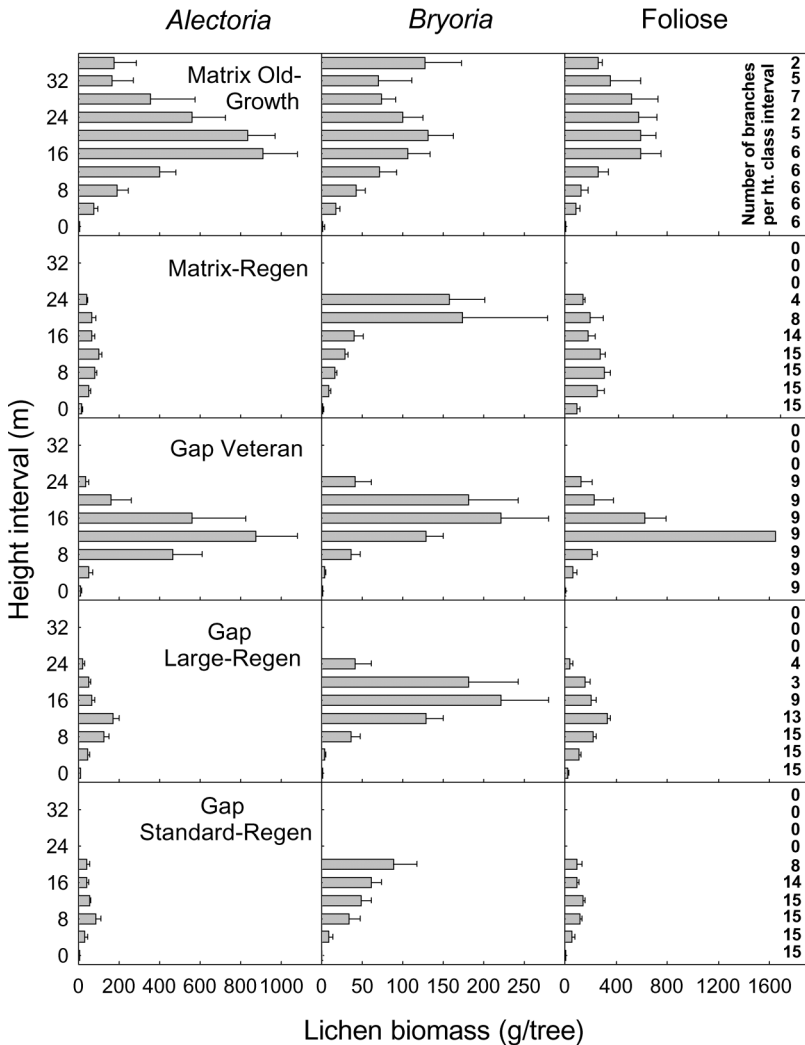[c] n = 6 for M–OG, n = 3 for G–V.

FIGURE 3.   Vertical distribution of the *Alectoria*, *Bryoria*, and Foliose functional group expressed as mean lichen biomass per height interval for matrix regen, matrix old growth, gap large regen, gap veteran, and gap standard regen type trees. Error bars represent the standard error of the mean and the numbers along the right hand axis indicate total sample size (number of branches) for each height class interval of that tree class.

Viking West gap stand. No G–V trees were assessed in the Viking East gap stand for safety reasons.

Matrix old growth trees supported significantly more lichen biomass than veteran trees, with the Cyanolichen functional group being the main factor contributing to this result (Table 5). There was no difference in lichen biomass between matrix old growth and veteran trees for the *Alectoria*, *Bryoria*, and Foliose functional groups. M–OG and G–V trees were less stratified than regen trees in the vertical distribution of lichen functional groups. Peak biomass of Alectoria and Foliose lichen functional groups was found in the mid canopy (Figs. 3–4) of M–OG and G–V trees. For *Bryoria*, peak abundance was seen in the 16–20 height interval of G–V trees (defined as upper canopy for G–V these

trees based on their stature), whereas for M–OG trees, although, although *Bryoria* abundance also peaked in the 16–20 height interval (defined as mid-canopy for M–OG trees based on their stature) a secondary peak of abundance was seen in the extreme upper canopy (although the number of replicate branches at this height was low).

Gap veteran vs. gap large regen.—G–V trees were older and larger in diameter than G–LR trees, however, there was no difference in tree height (Table 4). G–V and G–LR trees did not differ significantly in total number of branches or summed branch length (Table 5). Branch density was greater in G–LR trees and branch diameter was greater in G–V trees (Table 4).

