

Spatial distribution and succession of epiphytes on *Tsuga heterophylla* (western hemlock) in an old-growth Douglas-fir forest

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Abstract: We examined the distribution and abundance of nonvascular epiphytes on western hemlock trees in an old-growth coniferous forest focusing on patterns of epiphyte distribution at different spatial scales, epiphyte abundance amongst trees differing in size, and crown structures associated with epiphyte abundance. Total epiphyte cover was greatest in four canopy microhabitats: the upper canopy strata, crowns of large trees, lower crown branches, and inner branch plots. Epiphyte functional groups were stratified vertically within the stand and horizontally within branches. Alectorioid and "other" lichens were most abundant in the upper canopy and outer branch plots. Cyanolichens and *Sphaerophorus globosus* (Huds.) Vain. were most abundant in the lower to mid canopy. Although cyanolichens were most abundant in middle branch plots, *Sphaerophorus* was most abundant in inner branch plots. Bryophytes were most abundant in the lower canopy and inner branch plots. At the stand level, canopy height and tree size were the main influences on epiphytes. Within trees, plots closer to the tree trunk and lower in the crown had the greatest abundance of epiphytes. In this forest, understory trees were colonized first by bryophytes, not by alectorioid and "other" lichens as is common for small trees in young stands.

Key words: epiphyte succession, lichens, western hemlock, old growth, forest canopy, crown structure.

Résumé : Les auteurs ont examiné la distribution et l'abondance des épiphytes non-vasculaires sur les tiges de pruches de l'ouest, dans une forêt coniférienne surannée, en mettant l'accent sur les patrons de distribution des épiphytes à différentes échelles spatiales, sur l'abondance des épiphytes parmi des arbres de différentes dimensions, ainsi que les structures des cimes associées aux épiphytes. La couverture totale d'épiphytes est la plus élevée dans quatre habitats de la canopée : la strate supérieure de la canopée, la cime des grands arbres, les branches basses des cimes, et les branches internes. Les groupes fonctionnels d'épiphytes se distribuent par strates verticales dans le peuplement et horizontalement sur les branches. Les lichens alectorioïdes et « autres » sont les plus abondants dans la canopée supérieure et sur les branches externes. Les cyanolichens et le *Sphaerophorus globosus* (Huds.) Vain. sont surtout abondants dans la canopée basse à moyenne. Bien que les cyanolichens soient très abondants sur les branches du milieu, le *Sphaerophorus* est le plus abondant sur les branches internes. Les bryophytes sont les plus abondantes dans la canopée inférieure et les branches internes. Au niveau du peuplement, la hauteur de la canopée et la dimension des arbres exercent le plus d'influence sur les épiphytes. Au niveau des arbres, les parcelles les plus près du tronc et les plus basses dans la cime montrent la plus grande abondance d'épiphytes. Dans cette forêt, les arbres en sous-étage sont d'abord colonisés par les bryophytes, et non par les lichens alectorioïdes et « autres », comme c'est souvent le cas chez les petits arbres dans les jeunes peuplements.

Mots clés : succession des épiphytes, lichens, pruche de l'ouest, forêt surannée, canopée forestière, structure des cimes.

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Introduction

Canopy epiphytes are a conspicuous and characteristic component of old-growth forests in the Pacific Northwest. They are involved in critical ecosystem processes such as primary production (Pike 1981; McCune 1993), nutrient cy-

cling (Lang et al. 1976; Pike 1978; Nadkarni 1984), and hydrology (Brown and Bates 1990; FEMAT 1993). Epiphytes also provide food, nesting material, and habitat for arboreal and terrestrial organisms (Maser et al. 1985; FEMAT 1993; Rominger et al. 1994). Despite their importance, relatively little is known about epiphyte ecology. Early studies of epiphytes in the Pacific Northwest focused on floristic surveys and baseline estimates of epiphyte biomass (Hoffman and Kazmierski 1969; Pike 1971; Denison et al. 1972; and Pike et al. 1975). Recent temperate forest canopy research has focused on relationships between forest structure and function, and the effects of habitat type and management practices on epiphyte communities (McCune 1993; Neitlich 1993; Clement 1995; Sillett 1995; Neitlich and McCune 1997).

Epiphytes are influenced by a variety of structural characteristics such as tree and branch size, forest age, substrate

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Table 1. Number of live trees, basal area, and tree density within the Wind River Canopy Crane Research Facility 4-ha plot.

