Canopy microclimate and arboreal lichen loading in subalpine spruce–fir forest

Jocelyn Campbell and Darwyn S. Coxson

Abstract: Hair lichen communities in Engelmann spruce (Picea engelmannii) – subalpine fir (Abies lasiocarpa) forests of the northern Cariboo Mountains (British Columbia) show distinct vertical zonation. Alectoria sarmentosa reaches peak abundance in the lower canopy (over 35 kg/ha) whereas Bryoria spp. lichens reach peak abundance in the upper canopy (over 250 kg/ha). These distribution patterns are accentuated by stand structure with trees growing in clumps retaining significantly higher lichen loading on a per branch basis compared to solitary trees. The vertical zonation of lichen communities is accompanied by distinct trends in canopy microclimate. Snowmelt events account for the largest proportion of observed thallus hydration in both Alectoria and Bryoria. Although canopy microclimate is surprisingly isothermal during rainfall events, the attenuation of thallus hydration after wetting is typically greater for lower canopy exposures. An important exception to this pattern is seen under midwinter conditions, when solar insolation is insufficient to sustain prolonged lower canopy snowmelt. Our data support the hypothesis that ventilation in upper canopy exposures is a contributing factor in the vertical zonation of Alectoria and Bryoria communities. Upper canopy Bryoria rely more heavily on snowmelt events to sustain thallus hydration, whereas lower canopy Alectoria utilize summer rainfall events to a greater extent. We hypothesize that physiological mechanisms, through which these patterns of canopy microclimate influence lichen zonation, may include an intolerance to prolonged wetting by Bryoria and higher resaturation respiration costs in Alectoria, which would limit it to more mesic canopy exposures. We believe that the observed distribution of canopy lichens ultimately reflects the long-term interaction of both physiological and successional processes (lichen colonization and dispersal) within the canopy.

Key words: canopy, epiphytes, lichens, microclimate.

Résumé : Les communautés de lichens filamentueux des forêts d’Engelmann (Picea engelmannii) et de sapin subalpin (Abies lasiocarpa) du nord des montagnes Cariboo (Colombie Britannique), montrent une nette zonation verticale. L’Alectoria sarmentosa atteint son maximum d’abondance dans la partie basse de la canopée (plus de 35 kg/ha) alors que les lichens du genre Bryoria atteignent leur maximum dans la partie haute de la canopée (plus de 250 kg/ha). Ces patrons de distribution sont accentués par la structure du peuplement, les arbres poussant en groupe retenant une charge de lichens significativement plus lourde, sur une base par branche, comparative aux arbres isolés. La zonation verticale des communautés de lichens s’accompagne de tendances distinctes dans le microclimat de la canopée. Les événements de fonte de neige expliquent une majeure partie de l’hydratation observée des thalles, chez l’Alectoria aussi bien que chez les Bryoria. Bien que le microclimat de la canopée soit étonnamment isotherme au cours des précipitations sous forme de pluie, l’atténuation de l’hydratation des thalles après mouillage est typiquement plus importante pour les sites de la canopée inférieure. On observe une importante exception à ce patron sous les conditions mi-hivernales, lorsque l’ensoleillement est insuffisant pour soutenir une fonte prolongée dans la canopée inférieure. Les données supportent l’hypothèse que la ventilation des sites de la canopée supérieure est un facteur qui contribue à la zonation dans les communautés d’Alectoria et de Bryoria. Les Bryoria de la canopée supérieure dépendent plus fortement des événements de fonte de la neige pour assurer l’hydratation des thalles, alors que les Alectoria de la canopée inférieure utilisent beaucoup plus les pluies estivales. Les auteurs formulent l’hypothèse que les mécanismes physiologiques, par lesquels ces patrons de climat dans la canopée influencent la zonation des lichens, pourraient inclure une tolérance à l’hydratation prolongée chez les Bryoria et un coût plus élevé de restauration de la respiration chez les Alectoria, ce qui pourrait les limiter à des sites plus mésiques de la canopée. Les auteurs croient que la distribution observée des lichens dans la canopée reflète ultimement l’interaction à long terme de processus physiologiques et successionnels (colonisation lichénique et dispersion) à l’intérieur de la canopée.

Mots clés : canopée, épiphytes, lichens, microclimat.


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Introduction

Early investigations of high elevation forests within the Cariboo Mountains of east-central British Columbia revealed abundant epiphytic lichen communities (Edwards et al. 1960) composed primarily of Alectorioid lichens (Alectoria and Bryoria spp.). The detailed structure of these arboreal...
lichen systems has largely remained unexplored, as access constraints have restricted upper canopy observations. More recently, Goward (1998) has postulated a series of factors that may influence the distributional ecology of these epiphytic lichen communities in high elevation coniferous forests. A primary consideration that Goward brings forward is the interaction of canopy microclimate with canopy structure, speculating that duration of wetting within the canopy may be a primary determinant of the distributional ecology of the lichen genus Bryoria.

Although it is difficult to discriminate between structural and environmental influences on epiphytic communities, there is considerable evidence documenting the importance of microclimate to epiphyte abundance (Halonen et al. 1991; Yarranton 1972). The two most influential environmental variables affecting lichen abundance are availability of solar radiation and moisture (Boucher and Stone 1992). Lichens are highly tolerant of frequent wetting and drying cycles and are capable of dormancy in response to moisture stress, but they are only photosynthetically active when wet. Growth rate is therefore intrinsically tied to the amount of precipitation that the canopy receives (Armstrong 1993; Renhorn and Esseen 1995).

Radiant loading is also postulated to play a strong part in controlling the distribution of Alectorioid lichens. Bryoria, for example, has a wide ecological amplitude and tends to colonize more open sites (Edwards et al. 1960). Alectoria, on the other hand, is tolerant of diffuse light and is commonly found in the lower canopy and in more dense forests.

The microclimate experienced by arboreal lichens is ultimately determined by the interaction between regional climate and forest canopy structure (Halonen et al. 1991). Tree architecture plays a significant role in influencing the patterns of lichen distribution and abundance (Edwards et al. 1960) along vertical gradients in the canopy. Previous studies in coastal coniferous forests of the Pacific North-west have shown distinct vertical gradients in epiphyte abundance along which epiphyte functional groups (including bryophytes, fruticose lichens, foliose, green lichens, and cyanolichens) replace one another as the most abundant in the canopy (McCune et al. 1997; Sillett and Neitlich 1996).

We have now examined this complex of interactions between canopy structure and canopy microclimate and its effect on the arboreal lichen communities of Engelmann spruce – subalpine fir (ESSF) forest stands in the northern Cariboo Mountains of north-central British Columbia. We document architectural features (branch diameter, aspect, length, and slope) that characterize the canopy structure of ESSF stands and examine corresponding height-related, vertical zonation of lichen functional groups and canopy microclimate. We also examine the effects of prior stand development, as reflected in the growth of ESSF trees within “groups” or “clumps”, a common phenomenon in “sub-alpine forested parklands” of north-central B.C. Our findings have significant implications for the management of these high-elevation forests and provide possible guidelines for the implementation of selection harvesting systems where retention of canopy lichen communities is a management concern.