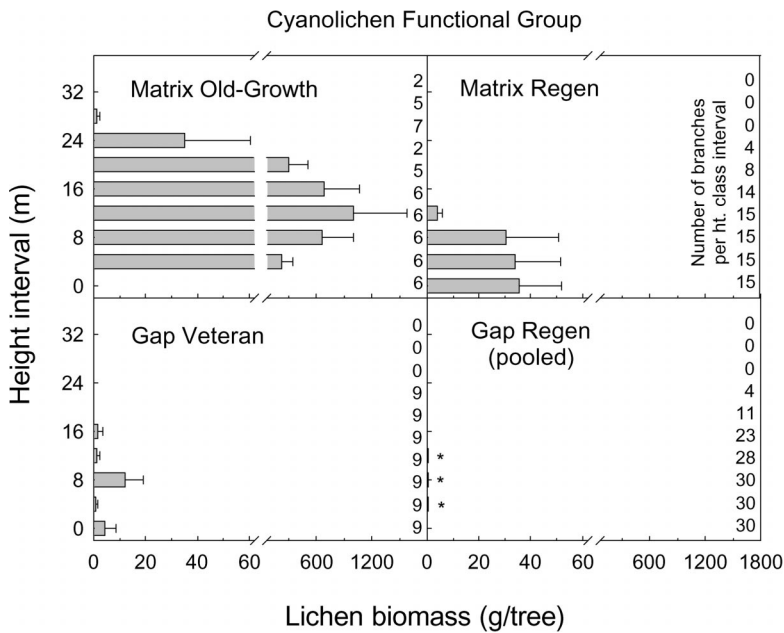Total lichen loading was three times greater in

FIGURE 4.   Vertical distribution of the Cyanolichen functional group expressed as mean lichen biomass per height interval for matrix old growth, matrix regen, gap veteran, and gap regen type trees. Error bars represent the standard error of the mean and the numbers along the right axis indicate total sample size (number of branches) for each height class interval of that tree class. Asterisk indicates trace amounts of lichen biomass (< 0.3 g/tree) by height class interval.

G–V compared to G–LR trees (Table 5). The *Alectoria* and Foliose functional groups were more abundant in G–V trees, while there was no difference in the *Bryoria* functional group between the two tree classes (Table 5).

Lichen functional groups in G–V and G–LR trees had similar vertical distributions (Fig. 3). The Alectoria and Foliose functional groups peaked in the mid canopy. The *Bryoria* functional group peaked from between 16 to 20 m in height within the canopy of both G–V and G–LR trees (within the upper canopy category as defined for these two classes of trees).

Matrix regen versus gap large regen lichen loading.—Results for the structural analysis, comparing G–LR and M–R trees, are summarized in Tables 4–5. There were no differences in tree height, dbh or age, however, G–LR trees had a greater number of branches (x = 130.9) than M–R trees (x = 98.0). Mean branch diameter (at 2.9 cm) was greater in M–R trees throughout the canopy, while branch density (at 6.4 branches/m) was greater in G–LR trees at all levels except the lower canopy. Branch lengths were summed to measure total length (in meters) of available substrate for lichen. There was no difference in the mean of total summed branch lengths between G–LR (188.7 m) and M–R trees (199.6 m). This was true in the mid and upper can-

opy, however, in the lower canopy M–R trees had a greater mean summed branch length (at 57.9 m).

Within G–LR and M–R tree classes, branch diameter, density, and summed branch length were compared between tree classes for the three canopy strata (Tables 4–5). In G–LR trees, mean branch diameter in the lower canopy was smaller (1.9 cm) than mean branch diameter in the mid and upper canopy (2.5 and 2.4 cm, respectively). Summed branch length was shorter in the low canopy compared to the mid and upper canopy. In M–R trees branch density in the lower canopy was less than in the mid and upper canopy. The summed branch length in the mid canopy was larger than that of the upper canopy.

M–R and G–LR trees did not differ significantly in total lichen biomass (Tables 6–7). A breakdown by functional group revealed that the *Bryoria* functional group was much more abundant on G–LR trees (at 483.0 g/tree) versus M–R trees in gap stands (at 171.2 g/tree), while G–SR trees had a slightly lower lichen loading of Bryoria (at 140.0 g/tree) compared to M–R trees. The cyanolichen functional group was more abundant in the old-growth matrix stands, both for larger trees with an old-growth form (M–OG vs. G–V) and for younger regenerating trees (M–R vs. pooled G–SR and G–LR).

TABLE 6. Estimated lichen biomass (mean g lichen/tree) by functional group in matrix old growth (M–OG), matrix regen (M–R), gap veteran (G–V) trees, gap large regen (G–LR), and gap standard regen (G–SR). Standard deviations are in parentheses.

Lichen Functional Group	Tree Class				
	M–OG $n = 9$	M–R $n = 15$	G–V $n = 6$	G–LR $n = 15$	G–SR $n = 15$
Alectoria	3376.0(1305.4)	330.7(183.9)	2100.1(1355.9)	443.6(182.7)	199.3 (136.9)
Bryoria	565.1(161.0)	171.2(242.5)	496.9(268.1)	483.0(309.9)	140.0 (78.9)
Foliose	2909.5(1421.5)	1130.9(568.9)	2795.7(2237.0)	983.8(317.1)	378.4 (117.3)
Cyanolichen	2898.0(4867.2)	103.6(56.1)	20.0(22.6)	—	0.84(0.28)[1]
Total biomass	9961.6(4756.9)	1632.8(861.0)	5412.7(2113.2)	1910.3(666.9)	717.7 (287.5)

[1] Cyanolichen biomass values pooled for G–LR and G–SR trees.