Species	No. of live trees	Basal area (m ² /ha)	Tree density (stems/ha)
<i>Cornus nuttallii</i> Aud	13	0.01	6.5
<i>Thuja plicata</i> Donn. Red	120	16.36	60.0
<i>Abies amabilis</i> (Dougl.) Forbes	188	1.13	94.0
<i>Abies grandis</i> (Dougl.) Forbes	17	0.95	8.5
<i>Abies procera</i> Rehder	2	0.11	1.0
<i>Pinus monticola</i> Dougl.	2	0.09	1.0
<i>Pseudotsuga menziesii</i> (Mirbel.) Franco	143	35.15	71.5
<i>Tsuga heterophylla</i> (Raf.) Sarg.	888	25.54	444.0
<i>Taxus brevifolia</i> Nutt.	346	2.00	173.0
Total	1719	81.35	859.5

Note: Numbers include all trees greater than 5 cm in diameter.

type, relative position, and microclimate (i.e., light, temperature, moisture) (Armstrong 1981; Lesica et al. 1991; Esseen et al. 1996; Shirazi et al. 1996). Studies comparing epiphyte abundance between stands that vary in age and management strategies have documented a strong relationship between stand age and epiphyte biomass, particularly for nitrogen-fixing lichens (cyanolichens), which are dominant in old forests but nearly absent from young stands (McCune 1993; Neitlich 1993). However, the majority of epiphyte research has focused on large Douglas-fir (*Pseudotsuga menziesii* (Mirbel.) Franco) trees and some hardwood species (Nadkarni 1984; Clement 1995; Sillett 1995). Although Douglas-fir is often the largest species in many stands, shade-tolerant species such as western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) often dominate old-growth forests in terms of total number of individuals, vegetative surface area, and volume (Van Pelt and North 1996). Epiphyte distribution and abundance on species other than Douglas-fir or among small trees has been documented in only a small number of studies, some of which have been used to speculate on epiphyte succession (McCune 1993; Lesica et al. 1991; Neitlich 1993).

Chronosequences of stand ages have also been used to generate hypotheses about epiphyte succession in Pacific Northwest coniferous forests (McCune 1993; Neitlich 1993). However, applying models of succession developed from a series of stand ages to individual trees within a single old-growth stand is problematic because trees in a given age class in old growth do not experience the same environmental conditions as trees of a similar age in even-aged or managed stands. As a stand ages, changes in the forest structure modify environmental conditions. Also, using height classes for chronosequences may not be appropriate because tree size is often a poor indicator of age in old-growth forests. The diversity of both tree size and age, along with microclimate variability within a single old-growth forest stand, will result in varied patterns of epiphyte succession within a single stand.

In this study, we quantified the distribution patterns of epiphytic lichens and bryophytes on western hemlock.

Within a single stand, individual western hemlock trees between 4 and 51 m in height were intensively sampled to test two hypotheses: (i) the distribution and abundance of epiphyte functional groups varies with height class and relative canopy position (position within the tree crown and branch) and (ii) structural characteristics of individual branches and trees (branch size and position) are related to epiphyte abundance. Our objectives were to (i) extensively sample trees to quantify patterns of epiphyte distribution at distinct spatial scales (within branches, within trees or "crown zones," and within the forest canopy), (ii) compare epiphyte abundance among trees differing in size, and (iii) identify structural elements correlated with epiphyte abundance. This information could improve our understanding of the effects of substrate quantity and quality on epiphyte diversity and abundance in structurally complex, mixed-species, old-growth forest canopies.

Materials and methods

Study site

Research was performed between June 1996 and July 1997 at the Wind River Canopy Crane Research Facility (WRCCRF) located within the Thornton T. Munger Research Natural Area (RNA) in Washington State, U.S.A. The facility is a cooperative scientific venture of the University of Washington, the U.S. Forest Service Pacific Northwest Research Station, and the U.S. Forest Service Gifford Pinchot National Forest. The site contains a 4-ha study plot centered on a 74.5-m Liebherr HC 550 crane that provides access to 2.3 ha of old-growth forest.

The WRCCRF is a moist temperate coniferous forest with cool, wet winters and dry summers (Waring and Franklin 1980). The study site has a mean annual precipitation of 2528 mm with much of the winter precipitation in the form of snowfall (WRCCRF 1995). The mean annual temperature is 8.7°C with July and January average temperatures of 17.5 and 0.0°C, respectively, (Kemp and Schuller 1982; WRCCRF 1995). Vegetation in this low elevation, old-growth Douglas-fir/western hemlock forest is transitional between *Tsuga heterophylla*/Gaultheria shallon Pursh. and *Abies amabilis* (Dougl.) Forbes/Gaultheria shallon (Franklin and Dyrness 1988). Emergent Douglas-fir trees up to 500 years old dominate the upper canopy; western hemlock fills in the middle and lower canopy (Table 1).