**Methods and materials**

**Study area**

Our research was conducted in north-central British Columbia, Canada, at Pinkerton Mountain in the Bowron Valley near Prince George (Fig. 1). The site is within the Engelmann spruce – subalpine fir biogeoclimatic zone (Meidinger and Pojar 1991), part of the oroboreal subzone (Tuhkanen 1984), on a south-facing gentle slope at approximately 1450–1475 m in elevation. The forest stand had an average density of 572.6 stems/ha (>17.5-cm diameter at breast height (DBH)), of which 73% were Abies lasiocarpa and 27% were Picea engelmannii (Anonymous 1995). Tree heights in the multi-cohort stand ranged from 1-m seedlings to 30-m trees up to approximately 350 years old. Stand structure in these high-elevation “wet-belt” forests of north-central B.C. is characterized by discrete groupings of trees, not unlike “sub-alpine forested parkland” in timberline environments (Arno 1984). Site mapping indicates that 62% of trees in the stand at our study site were growing in clumps with closely associated canopies separated by gaps of approximately equal size (e.g., see Figs. 2 and 3).

**Lichen biomass sampling**

Canopy sampling was designed to reflect the “grouped” nature of tree growth in this stand; trees that were growing in groups with overlapping crowns (clumps) were designated as our primary sampling unit. Eight study clumps were randomly chosen for characterization of arboREAL lichen loading from a pool of prospective study clumps, each selected via an assessment of climbing hazards and the structural makeup of the clump (Campbell et al. 1999). At each of these eight study sites, an additional single adjacent tree (no crown overlap) was selected randomly (again, from a pool of eligible trees). Each single tree chosen was within 30 m of the reference clump. There were 62 trees (larger than 2 m) within these eight sites, of which 40 were accessed using the single rope technique (Perry 1978); all others were assessed from the ground. For each branch with a basal diameter greater than 2 cm, height above ground was measured using a 50 m tape suspended from the top branch to the ground surface. Branch basal diameters were measured using a hand ruler. Branch aspect and slope (to the nearest degree with a compass), and length (to the nearest half metre) were subsequently measured on a 15% subsample of branches; five percent of these were the branches selected with probability proportional to prediction for biomass sampling, described below. To increase the subsample size and insure that it represented the entire canopy, architectural measurements were taken on an additional 10% of the branches, randomly selected within three height zones.

Epiphytic lichens were divided into three sampling groups after Campbell et al. (1999), based on a modification of functional groups presented by McCune (1993). These sampling groups were 1) Alectoria (mainly A. sarmentosa, but also including Usnea species, which were rare in the study area), 2) Bryoria (including B. capillaris, B. fremontii, B. fuscescens, B. glabra, and B. pseudofuscescens), and 3) foliose lichens (including Cetraria platyphylla, Hypogymnia imshaugii, Hypogymnia metaphysodes, Hypogymnia occidentalis, Hypogymnia physisodes, Hypogymnia rugosa, Hypogymnia tubulosa, Parmelia sulcata, and Platismatia glauca). Sampling (or functional) groups were used rather than taxonomic groups because of their growth forms, their use as forage, and common ecological roles that define their presence in the canopy (McCune 1993).

Three other functional groups commonly used in epiphyte studies that we did not include in this research are bryophytes, cyanolichens, and crustose lichens. Bryophytes and cyanolichens were not included because they were rare or absent in the study area. Crustose lichens were excluded because of time constraints.

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The biomass of *Alectoria*, *Bryoria*, and foliose lichen was estimated throughout the canopy using the "clump method" (Stevenson 1978), where the amount of lichen on a given branch was compared to a standard "clump" of lichen of known size and weight. The amount of fruticose lichen (*Alectoria* and *Bryoria*) was estimated according to how many multiples of a standard, 2.5 g (dry weight) clump of lichen were present (Stevenson and Enns 1993; Campbell et al. 1999). *Alectoria* and *Bryoria* were separated subsequently into individual functional groups by estimating the percentage of *Bryoria* in that clump. A similar method was used for estimating the amount of foliose lichens using a "card" of known dimension (8.5 × 8 cm), which represented approximately 1.5 g of foliose lichen. Consistency was crucial and was maintained by frequently comparing our estimates to the standards and to each other's estimates.

Accuracy and precision of these methods were verified by comparing and correcting the estimates of lichen biomass with the lichen removed from a 5% subsample of branches. Branches were selected using probability proportional to prediction (3P) sampling, where the probability of any given branch being included in the subsample is proportional to the estimate of lichen on that branch (Cochrane 1977; Pike et al. 1977; Stevenson 1979). The normality of *Alectoria* and foliose lichen biomass was improved with a log transformation. A natural log transformation was used for *Bryoria* biomass. A constant ($K = 1$) was added to all estimates prior to transformation to avoid taking the logarithm of zero. Simple regression models were calculated for each functional group to describe the relationship between the measured and estimated lichen biomass on the 5% subsample of branches obtained through 3P sampling.

Any bias introduced by correcting estimates with log or natural log transformed data was reintroduced by adding a constant ($s^2/n$) to the regression equation (Casella and Berger 1990). The resulting regression equations (log/ln ($Y + 1) = Y_0 + a\log/ln(X + 1) + s^2/n$; where $Y$ is the regression corrected lichen biomass for each branch, $X$ is the estimated lichen biomass for each branch, and $s^2/n$ is the natural log and log normally distributed errors) (Table 1) were applied to the estimates of lichen biomass for the entire population, providing a log/ln transformed corrected estimate for statistical analysis. Estimates were converted back to grams per branch by taking the antilog of the output of the regression.

The corrected lichen biomass (g/branch) was converted to kg/ha using the average number of branches per tree and number of stems/ha for each tree size class (small, 0–5 m tall; medium, >5–15 m tall; and, large, >15 m tall). Tree structure variables were categorized at the branch level into the following categories for graphical and statistical analysis: branch height = 2.5 m; diameter = 1.0 cm; length = 0.5 m; slope = 10°; and aspect = 12 directions (N, NNE, ENE, E, ESE, SSE, S, SSW, WSW, W, WNW, NNW).

Separate variances t-tests were used to detect differences in lichen biomass between tree species and between clumped and solitary trees. One way analysis of variance tests with a Bonferroni
adjustment were used to detect significance in the relationships between tree size and lichen biomass. Nested analysis of variance models (branch diameter nested within height in the tree nested within the individual trees) with subsequent hypothesis testing within the general linear model indicated significant changes in biomass with increasing branch height and diameter. All statistics were conducted at a significance level of $p < 0.05$ and effect sizes were reported for each test (Cohen 1992). Averages were given as mean ± SE.