There were no significant differences in the biomass of Alectoria and Foliose functional groups between G–LR and M–R stands (Table 7). In contrast, the Bryoria functional group lichens showed significant differences between M–R and G–LR trees. Each of the comparisons between G–LR and G–SR trees were significant, excluding cyanolichens that were largely absent from the gap stand trees. The non-foliated portion of tree crowns contained more lichen biomass than the foliated portion (grams of lichen per region of branch) in both G–LR trees and M–R trees (Table 8). The *Alectoria* and Foliose functional groups contributed more to the large biomass in the non-foliated region than did *Bryoria*. The *Bryoria* functional group was more abundant in the foliated region of matrix stands but was not significantly different between foliated and non-foliated regions in gap stands.

Representation of lichen loading on the basis of grams lichen per meter of branch showed no significant differences in total lichen loading between foliated and non-foliated regions of the tree crown for both stand types (Table 9). However, analysis by functional group revealed that *Bryoria* was significantly more abundant in the foliated region in matrix stands and Alectoria was significantly more abundant in the non-foliated region for two of the three measured gap stands (at Hungary and Viking East).

The biomass of the *Bryoria* functional group peaked in the upper-canopy of G–LR trees (above 16 m in height), while the *Alectoria* and Foliose functional groups peaked in the mid canopy (from 8 to 16 m in height) of the G–LR trees (Fig. 3). Although the Foliose lichen functional group was most prominent in the mid canopy of M–R and G–LR trees, its distribution was broad compared to that of the *Bryoria* and *Alectoria* functional groups for both stand types. The *Bryoria* functional group showed greatest abundance in the 20–24 m height class interval of the M–R trees (this height class interval defined as part of the upper canopy for M–R trees, see Table 1, Fig. 3). Further, *Bryoria* abundance fell only slightly in next higher (top) height

class interval of the M–R trees (24–28 m above ground). In contrast, in the G–LR trees, *Bryoria* abundance peaked in the 16–20 m height class interval (this also defined as part of the upper canopy in the G–LR trees) (Fig. 3), but showed a large decline in abundance in each of the next two higher height class intervals. The biomass of the cyanolichen functional group peaked in the lower canopy of M–R trees (below 16 m in height), although the distribution (albeit at very much lower abundance values) was skewed more towards the middle canopy (from 8 to 16 m) of G–LR trees (Fig. 4). Due to the different statures of the gap and old-growth canopies the mid-canopy position of the gap stand (defined as from 8 to 16 m in height) overlaps with the height range of the lower canopy as presently defined (from 0 to 12 m) in the old-growth matrix stand.

Gap large regen vs. gap standard regen.—Large and standard regen trees did not differ significantly in age. G–LR trees were larger than G–SR trees in height and dbh, and had more branches (Table 4). Branch density was significantly greater in G–LR trees in all regions of the crown. G–LR trees had larger overall branch diameter, however, this effect was evident only in the mid canopy. Mean summed branch length was significantly greater for G–LR trees than for G–SR trees, excluding the upper canopy where there was no effect.

Within G–LR trees, comparisons across canopy strata revealed smaller diameter branches and a shorter summed branch length in the lower canopy (Table 4). Branch density increased in each canopy region with height. In G–SR trees, a similar pattern existed for summed branch length and branch density, however, there was no difference in branch diameter across canopy strata.

The *Alectoria*, *Bryoria*, and Foliose functional groups were present on all gap regen trees sampled. The Cyanolichen functional group occurred on 13% of the G–SR trees (one tree from each of the Viking West and Hungary sites) and 7% of the G–LR trees (one tree from the Hungary site). Large regen trees supported more lichen biomass than standard regen

trees (Table 5). This was true for all functional groups considered.

The pattern of lichen distribution in foliated and non-foliated regions was similar in G–LR and G–SR trees, excluding the Viking West gap stand which had a significant between site effect in the foliated region (Tables 6–7). Overall, both tree classes had more total lichen biomass in the non-foliated region of the tree crown, when expressed as grams of lichen per region of branch. The *Bryoria* functional group was the only group showing no difference in distribution between foliated and non-foliated regions.

Analysis on the basis of grams lichen per meter of branch showed no difference in total lichen biomass between foliated and non-foliated regions. However, the *Alectoria* functional group remained more abundant in non-foliated regions of the tree crown for both tree classes. In G–SR trees, the Foliose functional group at one of the sites was more dominant in the non-foliated region, while the other two sites showed no difference. Again, there was no difference in distribution of the Bryoria functional group between foliated and non-foliated regions.

The *Alectoria* and Foliose functional groups showed similar patterns of vertical distribution in G–LR and G–SR trees (Fig. 3). Both groups had peak biomass in the mid canopy. In contrast, the The *Bryoria* functional group peaked in the upper canopy (above 16 m) of both M–R and G–S trees (Fig. 3). In G–SR trees, the *Bryoria* functional group tended to increase with height right to the canopy top, reaching maximum biomass in the top few meters of the tree. In contrast, in G–LR trees, *Bryoria* biomass increased with height to approximately eight meters from the top of the tree, where it then decreased towards the tip of the tree.

Stand-level projections.—Total lichen loading, when expressed on a stand level basis, was marginally higher in the old growth stands than in the gap stands, at 1,332 versus 1,080 kg of lichen/ha respectively. The Cyanolichen functional group was the main contributor to this result (Fig. 5). While matrix old growth stands supported more Cyanolichen and Alectoria functional group biomass, gap stands contained more Bryoria and Foliose functional group biomass.