Sampling methods

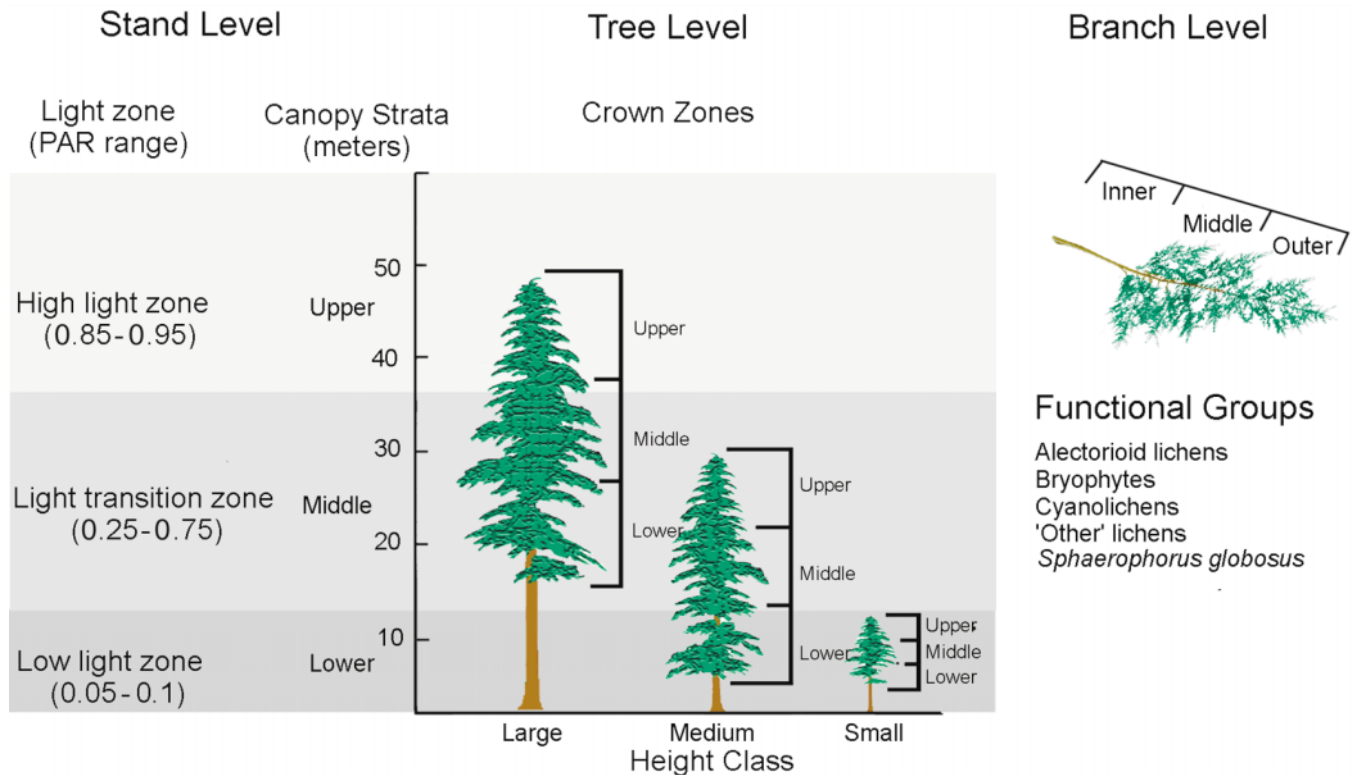
Tree selection

All live, mistletoe-free western hemlock trees greater than 5 cm in diameter at breast height (dbh) were considered for sampling. Trees were rated on their accessibility from the crane gondola, and the first 10 trees falling into each of three height classes were selected for sampling (30 total). Height classes were established based on previously quantified light levels within the study site (Parker 1997) (Fig. 1). Below 12 m, photosynthetically active radiation (PAR) is consistently low. Above 37 m, PAR is consistently high. At heights between 12 and 37 m, light intensity is variable with some sites receiving high levels of incoming solar radiation and others receiving very little. The height classes are referred to as small (<12 m), medium (12–35 m), and large (>37 m). The upper, middle, and lower canopy strata of the forest are defined in relation to the light zones.

Tree and branch sampling

Among all 30 trees, a total of 961 branches was measured for structural characteristics and sampled for epiphytes. Small trees

Fig. 1. Overview of the study design and stratification of sampling units. The canopy strata and height classes were defined based upon known light levels or photosynthetically active radiation at the study site (Parker 1997). The height classes were small (<12 m), medium (12–37 m), and large (>37 m). Tree crowns were divided into three equal “crown zones,” and all sampled branches were classified into one of three zones. The percent cover of epiphyte functional groups was estimated at three positions along each branch.



were accessed with ladders. Large and medium trees required use of the canopy crane for access. On small trees, all live branches greater than 2 mm in diameter were sampled. On large trees, 15% of live branches greater than 1 cm in diameter was sampled. The total branch length, foliage length, branch height (at base), and foliage height (at tip) were measured on all sample branches. Branch length was measured as the horizontal distance from the trunk to the branch tip. Foliage length was measured as the horizontal distance from the point at which the foliage began to the tip of the branch.