Effect sizes ($d$) for the separate variances $t$-tests were calculated from the mean differences divided by the population standard deviation and interpreted on a scale of small (0.20), medium (0.50), and large (0.80). ANOVA effect sizes ($\eta^2$) were calculated from the between group degrees of freedom ($df_{\text{group}}$), the $F$ statistic, and the population sample size ($N$) (eq. 1) and then interpreted on a scale of small (0.10), medium (0.25), and large (0.40) (Cohen 1992).

$$\eta^2 = \frac{F \times df_{\text{group}}}{N - 1}$$

The overall importance of canopy structural variables in explaining lichen biomass loading was examined by using the Relative Pratt index (Pratt 1987; Thomas et al. 1998), which partitions the overall $R^2$ between the explanatory variables. The index attributes a proportion of the $R^2$ to each variable and then orders them in terms of the relative magnitude of the index value. A small index value ($D < 1/dp$, where $p$ is the number of explanatory variables) indicates that a variable is relatively unimportant in predicting the distribution of lichens in the canopy. The Relative Pratt index was calculated from a best subsets regression model (eq. 2), where $r$ is the correlation coefficient, $B$ is the standardized regression coefficient and $R^2$ is the coefficient of determination.

$$D_j = B 	imes r / R^2$$

Lichen microclimatic measurements

Microclimatic conditions experienced by Alectoria and Bryoria lichen thalli were assessed at two heights within the canopy, from between 4–6 m above the forest floor (designated lower canopy exposures) and from between 12–15 m above the forest floor (designated upper canopy exposures). Additionally, microclimatic measurements were partitioned between north and south facing aspects on each tree. Instrumentation focused on canopy-based measurements of thallus temperature (°C), moisture (percent thallus moisture content), and incident photosynthetically active radiation (PAR, $\mu$mol·m$^{-2}$·sec$^{-1}$). PAR was measured with LI-COR quantum sensors placed adjacent to lichen thalli, the upper sensor surface held level within a gimbal mount.

Thallus-based instrumentation was installed on six codominant or dominant trees in three separate clumps, on north and south aspects, respectively. Replicate measurements were taken on two thalli from each functional group (Alectoria and Bryoria) for each height stratum aspect location.

Lichen thallus temperatures were measured using fine wire thermocouples (0.001 in.; Type T) appressed to the surface of individual lichen strands within the centre of pendulous clumps of Bryoria and Alectoria. Thallus moisture content was assessed using proxy measurements, based on the determination of electrical conductivity across lichen thalli using attached micro-clips (after Coxson 1991). These measurements are based on the principle that wet lichens will have a higher conductivity to electrical currents than dry lichens. The return of a 4 V AC excitation, applied in a 10 ms pulse during each sampling episode (every 10 min during hydration periods), was used to determine impedance (opposition to the flow of an alternating current) across lichen thalli.

Representative calibration curves for impedance response in Alectoria and Bryoria (Fig. 4) show that this technique can discriminate, quite effectively, between small differences in lichen moisture content. It is a non-linear response, with the greatest sensitivity at very low thallus moisture content thresholds (where electrical conductivity falls off very rapidly on drying) and at very high thallus moisture content thresholds (where surface and intracellular water films result in quite high electrical conductivity).

Polynomial equations were used to predict the percent relative water content of lichen thalli based on field measurements of importance (expressed on a percent relative basis for dry lichen thalli) across each instrumented lichen thalli. Instrumented lichen thalli were calibrated on an individual basis at regular intervals (every 3–6 months) to determine the signal return from fully hydrated lichen thalli (100% impedance setpoint).

We also examined time series and equilibrium response rates of Alectoria and Bryoria thalli to ambient relative humidity (RH) under controlled conditions (Fig. 5). Bryoria demonstrated significantly faster rehydration when held under conditions of saturating atmospheric humidity, although neither lichen functional group had fully reached equilibrium thallus hydration after 48 h humidity exposure (Fig. 5a). Both lichen functional groups showed a rapid decline in equilibrium thallus hydration as atmospheric humidity fell below 70% RH (Fig. 5b). All lichen biomass measurements in the present study were taken after lichen thalli had been held over Drierite™ (ambient atmospheric RH of 12%) for 48 h, thus controlling for effects of ambient RH.

Selected stand-level climatic measurements were taken from a 12 m instrumentation tower placed in the centre of a small opening in the forest canopy between instrumented “clumps” of trees. Windspeed and wind direction were measured at 12 m using an R.M. Young anemometer (R.M. Young Co., Traverse City, Mich.). Air temperature was measured at 4 and 12 m using unshielded infrared sensors (Type T) appressed to the surface of lichen thalli (100% impedance setpoint). The return of a 4 VA C excitation, applied in a 10 ms pulse during each sampling episode (every 10 min during hydration periods), was used to determine impedance (opposition to the flow of an alternating current) across lichen thalli.

<table>
<thead>
<tr>
<th>Functional group</th>
<th>Regression equation</th>
<th>$R^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Alectoria</td>
<td>log $(Y + 1) = 0.075 + 0.992 \times \log (X + 1) + 0.001$</td>
<td>67.9%</td>
</tr>
<tr>
<td>Bryoria</td>
<td>$\ln (Y + 1) = 0.790 + 1.102 \times \ln (X + 1) + 0.071$</td>
<td>76.1%</td>
</tr>
<tr>
<td>Foliose</td>
<td>log $(Y + 1) = 0.136 + 0.969 \times \log (X + 1) + 0.003$</td>
<td>61.3%</td>
</tr>
</tbody>
</table>

Table 1. Regression equations for predicting lichen biomass loading from visual estimates by lichen functional group.
and fall equinoxes. A threshold of 20% thallus hydration (percent relative water content) was used to separate records for “dry” lichens versus those for “wet” or hydrated lichens. This threshold corresponds to the point below which little physiological activity (gas exchange) is detectable in these species (D.S. Coxson, personal communication).

**Results**

**Lichen loading**

Large and medium *A. lasiocarpa* trees supported more lichen biomass than *P. engelmannii* trees (Table 2) of the same size. A comparison of small trees (0–5 m) showed greater lichen biomass in *P. engelmannii*; however, the sample sizes for small trees were too low to produce an effect on the overall lichen biomass at the branch, tree, or ecosystem level. All three functional groups were less abundant in small trees than in the lower canopy (0–5 m) of large and medium *A. lasiocarpa*. More lichen was also found in the middle canopy of dominant *A. lasiocarpa* than in medium sized trees at the same height. The effect of tree size on lichen biomass in the middle canopy of *P. engelmannii* mirrored that seen in the *A. lasiocarpa* sample trees. *Bryoria* was prolific in the upper canopy of both tree species and more abundant than either *Alectoria* or foliose lichen in large trees. Foliose lichens were most abundant in the lower canopy of medium sized trees and in the middle canopy of the large trees of both species. *Alectoria* biomass peaked in the lower canopy of large *A. lasiocarpa* and *P. engelmannii*. The total contribution of *Alectoria* toward epiphyte biomass of the stand (8.9%) was much lower than that of either *Bryoria* (60.7%) or foliose lichens (30.4%).

A comparison of the lichen biomass in trees taller than 10 m in the clump with solitary trees (those growing without crown interaction with other trees) of comparable size revealed that *Bryoria* was significantly more abundant in clumped trees (Fig. 6). This was true for both the total tree population \( (t(6.4) = 5.465, p = 0.001, d = 1.74) \) and for *A. lasiocarpa* trees only \( (t(7.8) = 4.177, p = 0.003, d = 1.57) \). There were no solitary *P. engelmannii* trees in our sample with which to compare the clumps; this was a reflection of the species composition of the stand. There were no differences in *Alectoria* or foliose lichen biomass with tree clumping.