DISCUSSION

Total lichen loading was surprisingly comparable for the *Alectoria*, *Bryoria*, and Foliose functional groups when comparisons were made between regenerating trees of similar size and structure from gap stands, and those from the understory of the surrounding old-growth forest matrix. These results

TABLE 7. Tukey's post-hoc comparisons (*t* values and probability) for lichen loading (g lichen/tree) by functional group between stand types [Matrix regen (M–R), matrix old growth (M–OG), gap large regen (G–LR), gap standard regen (G–SR), gap veteran (G–V)]. Significant values are indicated in bold.

Lichen Functional Group		Sample Tree Comparisons by Class										
	M–OG vs M–R		M–OG vs G–V		M–R vs G–LR		G–V vs G–LR		G–LR vs G–SR		(G–SR and G–LR pooled) vs M–R	
	t	p	t	p	t	p	t	p	t	p	t	p
Alectoria	9.020	**< 0.001**	−1.827	0.091	1.686	0.103	2.982	**0.030**	4.144	**< 0.001**	—	—
Bryoria	3.641	**0.002**	−0.534	0.605	3.069	**0.005**	0.096	0.924	4.153	**< 0.001**	—	—
Foliose	4.349	**0.005**	−0.121	0.905	−0.875	0.389	4.396	**< 0.001**[a]	5.540	**< 0.001**	—	—
Cyanolichen	2.473	**0.027**	−2.623	**0.021**[b]	—		—		—		2.043	0.060
Total Biomass	9.389	**< 0.001**	−2.182	**0.048**	0.987	0.332	3.966	**0.009**	5.858	**< 0.001**	—	—

[a] Values of *t* and *p* were obtained from log$_{10}$ transformed data.
[b] *n* = 6.

TABLE 8. Tukey's post-hoc comparisons (*t* values and probability) for mean lichen biomass (mean g lichen/branch region) in foliated and non-foliated regions of the tree crown in regen tree classes: matrix regen (M–R), gap large regen (G–LR), and gap standard regen (G–SR). Standard deviations are in parentheses. Significant values are indicated in bold.

	Crown Region by Tree Class											
	M–R (n = 5)				G–LR (n = 5)				G–SR (n = 5)			
Functional Group by Site*	Foliated	Non-foliated	t	p	Foliated	Non-Foliated	t	p	Foliated	Non-foliated	t	p
Alectoria[a]												
All Sites (pooled data)	118.3 (76.3)	212.4 (136.7)	2.328	**0.027**								
Hungary Site Only					58.5 (15.6)	365.0 (135.9)	−5.010	**0.001**	33.9 (9.5)	130.4 (62.6)	−3.409	**0.009**
Viking East Site Only					41.4 (18.6)	320.8 (128.6)	−4.809	**0.001**	17.5 (3.7)	111.3 (63.3)	−3.312	**0.011**
Viking West Site Only					224.7 (124.1)[b]	320.3 (120.4)	−1.235	0.252	150.6 (119.0)[b]	154.3 (75.0)	−0.059	0.954
Bryoria[a]												
All Sites (pooled data)	89.8 (71.6)	81.3 (181.8)	−2.333	**0.027**[c]	189.9 (120.3)	293.1 (223.9)	−1.574	0.127	65.1 (33.5)	74.9 (51.7)	−0.617	0.542
Foliose[a]												
All Sites (pooled data)	293.0 (140.9)	837.9 (456.6)	4.417	**< 0.001**	280.2 (144.2)	703.6 (244.5)	−5.777	**< 0.001**	94.0 (41.7)	340.5 (110.6)	−4.663	**0.002**
Hungary Site Only									74.4 (28.8)	208.4 (73.3)	−3.809	**0.005**
Viking East Site Only									164.5 (48.8)[b]	253.5 (88.0)	−1.978	0.083
Viking West Site Only												
Total Biomass[a]												
All Sites (pooled data)	501.1 (244.4)	1131.7 (669.9)	−3.43	**0.002**	578.3 (277.3)	1332.0 (517.4)	4.974	**< 0.001**	195.5 (34.6)	531.8 (226.5)	3.283	**0.011**
Hungary Site Only									149.8 (30.3)	407.4 (151.0)	3.741	**0.006**
Viking East Site Only									384.7 (186.8)[b]	484.0 (211.9)	0.786	0.455
Viking West Site Only												

* Data reported by site were not pooled because of a significant effect between sites.

[a] Data for the three sites pooled, n = 15.

[b] Significant effect in the ANOVA between sites, ∞ = 0.05.

[c] Values of *t* and *p* were obtained from $\log_{10}$ transformed data, but means and standard deviations are from untransformed data.