Branch sampling consisted of “vertical drops” in the crane gondola down 2 to 4 sides of each tree crown. Sampling intervals of 3 m for large trees (2 m for medium trees) were used and resulted in a sample of approximately 30 branches per tree. For each vertical drop, the crane gondola was positioned above an area that appeared accessible throughout the length of the crown. The nearest live branch within 30° to either side of the gondola was selected for sampling. This procedure continued throughout the tree crowns until further downward movement was not possible. The total number of branches was counted on a subset (7–10) of the medium and large trees to determine the proportion of crown branches sampled for epiphytes.

All sampled trees were cored to estimate tree age. Cores were taken at a height of 30.5 and 45.7 cm for medium and large trees, respectively. Annual growth rings were counted using a dissecting scope. Tree ages from cores that were laterally offset from the center or fell short of the center were adjusted following standard methods (Applequist 1958; USDA Forest Service 1987).

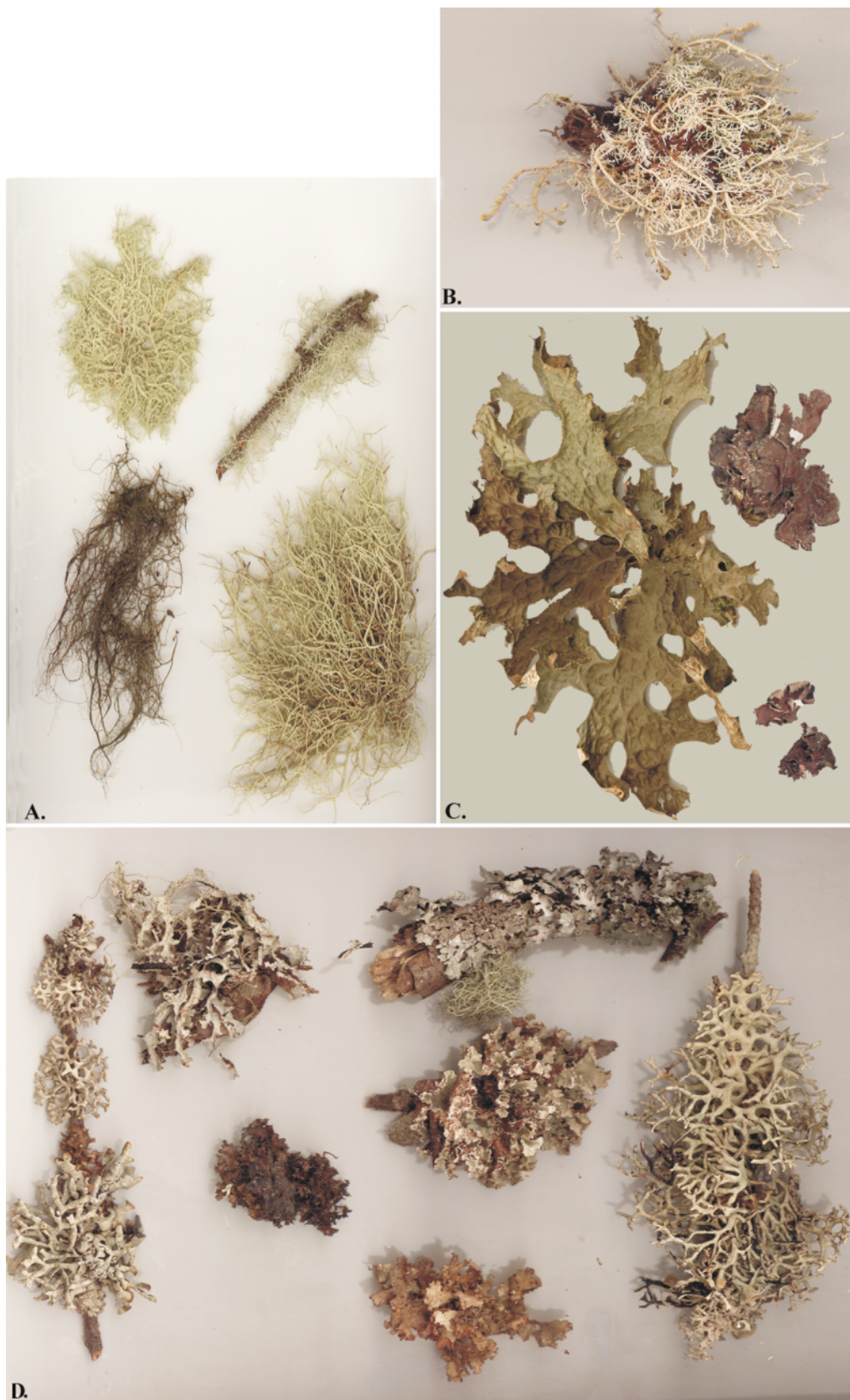
Epiphyte sampling

Epiphytes were classified into functional groups following McCune (1993). Epiphyte functional groups were comprised of