In addition to being influenced by stand composition, lichen functional groups showed a marked response to height gradients in the canopy (Fig. 7). *Alectoria* exhibited a general decrease in biomass with increasing height in the canopy of both tree species. There was an initial increase in *Alectoria* biomass with height in *A. lasiocarpa* to an average peak of 4.00 ± 0.30 g/branch between 5.0–7.5 m. This peak was followed by a significant decline to a minimum of 0.19 ± 0.00 g/branch in the upper canopy \( (F(117, 238) = \)
A similar trend was seen in *P. engelmannii* canopies (*F*(60, 142) = 5.381, *p* < 0.0001, *h*² = 0.20), but there was a slightly smaller maximum average branch loading of 2.89 ± 0.54 g/branch in *P. engelmannii*.

*Bryoria* displayed a trend opposite to that of *Alectoria* (Fig. 7). It increased in abundance with increasing height in the canopies of both *A. lasiocarpa* (*F*(117, 238) = 3.284, *p* < 0.0001, *h*² = 0.09) and *P. engelmannii* (*F*(60, 144) = 5.014, *p* < 0.0001, *h*² = 0.18). The interesting difference in the response of *Bryoria* to the tree species was in the upper canopy. *Bryoria* decreased significantly from a peak average biomass of 25.75 ± 1.47 g/branch between 17.5 and 20 m to 12.22 ± 3.82 g/branch in the top branches of *A. lasiocarpa*.

In contrast, *Bryoria* biomass in the upper canopy of *P. engelmannii* trees did not taper off, but remained at a relatively constant maximum of approximately 30 g/branch from 17.5 m to the top.

Foliose lichen biomass loading (Fig. 7) increased significantly with branch height up to approximately 7.5 m (2.6 ± 0.3 g/branch) and subsequently decreased to a minimum of 1.3 ± 0.1 g/branch in *A. lasiocarpa* (*F*(117, 236) = 3.523, *p* < 0.0001, *h*² = 0.10). In contrast, foliose lichens did not appear to peak in *P. engelmannii* trees, instead exhibiting a gradual and significant decrease with increasing height in the spruce tree (*F*(59, 144) = 2.194, *p* < 0.0001, *h*² = 0.06).

Transformation of the denominator for lichen loading to area-based measures (kg/ha) shows a slightly different pattern of lichen loading with height in the canopy (Fig. 7). For instance, the greatest lichen loading per branch occurs near 20 m in the canopy for the *Bryoria* functional group. However, the greatest overall loading, at a stand level, occurs near 16–18 m, reflecting the greater branch density at this height.

**Table 2.** The mean (± SE) and total biomass at the branch, tree, and stand level of *Alectoria*, *Bryoria*, and foliose lichen functional groups for small (0–5 m), medium (>5–15 m) and large (>15 m) *Abies lasiocarpa* and *Picea engelmannii* trees. Sample sizes are indicated in parentheses for each category.

<table>
<thead>
<tr>
<th>Tree size</th>
<th>Lichen functional group</th>
<th>Total Lower</th>
<th>Middle</th>
<th>Upper</th>
<th>Total Lower</th>
<th>Middle</th>
<th>Upper</th>
<th>Total Lower</th>
<th>Middle</th>
<th>Upper</th>
<th>Total Lower</th>
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<th>Total Lower</th>
<th>Middle</th>
<th>Upper</th>
<th>Total Lower</th>
</tr>
</thead>
<tbody>
<tr>
<td>Small</td>
<td>Alectoria</td>
<td>0.6±0.05</td>
<td>2.9±0.1</td>
<td>1.4</td>
<td>5.2±0.3</td>
<td>3.8±0.4</td>
<td>1.5</td>
<td>9.5±0.7</td>
<td>6.4±0.3</td>
<td>1.1</td>
<td>17.4±0.7</td>
<td>12.9±0.5</td>
<td>4.5</td>
<td>30.2±0.4</td>
<td>22.7±0.8</td>
<td>7.5</td>
<td>52.3±0.5</td>
<td>38.8±1.1</td>
<td>13.9</td>
<td>81.6±1.8</td>
<td></td>
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</tr>
<tr>
<td></td>
<td>Bryoria</td>
<td>2.3±0.11</td>
<td>19.5±4.1</td>
<td>5.4</td>
<td>34.0±4.4</td>
<td>26.5±3.5</td>
<td>6.9</td>
<td>68.0±3.5</td>
<td>39.4±2.4</td>
<td>10.9</td>
<td>114.9±4.9</td>
<td>80.2±3.0</td>
<td>34.7</td>
<td>229.3±5.7</td>
<td>171.7±4.8</td>
<td>57.6</td>
<td>352.1±7.5</td>
<td>250.9±7.0</td>
<td>101.2</td>
<td>413.2±14.3</td>
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<tr>
<td></td>
<td>Foliose</td>
<td>2.6±0.3</td>
<td>22.3±4.7</td>
<td>6.1</td>
<td>34.9±4.0</td>
<td>26.9±3.9</td>
<td>6.9</td>
<td>68.8±4.0</td>
<td>39.0±2.5</td>
<td>10.9</td>
<td>115.8±4.9</td>
<td>81.0±3.0</td>
<td>34.7</td>
<td>231.6±5.7</td>
<td>173.8±4.8</td>
<td>57.8</td>
<td>362.3±14.3</td>
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<tr>
<td>Medium</td>
<td>Alectoria</td>
<td>4.8±2.6</td>
<td>14.4±3.4</td>
<td>1.5</td>
<td>16.3±3.6</td>
<td>12.0±3.1</td>
<td>2.4</td>
<td>30.5±3.7</td>
<td>24.4±3.2</td>
<td>4.7</td>
<td>60.3±3.9</td>
<td>40.4±3.2</td>
<td>19.5</td>
<td>119.2±4.4</td>
<td>84.8±3.3</td>
<td>34.6</td>
<td>238.6±14.6</td>
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<tr>
<td></td>
<td>Bryoria</td>
<td>17.9±10.8</td>
<td>58.3±4.7</td>
<td>5.4</td>
<td>63.5±4.8</td>
<td>47.9±3.9</td>
<td>7.4</td>
<td>71.4±4.9</td>
<td>54.8±3.8</td>
<td>12.6</td>
<td>138.6±5.7</td>
<td>98.6±4.2</td>
<td>39.2</td>
<td>276.4±14.5</td>
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<td></td>
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<tr>
<td></td>
<td>Foliose</td>
<td>5.6±3.2</td>
<td>16.8±3.8</td>
<td>1.7</td>
<td>8.8±1.0</td>
<td>5.4±0.8</td>
<td>5.0</td>
<td>21.0±1.6</td>
<td>12.0±1.2</td>
<td>4.9</td>
<td>37.9±1.8</td>
<td>27.0±1.2</td>
<td>10.9</td>
<td>75.8±1.8</td>
<td>44.0±1.2</td>
<td>11.9</td>
<td>131.7±1.4</td>
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<tr>
<td>Large</td>
<td>Alectoria</td>
<td>0.6±0.05</td>
<td>2.9±0.1</td>
<td>1.4</td>
<td>5.2±0.3</td>
<td>3.8±0.4</td>
<td>1.5</td>
<td>9.5±0.7</td>
<td>6.4±0.3</td>
<td>1.1</td>
<td>17.4±0.7</td>
<td>12.9±0.5</td>
<td>4.5</td>
<td>30.2±0.4</td>
<td>22.7±0.8</td>
<td>7.5</td>
<td>81.6±1.8</td>
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<td></td>
<td>Bryoria</td>
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<td>26.5±3.5</td>
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<td>68.0±3.5</td>
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<td>114.9±4.9</td>
<td>80.2±3.0</td>
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<td>229.3±5.7</td>
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<td>57.6</td>
<td>352.1±7.5</td>
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<td></td>
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<td>2.6±0.3</td>
<td>22.3±4.7</td>
<td>6.1</td>
<td>34.9±4.0</td>
<td>26.9±3.9</td>
<td>6.9</td>
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<td>5.4±0.8</td>
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<td>28.9±1.6</td>
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<tr>
<td></td>
<td>Bryoria</td>
<td>6.6±3.2</td>
<td>20.5±3.8</td>
<td>2.0</td>
<td>8.8±1.0</td>
<td>5.4±0.8</td>
<td>5.0</td>
<td>33.0±1.6</td>
<td>20.2±1.2</td>
<td>4.9</td>
<td>58.1±1.8</td>
<td>33.6±1.2</td>
<td>11.5</td>
<td>103.2±1.4</td>
<td>59.2±1.2</td>
<td>15.9</td>
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<tr>
<td></td>
<td>Foliose</td>
<td>1.4±0.3</td>
<td>4.8±0.8</td>
<td>1.7</td>
<td>8.8±1.0</td>
<td>5.4±0.8</td>
<td>5.0</td>
<td>21.0±1.6</td>
<td>12.0±1.2</td>
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<td>44.0±1.2</td>
<td>11.9</td>
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</table>