TABLE 9. Lichen biomass (mean g lichen/m of branch region) for foliated and non-foliated regions of the tree crown in regen tree classes: Matrix regen (M–R), gap large regen (G–LR), and gap standard regen (G–SR). Standard deviations are in parentheses. Significant values are indicated in bold.

| Functional Group by Site* | Crown Region by Tree Class | | | | | | | | | | | |
| | M–R (n = 5) | | | | G–LR (n = 5) | | | | G–SR (n = 5) | | | |
	Foliated	Non-Foliated	t	p	Foliated	Non-Foliated	t	p	Foliated	Non-Foliated	t	p
Alectoria												
Hungary Site Only	2.3 (1.3)	1.4 (0.3)	−1.542	0.162	1.0 (0.2)	2.2 (0.6)	−4.425	**0.002**	0.9 (0.2)	1.5 (0.3)	−3.401	**0.009**
Viking East Site Only	2.4 (1.8)	2.2 (0.7)[a]	−0.184	0.859	0.8 (0.2)	2.7 (1.1)	−3.692	**0.006**	0.7 (0.1)	2.6 (1.3)	−3.224	**0.012**
Viking West Site Only	1.4 (0.3)	1.2 (0.3)	−1.113	0.298	4.4 (3.5)[a]	3.3 (1.5)	0.625	0.549	4.7 (3.3)[a]	4.8 (1.9)[a]	−0.059	0.955
Bryoria[b]												
All Sites (pooled data)	1.3 (0.7)	0.5 (0.9)	−2.761	**0.010**	3.3 (1.9)	2.2 (1.3)	1.701	0.100	2.2 (0.8)	1.6 (1.2)	1.395	0.174
Foliose[b]												
All Sites (pooled data)	5.2 (3.5)	6.3 (2.0)	1.061	0.298	4.8 _n(2.6)	5.5 (1.0)	−1.003	0.324				
Hungary Site Only									2.6 (0.9)[a]	4.1 (0.5)[a]	−3.333	**0.010**
Viking East Site Only									3.4 (1.9)	5.0 (2.3)	−1.191	0.268
Viking West Site Only									5.8 (1.9)[a]	8.0 (1.8)[a]	−1.818	0.107
Total Biomass[b]												
All Site (pooled data)	8.6 (4.6)	8.4 (2.6)	−0.098	0.923	10.1 (5.3)	10.4 (2.7)	−0.232	0.818				
Hungary Site Only									5.5 (0.6)	6.3 (1.0)[a]	−1.445	0.187
Viking East Site Only									6.6 (2.4)	9.7 (4.0)	−1.457	0.183
Viking West Site Only									12.6 (4.0)[a]	15.0 (4.3)[a]	−0.896	0.396

* Data reported by site were not pooled because of a significant effect between sites.

[a] Significant effect in the ANOVA between sites, ∞ = 0.05.
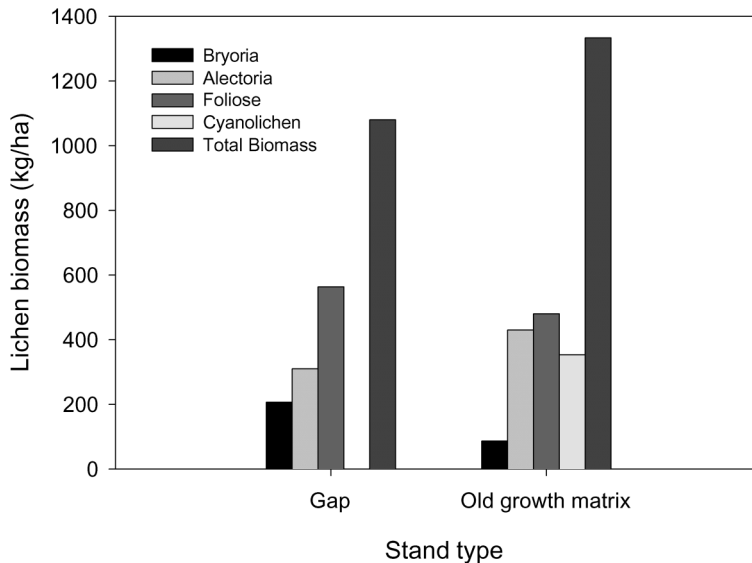
[b] Data for the three sites pooled, n = 15.

FIGURE 5.   Arboreal lichen biomass (by lichen functional group) expressed on a stand level basis (kg/ha) for gap and old-growth matrix stand types.

would initially seem to contradict current literature, which reports that trees in old growth stands support much more lichen than trees in stands with second growth characteristics (Esseen et al. 1996; Lesica et al. 1991; McCune 1993). This study, however, differs from these earlier works in that sampling occurred on comparable units (regenerating trees) in both stand types, and that these regenerating trees in the gaps were confined to small 1–3 ha patches, derived naturally following insect-defoliation disturbance events in the late 1800's. As a consequence, these patches of regenerating trees have remained wholly embedded within the surrounding old-growth forest matrix during their period of development. On the other hand, our finding that matrix old-growth trees had a much higher lichen biomass loading than did the remaining veteran trees in our gap stands does support (in a natural setting) the previous findings of these studies that lichen loading can decline on isolated old-growth trees surrounded by harvested (second growth) areas in managed stands.

McCune (1993) and Uliczka and Angelstam (1999) showed that tree structure and age have a major influence on lichen loading. These findings still apply in the interpretation of our results. However, it is valuable to recognize the differences observed in the individual lichen functional groups to understand the process of lichen colonization. The composition, abundance, and distribution of the lichen functional groups examined appear to be differentially affected by tree structure and microclimate, and could be related to dispersal capability.