species sharing similar ecological roles and morphology (Fig. 2). Alectorioids are pendulous lichens belonging to the genera *Alectoria*, *Bryoria*, and *Usnea*. Bryophytes include all mosses and liverworts. Cyanolichens are foliose nitrogen-fixing macrolichens (e.g., *Lobaria*, *Pseudocyphellaria*, and *Stictia*), which contain cyanobacteria in their thalli. All remaining macrolichens are included in the “other” lichen category with the exception of a single species, *Sphaerophorus globosus*, which was placed in a separate group (Clement 1995; Sillet and Goslin 1999). This fruticose species has a distinct distribution pattern compared with the remainder of the “other” lichens. Crustose lichens were not considered in this study.

A maximum of three epiphyte samples was taken on each of the 961 sampled branches. Each branch was divided into three regions: inner, middle, and outer. The inner branch region was defined as the area of bare branch, devoid of foliage. The middle and outer plots were those containing foliage, and were located adjacent to the area where foliage began and ended, respectively. The outer quadrat was placed 10 cm back from the tip to avoid sampling the current year's growth. A frame attached to an extendable pole was placed within each zone, laid flat, and the percent cover of epiphytes was estimated on the upper branch surface. On branches in the upper canopy where foliage extended from the branch tip all the way to the tree trunk, inner plots did not exist because, by definition, they were the areas adjacent to the trunk devoid of foliage. In such instances, only middle and outer branch samples were taken, which resulted in a total sample size of 2701 plots out of a possible total of 2883 (961 branches × 3 plots per branch). Quadrat sizes differed to account for the large variation in limb size of understory and overstory trees. For small trees, a 10 × 25 cm quadrat was used (Pike et al. 1977); for medium and large trees, a 20 × 50 cm quadrat was used. Separate cover estimates were made

Fig. 2. Representatives of the lichen functional groups as defined by McCune (1993). (A) Alectorioid lichens (*Usnea* spp.; *Bryoria* sp., lower left). (B) *Sphaerophorus globosus*. (C) Cyanolichens (*Lobaria pulmonaria*, left; *Sticta* sp., upper right; and *Nephroma* sp., lower right). (D) "Other" lichens (*Hypogymnia* spp., far left and far right; *Platismatia herrei*, upper center; *Tuckermannopsis* spp., lower center; and *Parmelia sulcata*; upper and center right).



for each functional group and total epiphyte cover. Relative percent cover was calculated based on the area of the quadrat frame, the percent of the frame used, the percent foliage and twigs within the area used, and the percent cover of epiphytes (Lyons 1998).

Data analysis

Univariate analyses were non-parametric because branch and plot variables were not normally distributed (Kolmogorov–Smirnov goodness-of-fit test). Individual plots were averaged to generate branch and tree averages. Average epiphyte cover per height class, crown zone, and canopy strata were also calculated. A Kruskal–Wallis test was used to examine differences in epiphyte abundance within height classes, crown zones, relative position within a tree crown, and canopy strata. A Mann–Whitney test was used to test for proportional differences in epiphyte abundance between substrate types (i.e., small, medium, or large tree) within a given stratum. Pearson correlation analysis was used for pairwise examination of tree structure variables (tree height, age, and branch density; $n = 30$) and epiphyte abundance. Spearman correlation analysis was used for the examination of branch structural variables (branch length, diameter, and height; $n = 961$) and epiphyte abundance. Tree age was normally distributed, and differences in tree age among height classes were examined with one-way ANOVA followed by a post-hoc Tukey test to determine whether the tree height classes could be used as surrogates for age classes.

Results

Epiphyte distribution and abundance

Epiphytes were present in 76% of all plots and 60, 80, and 96% of small, medium, and large tree plots, respectively. Epiphyte cover varied with absolute position (height above ground), substrate type (small, medium, or large tree), and relative crown position (upper, middle, and lower crown as well as inner, middle, outer plot position). There were significant differences in total cover at all spatial scales ($p < 0.001$).

Stand level

Total cover was greatest in the upper stratum and least in the lower stratum (Table 2). Epiphyte functional groups were stratified vertically in the canopy. Alectorioids and “other” lichens increased in abundance from the ground up, while bryophytes decreased, and cyanolichens and *Sphaerophorus* increased in abundance from the lower to middle canopy strata and then decreased above the middle canopy (Fig. 3). There were significant differences in the cover of epiphyte functional groups per canopy stratum ($p < 0.001$). “Other” lichens (77%) and bryophytes (78%) were the dominant groups in the upper and lower canopy strata, respectively. The greatest richness and evenness of epiphyte functional groups was found in the middle stratum.