**Fig. 6.** Lichen biomass (g/branch) by functional group for clumped and solitary trees, for all clump trees and *Abies lasiocarpa* trees only. Each bar represents the mean ± 1 SE for 1717 and 315 observations by branch for clumped and solitary trees respectively (all clump trees); and for 963 and 315 observations by branch for clumped and solitary trees respectively (*A. Lasiocarpa* only).
Fig. 7. Lichen biomass by height class interval for each of Alectoria, Bryoria, and foliose lichen functional groups in Abies lasiocarpa and Picea engelmannii. Each bar represents the mean ± 1 SE for branches within 2 m height class intervals. The total number of branches from the ground up within each height class interval was 171, 341, 363, 264, 234, 196, 214, 12, 77, and 36, respectively, for Picea engelmannii and 18, 71, 93, 103, 91, 124, 121, 112, 108, 75, and 72, respectively, for A. lasiocarpa.

Fig. 8. Lichen biomass loading by branch diameter for Alectoria, Bryoria, and foliose lichen functional groups in Abies lasiocarpa and Picea engelmannii. Individual bars show the mean ± 1 SE for lichen biomass within 1 cm diameter class intervals for 1198, 896, 395, 127, and 39 branches from smallest to largest age classes, respectively, for Abies lasiocarpa and for 438, 347, 175, 74, and 29 branches from smallest to largest age classes, respectively, Picea engelmannii.

height. Similarly, foliose lichen loading shows a more pronounced peak in stand level abundance, between 5 and 10 m in height, when the denominator is plotted in area-based units (kg/ha).

The diameter of branches had a significant (but less marked) effect on the distribution of lichen biomass in both tree species (Fig. 8). Although Alectoria biomass did significantly change with branch diameter in both tree species (A. lasiocarpa, F(238, 2256) = 1.960, p < 0.0001, η² = 0.08; P. engelmannii, F(142, 871) = 1.841, p < 0.0001, η² = 0.09), the small effect sizes and graphical analysis revealed that there were no obvious trends in the distribution of this functional group with branch diameter. In contrast, Bryoria biomass increased significantly with increasing branch diameter (A. lasiocarpa, F(238, 2256) = 2.834, p < 0.0001, η² = 0.14; P. engelmannii, F(144, 871) = 3.226, p < 0.0001, η² = 0.23), reaching peak abundance on the largest branches in both tree species (28.39 ± 3.40 and 43.69 ± 4.14 g/branch on A. lasiocarpa and P. engelmannii branches, respectively). Unlike Alectoria and Bryoria, the response of foliose lichen biomass to branch diameter appeared to differ with host tree species. Whereas there was a significant difference in the distribution of foliose lichen biomass with increasing branch diameter in both species (A. lasiocarpa, F(236, 2256) = 3.199, p < 0.0001, η² = 0.16; P. engelmannii, F(144, 871) = 2.710, p < 0.0001, η² = 0.23), an overall increase in biomass was only visually apparent in A. lasiocarpa. Due to sample sizes, no significant trends in lichen biomass were revealed with changes in branch length, slope, or aspect.

The importance of each structural variable in describing lichen loading was evaluated using the Relative Pratt index (pooled stand data). Structural variables for Alectoria abundance were respectively ordered as branch height, length, diameter, and aspect (Table 3). The large index value (Dj) for branch height emphasized the importance of this variable. Conversely, branch slope was found to be unimportant in determining the distribution of Alectoria.

The Pratt index for Bryoria revealed that only branch height and diameter had an influence on the distribution of Bryoria in the canopy. The order of importance for the foliose lichen functional group was branch diameter, length, and aspect, with branch height and slope resulting in low index values (Table 3).

As indicated by the Pratt index ordering, aspect had a relatively small influence on lichen loading for Alectoria,
Table 3. Pratt index regression and correlation coefficients between canopy structural variables (branch aspect, diameter, height, length, and slope) and lichen biomass loading for Alectoria, Bryoria, and foliose lichen functional groups. Data is pooled for all study trees in experimental plots.

<table>
<thead>
<tr>
<th>Tree structural variable</th>
<th>Coefficients by lichen functional group</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Alectoria1</td>
</tr>
<tr>
<td></td>
<td>B</td>
</tr>
<tr>
<td>Branch aspect</td>
<td>0.16</td>
</tr>
<tr>
<td>Branch diameter</td>
<td>0.2</td>
</tr>
<tr>
<td>Branch height</td>
<td>-0.238</td>
</tr>
<tr>
<td>Branch length</td>
<td>0.168</td>
</tr>
<tr>
<td>Branch slope</td>
<td>-0.05</td>
</tr>
</tbody>
</table>

Bryoria, and foliose functional groups. Polar plots of lichen loading by aspect for individual trees and clump perimeter branches (Fig. 9) only show functional groups widely distributed across all vectors from the main trunk.