Lichen dispersal.—For the cyanolichen function-

al group, the availability of lichen propagules may be an important constraint on biomass accumulation in our gap stands. Dettki et al. (2000) noted that fruticose and foliose lichen abundance in second growth boreal forest stands, at 100 m from the edge of adjacent old-growth forests, ranged from only 22 to 61% of that at stand edges. However, their stand ages, from 35 to 78 yr after harvesting, were younger than those of our natural origin gap stands (trees from ca 100–120 yr in age). Peck and McCune (1997) reported over 200% greater accumulation of cyanolichen litter in second-growth stands that contained remnant trees and indicated that cyanolichen litter biomass was positively related to the number of remnant trees present.

Sillett and McCune (1998) demonstrated, using transplant studies, that ''old-growth cyanolichen species'' grew equally well and experienced the same percent mortality in second growth stands as in old growth stands in a coastal environment. Their results further point to limitations in dispersal capability, rather than microclimate factors, in explaining the poor representation of the Cyanolichen functional group in second growth stands. It should be cautioned, however, that our gap stands were much smaller than the second-growth stands of Sillett and McCune (1998), thus dispersal limitations may not be as serious a constraint for cyanolichens.

In the absence of lichen dispersal data, such as litterfall sampling transects across gap stands, we cannot state with certainty the degree to which cyanolichen propagules may be available over time in the gap stands. Although most trees within the gap stands were only 1–2 tree lengths from the adjacent

old-growth forest boundary, dispersal limitations may still be important for members of the cyanolichen group. Reinforcing this limitation may be the role (or lack thereof) of veteran trees in these gap stands. These remnants of previous (old-growth) forest cover in the gap stand in close proximity to many of the currently regenerating hemlock trees. However, the gap veteran trees appear to have lost most of their cyanolichen biomass after the previous stand-level disturbance event (on transition to a full-insolation environment) and thus no longer provide a major propagule source for cyanolichens. Of equal importance to cyanolichen establishment in the gap stands may be limitations of canopy microclimate and substrate availability. This perspective is reinforced by considering the relatively low cyanolichen loadings on the understory regen trees in the old-growth forest, even though these trees were typically in the immediate shadow of old-growth ''source'' trees, heavily loaded with cyanolichens.

Interestingly, the *Alectoria*, *Bryoria* and Foliose functional groups were apparently not limited by dispersal in the gap stands, as evident from the canopy lichen loading results. These findings are supported by comparable litterfall studies that show uniform distribution of *Alectoria* sp. and *Bryoria* sp. fragments across patch cuts 1–2 ha in size (Quesnel & Waters 1999). Dettki (1998) reported that thallus fragments of *Bryoria* sp. disperse efficiently up to 100 m, and Stevenson (1988) found dispersal distances of 400 m. Other studies have shown the Foliose functional group to be a primary colonizer and therefore not limited by dispersal (Esseen et al. 1996; McCune 1993; Peck & McCune 1997).

Canopy microclimate.—Many researchers have commented on the interaction of canopy microclimate gradients with distributional patterns of cyanolichen communities in old growth forest stands (Goward 1994; Lesica et al. 1991; McCune et al. 1997; Rosso et al. 2000). In a major study on canopy microclimate profiles Parker (1997) noted that for coastal wet-temperate old-growth rainforest (douglas-fir/western hemlock), the point in the mid-to lower canopy at which cyanolichen communities decline greatly in abundance coincides closely with the transition point from direct to diffuse light transmission. Although we have no profiles of light availability in our gap stands, Parker (1997) noted that young conifer stands place most of their foliage in the upper canopy, and thus the transition to a more poorly lit (diffuse transmission) environment occurs relatively higher in the canopy (compared to those of old-growth forest trees). This is consistent with the exclusion of cyanolichens from our gap stands, in that dispersing cyanolichen fragments

that lodged in the upper canopy of the gap stands would face a relatively xeric environment, perhaps even more so than the coastal environments of Sillett and McCune's (1998) transplants, given the continental location of our site. On the other hand, cyanolichen fragments that lodge in the lower canopy of the gap stand, may have insufficient light to facilitate their establishment and growth, due to the uniform and dense nature of stems on the gap stand. Thus, gradients of moisture and light availability may play opposing roles along vertical gradients within the canopy in excluding cyanolichens from the gap stands. In contrast, the cyanolichens (primarily *Lobaria pulmonaria*) that have established on regen trees in the lower part of the old-growth forest canopy may have greater light availability due to the generally more open (or irregular) nature of the old-growth forest matrix.

For lichens in the *Bryoria* functional group, their preference for middle to upper canopy height positions may be influenced more by their intolerance of prolonged wetting events (Goward 1998). The abundance of *Bryoria* falls off rapidly below 16 m in the old-growth forest trees, well above the point at which cyanolichen abundance declines. Presumably, below this height, conditions in the lower canopy are too mesic for *Bryoria*, due to reduced wind exposure and higher ambient humidities. Only the uppermost branches of the matrix regen trees reach beyond this 16 m boundary, hence their *Bryoria* loading is truncated into a relatively smaller region of the upper canopy of the matrix-regen trees. Although our data also show a secondary peak in *Bryoria* abundance on the uppermost branches of matrix old-growth trees, the number of replicate branches in this class interval is low (two), thus we cannot be sure that this is not simply an anomaly in the data set.