Total epiphyte abundance increased with height class. Large trees had approximately twice the total epiphyte cover of medium trees and nearly three times the cover of small trees (Table 2). There were also significant differences in the composition of epiphyte communities among height classes (Fig. 4). Small trees were dominated by a single functional group (bryophytes) while the other height classes exhibited a more diverse epiphyte community. Nearly half the epiphyte cover on medium trees was bryophytes, a third was “other” lichens, and the remainder was a combination of alectorioid lichens, cyanolichens, and *Sphaerophorus*. Within large

Table 2. Total epiphyte abundance by canopy stratum and height class.

Canopy strata	Height class			Total
	Small	Medium	Large	
Upper (>37 m)	—	—	20 (0.96)	20 (0.96)
Middle (12–37 m)	—	10 (0.73)	24 (1.22)	17 (0.74)
Lower (<12 m)	8 (0.58)	19 (2.76)	14*	10 (0.58)
Total cover	8 (0.58)	11 (0.80)	23 (0.93)	14 (0.46)

Note: Mean percent cover is given. Values in parentheses are one standard error.

*Based on the presence of a single large tree branch.

trees, epiphyte functional groups were more evenly distributed, but “other” lichens were considerably more abundant than the remaining functional groups.

Tree level

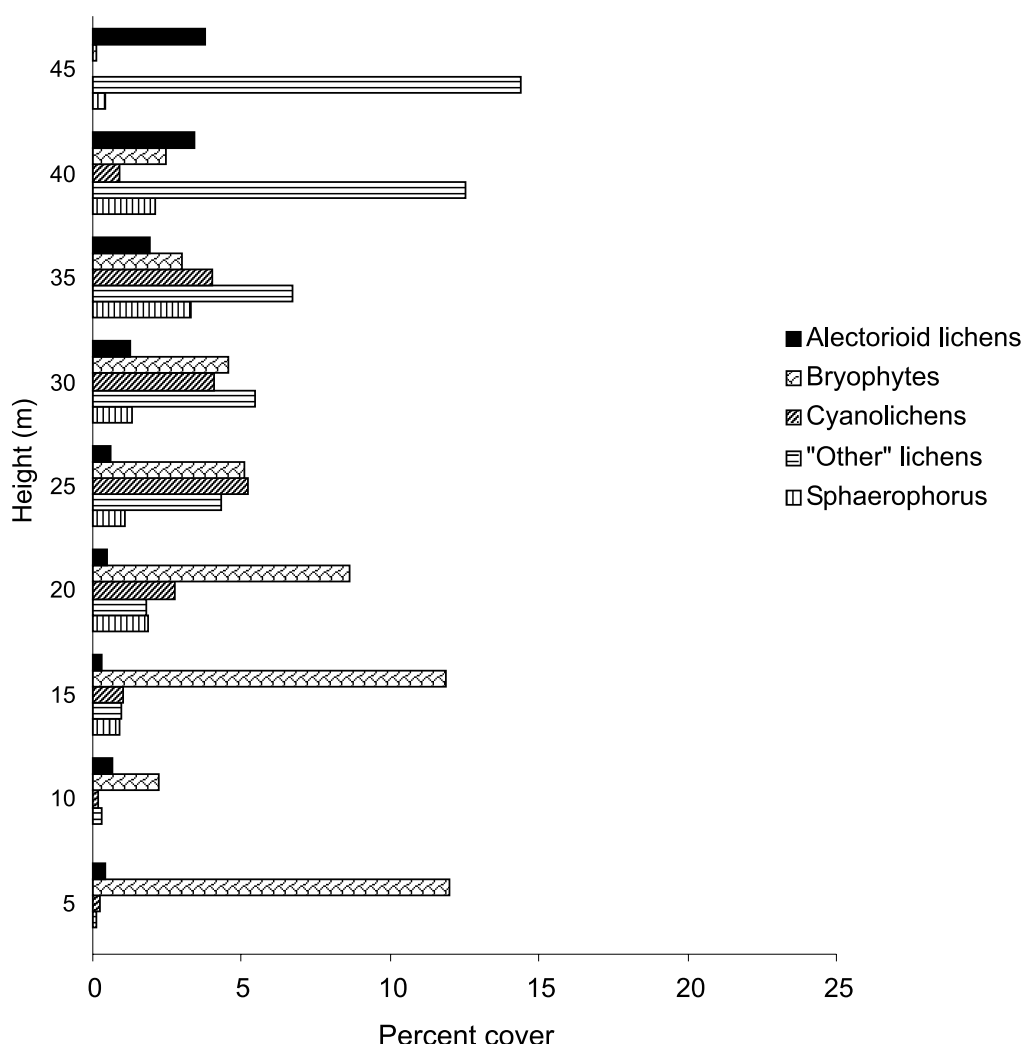
Within individual tree crowns among all height classes, epiphyte cover was greatest in the lower crown and smallest in the upper crown (Fig. 5). Within large trees, there was only a twofold increase in cover between the upper crown and the lower crown. In medium and small trees, there was a 4- and 17-fold increase in cover between upper and lower crown zones, respectively. The within-tree vertical distribution of epiphyte communities varied with height class (Fig. 5). “Other” lichens generally dominated the upper crowns of large and medium trees. Alectorioids were the most abundant functional group in the upper crowns of small trees. Bryophytes dominated the lower crowns of all trees. The abundance of cyanolichens, “other” lichens, and *Sphaerophorus* in lower tree crowns increased proportionally with height classes. Alectorioids were sparse in the lower crowns of all trees. The middle crown zone of each height class displayed the most even combination of epiphyte functional groups. Within the middle crowns of small trees, bryophytes comprised the bulk of the epiphyte cover, but in medium and large trees, “other” lichens, cyanolichens, and *Sphaerophorus* were proportionally more abundant.