Changes in structural characteristics of A. lasiocarpa and P. engelmannii were assessed along a vertical gradient in the canopy (Fig. 10). Branch diameter peaked (3.80 ± 0.07 cm) in the middle canopy of A. lasiocarpa. There was a gradual, but significant, decrease in branch diameter to both the base and the top of the canopy from the peak found at approximately 14 m (F(11, 2646) = 25.64, p < 0.0001, \( \eta^2 = 0.02 \)). In P. engelmannii, branch diameter fluctuated about the mean (3.58 ± 0.03 cm) without obvious trends along the vertical gradient. In contrast, height appeared to have a stronger effect on the density of branches in P. engelmannii than in A. lasiocarpa. There were significantly more branches in a 1-m section in the upper canopy of P. engelmannii than in the lower canopy (F(11, 1072) = 39.36, p < 0.0001, \( \eta^2 = 0.26 \)). Canopy height also had a more marked influence on the slope of branches in P. engelmannii trees than in A. lasiocarpa. Branches in the lower canopy of P. engelmannii were significantly more downwardly sloped (58.50 ± 6.1°) than those at the top of the tree (6.82 ± 2.4°; F(11, 159) = 5.15, p < 0.0001, \( \eta^2 = 0.16 \)). The vertical gradient had few discernible effects on the density and slope of branches in A. lasiocarpa. Both tree species showed an overall significant increase in the length of branches in the lower canopy (A. lasiocarpa, F(11, 495) = 4.028, p < 0.0001, \( \eta^2 = 0.03 \); P. engelmannii, F(11, 146) = 2.19, p = 0.018, \( \eta^2 = 0.02 \)). There were no discernible effects of canopy height on branch aspect in either tree species.

Lichen microclimate

Summary meteorological and microclimatic data are shown in Fig. 11. Mean annual air temperature at the Pinkerton Mountain site in 1997/98 was 8.1°C. The minimum air temperature recorded was -28.2°C, recorded in January 1998. Maximum air temperature briefly reached 30.8°C in July 1998. The maximum temperature of hydrated lichen thalli was much less, reaching only 18.2°C during wetting to drying transition events in July 1998. Cumulative daily PAR shows a strong seasonal pattern, ranging from less than 0.3 mol-m⁻²-day⁻¹ during the midwinter period to over 5 mol-m⁻²-day⁻¹ during the early spring period. Greatest wind gusts reaching near 5 m/sec⁻¹ during December 1997. Prevailing wind directions at the Pinkerton site were from the west to south-west, with northerly winds showing a secondary peak of frequency. Cumulative snow depth at Pinkerton reached over 2 m in the early spring of 1998.

Microclimate data from Oct 1997 (Fig. 12), during periods of lichen wetting from mixed snow and rain, shows a greater duration of total lichen hydration in the lower canopy. Side-by-side measures at given height profiles show very small differences in thallus temperature and hydration patterns (indistinguishable on plots in Fig. 12) between Alectoria and Bryoria functional group lichen thalli. Small differences in thallus temperature (up to 1.5°C) are seen in functional group comparisons between upper and lower canopy aspects.

During the mid-winter period (Fig. 13), lichen thalli experience periods of lichen hydration during snowmelt episodes. Again, side-by-side measures at given height profiles show very small differences in thallus temperature and hydration between lichen functional groups. Greater differences in temperature and hydration patterns are shown between upper and lower canopy exposures, with lower canopy thalli experiencing a reduced total duration of lichen hydration episodes (especially Alectoria thalli). Differences were also noted between duration and incidence of lichen hydration upon comparing north and south aspect lichen thalli. Figure 14 illustrates the greater duration of lichen hydration for south aspect Alectoria from lower canopy exposures.

Data from representative summer lichen hydration events (August 14–19, 1998; Fig. 15) show that thallus temperatures during rainfall events largely remain below 10°C. On returning to sunny conditions on August 19 rapid drying of both upper and lower canopy lichen thalli occurs with little or no dewfall on subsequent mornings. Differences between upper and lower canopy lichen hydration events are smallest in the summer datasets, with thalli in both aspects drying rapidly on transition to full insolation conditions. North-south aspect comparisons in the summer period (Fig. 16) show higher levels of thallus hydration in north-aspect Alectoria lichen, compared to south-aspect populations in the lower canopy.

Although levels of thallus hydration did fluctuate with...
changes in relative humidity, we saw relatively few dewfall events that brought levels of thallus hydration above a physiologically active threshold. Data for August 2–5, 1999 (Fig. 17) illustrates changes in thallus moisture content during a representative period of clear summer weather.

Seasonal patterns of lichen hydration duration by functional group (Fig. 18) indicate that the total duration of lichen hydration was significantly greater in lower canopy exposures for south aspect lichens during the summer season. During the winter period, Bryoria thalli show a greater duration of hydration at 4 m, however, these differences were not statistically significant ($p > 0.05$, Friedman two-way
Fig. 10. Tree structural characteristics (branch-diameter, -density, 
-length, and -slope) by branch height (2 m class interval) for 
Abies lasiocarpa (top) and Picea engelmannii (bottom). Individu-
als bars show the mean ± 1 SE for the number of branches indi-
cated in parenthesis below each bar. Branch diameter and branch 
density measurements are based on the same sample size as are 
branch length and branch slope measurements.

analysis of variance). Differences in the total duration of li-
chen hydration between upper and lower canopy exposures 
were not significant (p > 0.05, Friedman two-way analysis 
of variance) for lichen thalli on the north aspects of clumps.

When lichen hydration duration is summarized on a per 
event basis (Fig. 19), lower canopy south-facing aspects 
show higher total values for all species–seasonal combina-
tions (again excepting winter Alectoria measures). The larg-
est differences between upper and lower canopy hydration 
event duration are seen for summer Alectoria measurements 
on south-facing aspects, where upper canopy thalli show 
greater total per event hydration duration. Differences be-
tween upper and lower canopy per event wetting measure-
ments were not significant (p > 0.05, Friedman two-way 
analysis of variance) under all aspect and functional group 
combinations.

Discussion

Sillett and Neitlich (1996), McCune (1993), and McCune 
et al. (1997) discussed a vertical gradient in epiphyte bio-
mass that is intrinsically tied to epiphyte succession and 
therefore to the age and size of the host tree. It is logical 
then that the successional stages and distribution patterns of 
epiphytes evident in the ESSF ecosystem are different from 
those seen in coastal ecosystems where the trees are often 
twice the height of those at Pinkerton Mountain. The lichen 
distribution at Pinkerton Mountain corresponds with the ear-
lier successional stages detailed in the literature for coastal 
low-elevation forests. Foliose lichens are the first to colo-
nize (Stone 1989), followed by Alectorioid lichens 
(Alectoria and Bryoria); these are displaced to the higher 
canopy zones by the later successional cyanolichens and 
epiphytic bryophytes in older, more moist climates (McCune 
et al. 1997).

We profiled the vertical distribution of Alectorioid and 
foliose lichens in the ESSF. The 30 m canopy resembles that 
of the 30–60 m zone in coastal forests documented by 
McCune et al. (1997), suggesting that there is a change in 
epiphyte dominance from old-growth forest indicators such 
as cyanolichens to the earlier successional pendulous lichens 
in higher elevation ecosystems. This distribution supports 
the similar gradient hypothesis outlined by McCune (1993). 
This does not mean to say that stands in the ESSF may 
attain cyanolichen communities with greater age. Rather, the 
conditions of more open canopy structure that favour pendu-
lous lichens in the 30–60 m zone of coastal forests may be 
similar to those found in the shorter and more open ESSF 
forest stands at high elevation.