The gap large-regen (and gap veteran) trees, also show a trend of declining *Bryoria* abundance below ca 16 m height within the canopy. This may similarly be a constraint imposed by the presumed more mesic lower canopy conditions. However, unlike the matrix regen trees (which sit a canopy of dominant old-growth trees) the regenerating large gap stand trees are fully exposed in their upper canopy. Thus wind scouring can reduce lichen loading in the upper canopy of these trees. Additionally, the branches in these uppermost canopy positions are smaller, providing less substrate for lichen growth, thus our measures of lichen biomass (denominated as whole tree measures) will show reduced lichen biomass in this height class interval.

The Foliose functional group can be described as ubiquitous due to its presence at any height within the forest canopy. This quality would suggest that the Foliose functional group is not as severely con-

strained by profiles of canopy microclimate. The narrower distribution of the Foliose functional group observed in the lower canopy of gap regen trees is likely the result of tree structure. This was evident in the data for summed branch length in the lower canopy. With less substrate available for lichen colonization, there was less lichen biomass in this region of the tree (Esseen et al. 1996; Lyons et al. 1998). These structural differences between old-growth and gap regen trees probably reflect self-pruning in the crowded gap stand regen trees, which essentially are at a stem exclusion phase of development. In contrast, the old growth matrix trees grow in a stand environment with more large gaps and consequently greater understory light availability. As well, they do not face competition from a cohort of closely packed adjacent regenerating trees (as found in the gap stand); in fact, they often stand solitary within the understory of the old-growth forest stand.

Previous research has suggested that for the *Alectoria* functional group, access to a moist and relatively equable stand microclimate is important to attain high biomass values (Esseen et al. 1996; Lesica et al. 1991; Rominger et al. 1994). Certainly, in adjacent subalpine forests, *Alectoria* is strictly limited to the lower part of the forest canopy (Campbell & Coxson 2001). Results from this study, however, are less equivocal. The distribution of the *Alectoria* functional group was similar in regen trees from both stand types (and much lower in total abundance than in old-growth or gap veteran trees). This suggests that continuity of substrate availability (older substrates) may be an important variable controlling *Alectoria* abundance.

Canopy structural attributes.—Clement and Shaw (1999), Goward (1998), and Lyons et al. (1998) each noted that lichen functional groups have different distributions in foliated vs. non-foliated regions. Our study confirms that the majority of arboreal lichen biomass was located in the non-foliated region of regen tree crowns. However, we should not overlook the fact that the non-foliated portions of our regen tree crowns comprised twice the length of the foliated regions. When lichen distributions were expressed in terms of grams of lichen per meter of branch, we found no significant difference between lichen loading on foliated versus non-foliated branch regions. It would seem that the vertical distribution of foliage within the canopy may play a more important role in structuring stand level lichen loading than do gradients across the crowns of individual trees. For the lichen functional groups examined in this study, each would seem capable of growing on the different substrates provided by foliated and non-foliated regions, subject

to the larger constraints of vertical placement within the canopy.

One exception to this pattern was the apparent restriction of the *Alectoria* functional group to the more protected non-foliated regions of the regen tree crowns. This may reflect differences in age between foliated and non-foliated regions of the branch. Esseen et al. (1996) reported branch age was related to lichen mass. The oldest portion of branch is the non-foliated region near the bole of the tree, and may contain more lichen because of longer exposure to colonization.

The comparison of standard regen to large regen trees confirms previous findings that tree size, rather than age, is the better predictor of arboreal lichen biomass (Lyons et al. 1998) and that lichen colonization is limited on smaller trees because of less available substrate (Esseen et al. 1996). While lichen biomass was affected by tree size, the distribution pattern of lichen functional groups remained the same. The amount of available substrate seemed the most likely factor dictating the distribution of the *Alectoria* and Foliose functional groups. Peak biomass occurred where mean branch length was the longest, the mid canopy. This observation supports the findings of Esseen et al. (1996) and Lyons et al. (1998).

Veteran and gap regen trees, although different in age and structure, shared similar microclimatic conditions due to their relatively equal canopy position. The physical differences between veteran and gap regen trees did not affect biomass of the *Bryoria* functional group. This suggests there was an equal amount of suitable habitat for the *Bryoria* functional group in both tree classes. The abundance and distribution of the *Bryoria* functional group therefore appeared again to be dependent on vertical profiles in canopy microclimate, rather than on substrate quality. The gradients of canopy microclimate within these interior cedar-hemlock forests, especially for light, may be quite steep (after Parker 1997). This stands in contrast to adjacent, but higher elevation spruce-fir forests (Campbell & Coxson 2001), where vertical gradients of temperature, moisture and light availability were not pronounced, reflecting the very open stand structure and ready penetration of light to within the lower canopy.

Similarly, the vertical distribution pattern of the *Bryoria* functional group in old growth regen trees appeared to be influenced more by stand-level canopy stratification rather than the individual tree height. Stand-level canopy stratification may be defined by the boundary layer climate imposed by the surrounding old growth stand. Peak biomass for the *Bryoria* functional group occurred in the upper canopy of old growth regen trees that corresponded

with the stand-level peak for the *Bryoria* functional group. These findings support the idea that vertical distribution of the *Bryoria* functional group is strongly dependent on microclimate gradients.