Branch level

Epiphyte cover was differentially distributed along branches, with inner plots having the greatest cover and outer plots having the least (Fig. 6). Epiphytes were present in 83, 81, and 67% of inner, middle, and outer plots, respectively. There was a strong compositional gradient along branches, with significant differences in the abundance of epiphyte functional groups between plot positions ($p < 0.001$). The inner plots had the greatest abundance and diversity of epiphyte functional groups. Outer plots had the lowest abundance of epiphytes and were the least diverse. Although the cover of each functional group decreased with distance from the tree trunk, the proportional dominance of each functional group varied with position along the branch. Moving away from the trunk, the proportion of bryophytes and *Sphaerophorus* decreased, while the proportion of alectorioid and “other” lichens increased. The proportion of cyanolichens was greatest in the middle plot positions. These patterns were consistent for all three height classes.

The height classes appeared to vary in the rate at which new branch material was colonized. Among small trees, there was an 18-fold difference in total cover between inner

Fig. 3. Vertical distribution of epiphyte functional groups. Epiphyte functional groups include alectorioid lichens, bryophytes, cyanolichens, "other" lichens, and *Sphaerophorus globosus*.



and outer plots, but among large trees, this difference was only 7-fold. There was also a 15-fold difference in cover between upper and lower crown branches of small trees, while the difference in cover between upper and lower crown branches of large trees was less than 2-fold.

Structural differences between height classes

The height classes differed in basic structural characteristics including dbh, age, total number of branches, and branch density (Table 3). Tree height, dbh, and total number of branches increased with height class. Tree size was an unreliable indicator of tree age. The ANOVA revealed significant differences in age among the height classes ($p < 0.01$), but a post-hoc Tukey test indicated these differences were only significant between large and small trees ($p < 0.05$).

Crown structure and epiphyte abundance

At the tree level, total epiphyte abundance was positively correlated with tree height and age, and it was negatively correlated with branch density (Table 4). Abundance of all epiphyte functional groups except bryophytes was positively correlated with tree height and tree age. Abundance of

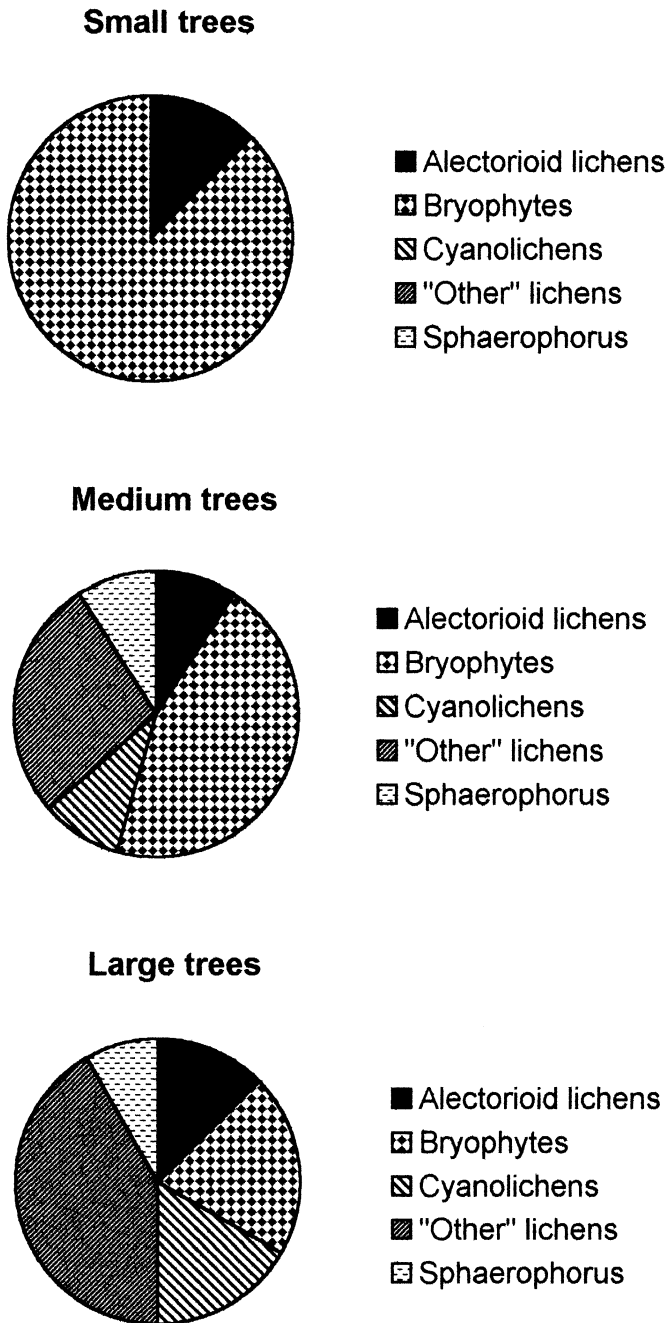
alectorioid lichens and "other" lichens was highly correlated with tree height.