In the ESSF zone, Alectoria and Bryoria dominate the 
canopy, and foliose lichens exhibit a less obvious distribu-
tion with height above ground. Cyanolichens and bryophytes 
are essentially absent. McCune (1993) also showed that cer-
tain foliose lichens were most abundant in the early mature 
forests considered in that study and that Alectoria sarmentosa 
and Bryoria spp. were present in all age categories, 
but reached maximal abundance in the medium-aged 
class forest. However, there was no distinct vertical zonation 
between these two genera in the Pseudotsuga menziesii for-
est. In contrast, Bryoria dominated the upper ESSF canopy 
at Pinkerton Mountain and was separated at approximately 
5–7 m from Alectoria, which increased in abundance from 
there to the lowest branches. Arseneau et al. (1997) and 
Rominger et al. (1994) also described separate responses for 
Alectoria and Bryoria to the vertical gradient. Many studies 
suggest environmental reasons for the distinct separation of 
Alectoria and Bryoria within the vertical canopy that was 
documented in the present study. The fact that the environ-
ment is thoroughly confounded with structure and succes-
sion (McCune 1993) makes it extremely difficult to explain 
the distribution of epiphytic lichens.

The marked increase in branch level Bryoria biomass with 
an increase in substrate availability (branch diameter) indi-
cates that canopy architecture can also play a significant role 
in determining the distribution of these lichens (Yarranton 
1972). These results concur with Lui et al. (2000), who 
found a relatively strong relationship between branch basal 
diameter and lichen biomass. However, the Pratt index val-
ues for fruticose lichens indicate that the presence of pendu-
lous forage lichens is determined much more by their 
vertical position in the canopy than by the size of the 
branch. The pendulous growth form of these lichens allows 
them to become attached to the host by a single holdfast. 
Substrate availability does not seem to limit Alectorioid li-
chen growth after initial colonization (Stone 1989; Renhorn 
1997). These results, coupled with the negligible index val-
ues for branch length, aspect, diameter, and slope, indicate that it is unlikely that branch and ecosystem loadings of *Alectoria* and *Bryoria* are in response to either structure or substrate availability alone.

For the foliose lichen functional group, however, branch diameter was the most important determining factor. An increase in substrate availability substantially increased foliose lichen biomass. This pattern substantiates the view that the large thallus of foliose lichens (relative to the more pendulous fruticose lichens) is strongly limited by available substrate (Stone 1989).

The increase of tree age and size within coniferous forest canopies has been postulated to exert a positive influence on lichen loading, due to the greater longevity and availability of bark substrates for lichen colonization (Selva 1994). Edwards et al. (1960) found that young trees in the ESSF had approximately 50 g/tree, intermediate aged trees held 100–1600 g/tree, and older trees had between 3100–8600 g/tree. Lichen loading at Pinkerton Mountain showed similar trends. Medium sized trees (5–15 m) constituted 45% of standing lichen biomass in the lower canopy (0–5 m), even though trees of this size class accounted for 22% of standing stems. Conversely, lichen loading on small trees (<5 m tall; 65% of standing stems) was less than 35% of lichen loading.

Fig. 11. Summary climate data for Pinkerton Mountain in 1997/98.
in the lower canopy. This finding concurs with much of the existing literature, which suggests that small trees do not make suitable habitat for arboreal lichens (Lang et al. 1980; Sillett and Neitlich 1996; Goward 1998). Although there is considerable variation in the size of medium sized trees, a comparison in the middle canopy reveals that large trees (>15 m in height, equivalent to about 45% of basal area in stand) host more lichen biomass (over 70% of total loading), both on a per branch basis and at the ecosystem level, than any other size class. The extraordinary contribution of large trees to the total standing epiphyte biomass may be attributed to the fact that Bryoria dominates the middle and upper canopy zones in this system and has a much greater total biomass than either Alectoria or foliose lichen.

One interesting trend in our data set was the relatively uniform (and high) loadings of Bryoria with increasing height in the upper canopy of P. engelmannii, whereas Bryoria loadings declined appreciably with height in the uppermost canopy of A. lasiocarpa. We believe that this may be an effect of branch size (as indicated by Pratt index significance rankings for branch diameter), reflecting the architecture of these species. Branch size tends to decrease

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Fig. 13. Lichen thalli microclimate (January 1998) for south-facing aspects of Alectoria and Bryoria lichen functional groups in upper (12 m) and lower canopy (4 m) exposures.

with height in A. lasiocarpa, whereas it remains relatively constant in the upper canopy of P. engelmannii. Curiously, branch length, which also decreases noticeably in upper canopy A. lasiocarpa, does not rank as a significant indicator for Bryoria loading. Upper canopy loading of Bryoria tends to be very matted in nature, not extending along the full length of branches. Wind scouring effects may be important in this regard, especially for the more narrow, spire-like architecture of A. lasiocarpa.

Goward (1998) suggested that lichen loading (especially of Bryoria spp.) within high elevation spruce-fir forests in British Columbia may be strongly shaped by lichen sensitivity to microclimate gradients, especially duration of hydration episodes. Goward postulated, in part, that Bryoria is found primarily in the upper canopy because high levels of solar radiation cause more rapid snow melt and moisture evaporation than would occur in the lower, less ventilated canopy. This hypothesis is supported by our datasets, which show reduced duration of lichen hydration (both total hours of hydration and hours hydrated per event) for Bryoria thalli in upper canopy exposures. Although these differences are not large in magnitude, even small differences in wetting and drying patterns can push lichen thalli into a situation of negative carbon gain, as documented by Moser and Nash (1978) for Cetraria cucullata.

Intolerance of prolonged wetting in Bryoria thalli may result from a breakdown of the symbiosis between algal and fungal bionts. Tysiaczny and Kershaw (1979) showed that the retention of sugars by algal bionts is limited to the relatively brief wetting to drying transitional periods for some lichen species. If Bryoria demonstrates this pattern of symbiont physiology, extended wetting events would result in the effective starvation of algal bionts. The ability to tolerate wetting and drying cycles may therefore be more important for
Bryoria in these upper canopy aspects (where conditions of light rains or dew alternate with drought-like conditions) than the total duration of wetting events themselves.

Interestingly, rehydration from dewfall events did not contribute appreciably to the duration of lichen hydration in our dataset. Although lichens do absorb atmospheric humidity under early morning conditions associated with dewfall events, they typically stay at levels of thallus hydration below those necessary for physiological activation. This corresponds to our summer field observations, where forest floor forbs and vegetation were frequently wet from dewfall, whereas lichen thalli in the canopy remained dry or only slightly hydrated. This may reflect the ease with which convective air exchange can occur around pendulous hair lichens. However, the surface properties of lichen thalli may also play a role. We note that under conditions of saturating humidity, thalli of Alectoria and Bryoria require 4–6 h to reach a point of physiological reactivation (slightly faster in Bryoria). Further, even small declines in ambient RH result in a sharp decrease in levels of thallus hydration. This avoidance of physiological reactivation during small-scale wetting events may limit the metabolic costs arising from restoring lichen function during rewetting. Solute leaching during rewetting (Coxson et al. 1992) and resaturation respiration (Coxson 1988) both impose metabolic costs on resaturation.