This stand-level influence on vertical stratification was not as marked for the *Alectoria* and Foliose functional groups on old growth regen trees. Lichen biomass has not developed to the same extent in the mid-canopy positions, irrespective of potentially favorable macroclimate at this height. Structural factors may therefore be more important in constraining biomass loading of these functional groups on old growth regen trees.

Stand level lichen loading.—The difference in standing crop of arboreal lichens in gap and old growth ICH stands was small, differing by only 250 kg/ha. McCune's 1993 study was one of the few that used sampling methodologies appropriate for extrapolation to the stand-level. He reported that old growth stands supported 2.6 times more lichen biomass than managed (second-growth) stands. In this study, as in McCune's, it was the larger representation of the Cyanolichen functional group that accounted for most of the biomass difference between the old growth and gap stands. The virtual absence of cyanolichens from the gap stands was one of the most interesting findings of the present study. Clearly the uniform nature of the gap stand, similar to that of second-growth stands, imposes severe constraints on cyanolichen growth. Our paired comparisons with regen trees under the canopy suggest that gradients in stand level microclimate, particularly light and moisture, may pose important limitation on the cyanolichen functional group.

Results for stand level loading of the other lichen functional groups complement findings in the literature. McCune (1993) reported that the Foliose functional group reached the greatest abundance in managed stands. Esseen et al. (1996), Lesica et al. (1991), and Rominger et al. (1994) found more *Bryoria* functional group lichens in second growth stands while the *Alectoria* functional group was more abundant in old growth stands. One cautionary note in this regard, however, is that the relatively high loading for Alectoroid lichens in the gap stands (including both of our *Alectoria* and *Bryoria* lichen functional groups) may reflect the greater availability of substrate (i.e., many small branches). We suspect that follow-up measurements would indicate that mean clump size in gaps is much smaller than that of the old growth stand. This may have serious negative implications for browse availability to by mountain caribou.

The relatively high total lichen loading in our gap stands (admittedly mainly Alectoroid and foliose lichens), nonetheless, stands in contrast to previous studies on lichens in second growth (managed) stands. These studies commonly report that old growth forests contain a much greater abundance of lichen (ranging from 2–6 times more), than adjacent managed stands (Enns et al. 1999; Esseen et al. 1996; Neitlich 1993). The main difference between this study and many others is the size of the regenerating forest patches. Many of the second growth stands used in the other studies originated from clearcuts larger than 50 ha. In contrast, this study examined relatively small 1–3 ha natural gap disturbances embedded in a matrix of old growth forest. This reduces the effects of dispersal limitations. Another difference between this and other studies is that trees were not removed after the disturbance event, unlike timber harvesting operations. This may change the availability of nutrients, moisture, and lichen propagules in the regenerating gap stands.

It should be noted that our projections of lichen loading were conservative. We do not, for instance, extrapolate lichen loading values from our measurements on hemlock to regenerating young cedar trees in the stand (which comprise about 50% of regenerating trees), although Enns et al. (1999) and Quesnel and Waters (1999) noted that young western red cedar trees support less lichen biomass than other conifers. In both gap and old growth stands there was a large proportion of trees smaller than 17 cm dbh that we did not include in stand-level projections. Lichen biomass contribution from these trees was considered negligible based on findings that lichen loading greatly decreased on trees of smaller diameter.

Implications for forest management.—One limitation of our study is that we have examined the development of stand level lichen loading at only one point in time and on only one coniferous forest species (at least within the gap stands). However, the time frame examined (ca 100–120 yr after stand initiation) is highly valuable to managers, in that this age corresponds closely to stand rotation ages being applied for forest harvesting in this region. Assuming that arboreal lichen communities will respond similarly to regeneration in a small partial cut as they have in our natural origin gap stands, our study would lead to the following predictions: 1) *Bryoria* functional group biomass will increase in partial cuts ranging from 1–3 ha in size, although mean clump size may decline (perhaps a significant constraint on lichen availability for forage and 2) lichen diversity will be dramatically lower in partial cuts due to the greatly decreased presence of the Cyanolichen functional group. A longer harvest rotation interval (approaching 200 yr) should ameliorate impacts on cyanolichen biodiversity as canopy structural characteristics shift more to an old-growth form. These findings parallel those of Ku-

usinen and Siitonen (1998), who found that longer harvest rotation intervals will also be needed in Scandanavian boreal forests to maintain canopy biodiversity.

A related issue may arise when using small patch cuts to maintain forage for mountain caribou. In our old growth ICH stands, caribou feed primarily on the lichen loaded branches of large rotten hemlock trees that fall in winter storms, and secondarily on lichen litterfall on the surface of the snow pack (Edwards et al. 1960; Rominger & Evans 2000). The younger trees within the gap stands will be more resistant to these windthrow events and will, in any case, provide far fewer lichens when they do fall. This may have a significant effect on the amount of available litterfall for caribou in second-growth or gap stands. To address this issue, we would suggest that litterfall studies be conducted in gap and old growth stands. Studies should also be conducted to determine the density of patch cuts on the landscape, sizes and shapes of patches, and stand types in which partial-cutting may be used effectively.

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