Microclimate data from Pinkerton Mountain highlights the importance of the winter period, when both Alectoria and Bryoria functional groups experience the greatest duration of wetting, and by extension, duration of metabolic activity. If physiological response patterns of Alectoria and Bryoria lichens are similar to those of other alpine and subalpine lichens (Coxson 1983), we might expect continued photosynthetic activity in hydrated thalli at temperatures well below 0°C. Kershaw (1975) demonstrated that dark colouration in corticolous lichen can enhance thallus temperature and allow greater utilization of snowmelt conditions. Although the dark colouration of Bryoria lichen thalli may enhance retention of solar radiation, when lichen thalli are hydrated, we see little difference in side-by-side temperature comparisons between lichen functional groups.
The finely dissected nature of lichen thalli in the *Alectoria* and *Bryoria* functional groups (and associated high rates of convective exchange and evaporative cooling) would seem to limit the influence of thallus colour on surface heating for pendulous lichen thalli.

This finding is similar to that of earlier measures on pendulous canopy lichens by Coxson et al. (1984). Greater differences are seen when comparisons are made between lichens in upper and lower canopy exposures or between north- and south-facing aspects at the same height. These trends may balance each other out seasonally, with south-facing aspects showing greater wetting during the mid-winter period, when low solar angles reduce meltwater effects on north-facing aspects; yet, these same south-facing aspects show reduced wetting during the mid-summer period, when insolation exposure leads to more rapid drying after precipitation events. Lichen loading seems to reflect this balancing of wetting duration, with no significant aspect effects either for individual trees or for perimeter measures on clumps.

When thalli are dry, radiant loading can play a greater role. Thalli temperatures of *Alectoria* and *Bryoria* in upper

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**Fig. 15.** Lichen thallus microclimate (August 1998) for south-facing aspects of *Alectoria* and *Bryoria* lichen functional groups in upper (12 m) and lower canopy (4 m) exposures.
canopy aspects can reach up to 20°C above air temperatures under still air conditions. It is likely, however, that most of this temperature elevation is due to the layer of still air surrounding coniferous foliage, as temperature differentials between thalli of the light-coloured Alectoria and the dark-coloured Bryoria were generally less than 0.5°C under these conditions.

In summary, although our field microclimatic data provides, for the first time, a detailed picture of operating environments for hair lichens in subalpine spruce–fir forests in western North America, our findings point more to the importance of seasonal variations in growth environment; snow melt events, in particular, rather than vertical gradients in canopy microclimate, are a primary factor that directly controls lichen growth rates. Indeed, our vertical profiles of canopy microclimate during periods of lichen hydration are surprisingly isothermal in nature. This finding stands in marked contrast to the clear gradients in lichen distribution patterns.

Why then, do both groups of lichens (Alectoria and Bryoria) not occur with equal abundance throughout the canopy? We should not discount canopy climate as a contributing factor. Although canopy conditions are quite isothermal during actual precipitation events, there is an attenuation of wetting in the lower canopy during drying periods after precipitation events, especially in the summer (presumably favouring lower canopy Alectoria growth). This pattern reverses in the mid-winter period, when snowmelt events are of longer duration in the upper canopy, again presumably favouring upper canopy Bryoria growth. We are now examining physiological response patterns in Bryoria to determine if differences in tolerance to prolonged periods of hydration preclude the establishment of Bryoria in the lower canopy, as suggested by Goward (1998).

Fig. 16. Comparative thallus microclimate for Alectoria functional group lichens on north- and south-facing aspects during July 1998.
Thus, it is clear that lichen dynamics (colonization and dispersal) within the stand must also be considered when examining vertical profiles of lichen distribution in old-growth subalpine spruce–fir forests. Esseen and Renhorn (1996) suggest that *Bryoria* more effectively colonizes branches in young stands, as they are finer and more readily fragmented under field conditions. This suggests that *Alectoria* may extend upwards into the canopy and gradually displace *Bryoria* as stands age. This trend, however, may be held in check by periodic storm events, which would differentially scour the longer *Alectoria* thalli from upper canopy exposures. Certainly, we would expect that patterns of distribution within the canopy for *Alectoria* and *Bryoria* are determined, in part, by lichen successional trends, driven by dispersal ability and stand structure, rather than physiological differences.

It is likely that both hypotheses (physiological versus successional control of lichen distribution patterns) are valid. Canopy operating environments will interact with lichen physiology to set limits to growth, both on a short-term basis and over longer time periods. Interestingly, Goward (1998) notes that dieback events in *Bryoria* have been observed during exceptionally wet summers in subalpine forests of southern British Columbia. Given the present distribution of *Bryoria* in the canopy, it would appear that operating environments for this species in the ESSF allow (or perhaps even require) greater utilization of snowmelt events, whereas *Alectoria* relies more heavily on summer precipitation events. This differential habitat use is an important element of the ecology of these lichen functional groups.

It is important to note that our measurements of canopy microclimate were restricted to lichen thalli growing within clumps of trees, where the extended perimeter of the effective outer crown may enhance both snow interception and snow melt during the winter period. We observed that lichen loading responded significantly to stand structure, suggesting that clumping may be a major determinant of lichen abundance in ESSF forests. *Bryoria* appeared to respond positively to the irregular clumping distribution of the trees at Pinkerton Mountain, exhibiting greater abundance per branch in clumped trees than in solitary trees of corresponding size in nearby canopy gaps (combined tree species data).

The greater overall lichen abundance in clumped trees within our study site has significant implications for stand structure and forest management practices in these high elevation ESSF forests. We hypothesize that the aggregation of trees in clumps creates a larger effective crown perimeter. This larger crown perimeter may confer a microenvironment on its member trees that is more similar in nature to late successional larger trees and thus more conducive to lichen growth and establishment. Although young trees that become established within this “integrated tree perimeter” experience slower growth rates than similarly aged trees developing in canopy gaps (Aplet et al. 1988), they may

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**Fig. 17.** Lichen thallus (*Alectoria* only) microclimate (August 2–5, 1999) for south-facing aspects in lower canopy (4 m) exposure.

![Graph showing PAR, temperature, and thallus hydration for Alectoria and Bryoria](image)

**Fig. 18.** Comparative lichen wetting duration (total days) for upper and lower canopy exposures (15 and 4 m, respectively), plotted by species functional group and season. Asterisk indicates significant differences between functional groups (*p* < 0.05, Friedman two-way analysis of variance) Each bar shows the mean ± 1 SE for six replicate measurements.

![Graph showing duration of lichen hydration (total days) for Alectoria and Bryoria](image)
Fig. 19. Comparative lichen wetting duration (h/event) for upper and lower canopy exposures (15 and 4 m, respectively), plotted by species functional group and season. There were no significant differences between groups (p < 0.05, Friedman two-way analysis of variance). Each bar shows the mean ± 1 SE for six replicate measurements.

Assume some characteristics of older trees, relative to lichen loading, due to microclimate modification effects within integrated crowns and higher availability of lichen propagules.

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