At the branch level, total epiphyte cover was highly correlated with branch diameter and length, and weakly correlated with branch height (Table 5). There was a positive correlation between the abundance of all functional groups and branch variables, with the exception of bryophytes. Bryophytes were negatively correlated with branch height. Abundance of "other" lichens was strongly correlated with branch variables, but abundance of the remaining functional groups was only moderately or weakly correlated with branch diameter and height.

Discussion

Previous studies in the Pacific Northwest have investigated epiphyte distribution and abundance on conifer trees, but none has focused on canopy epiphytes of western hemlock, the species with the greatest crown volume in many old-growth forests. Limitations of previous research include small sample size, access difficulties, and restriction of sampling to a small portion of the tree. Significant within-tree vertical and horizontal gradients in epiphyte abundance and

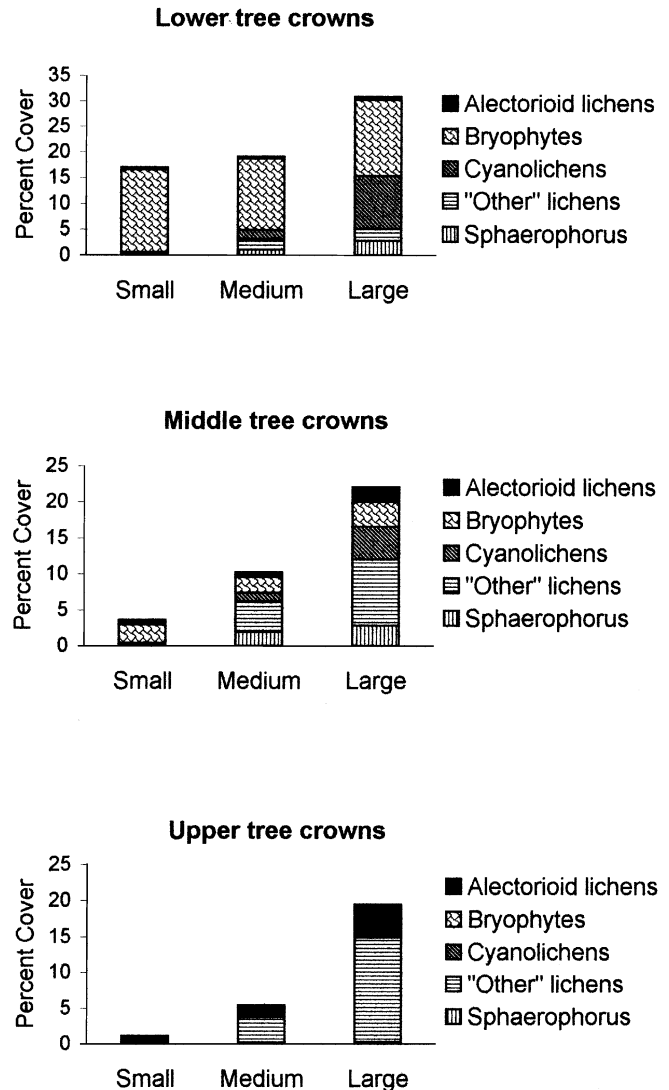
Fig. 4. Proportional abundance of epiphyte functional groups by height class: small (1–12 m), medium (12–37 m), and large (>37 m).



community composition were documented by a few studies with more extensive samples (Pike et al. 1977; Clement 1995). The canopy crane that we used afforded a much larger sample size of plots and trees than would have been possible with ground-based sampling or tree climbing techniques.

One limitation in this study is that specific environmental variables were not directly measured. Rather, sampling was structured around changes in light levels related to canopy structure (Parker 1997). With increasing height in the canopy, humidity declines, temperature and temperature extremes increase, throughfall increases, wetting and drying

Fig. 5. Proportional abundance of epiphytes per crown zone by height class: small (1–12 m), medium (12–37 m), and large (>37 m).

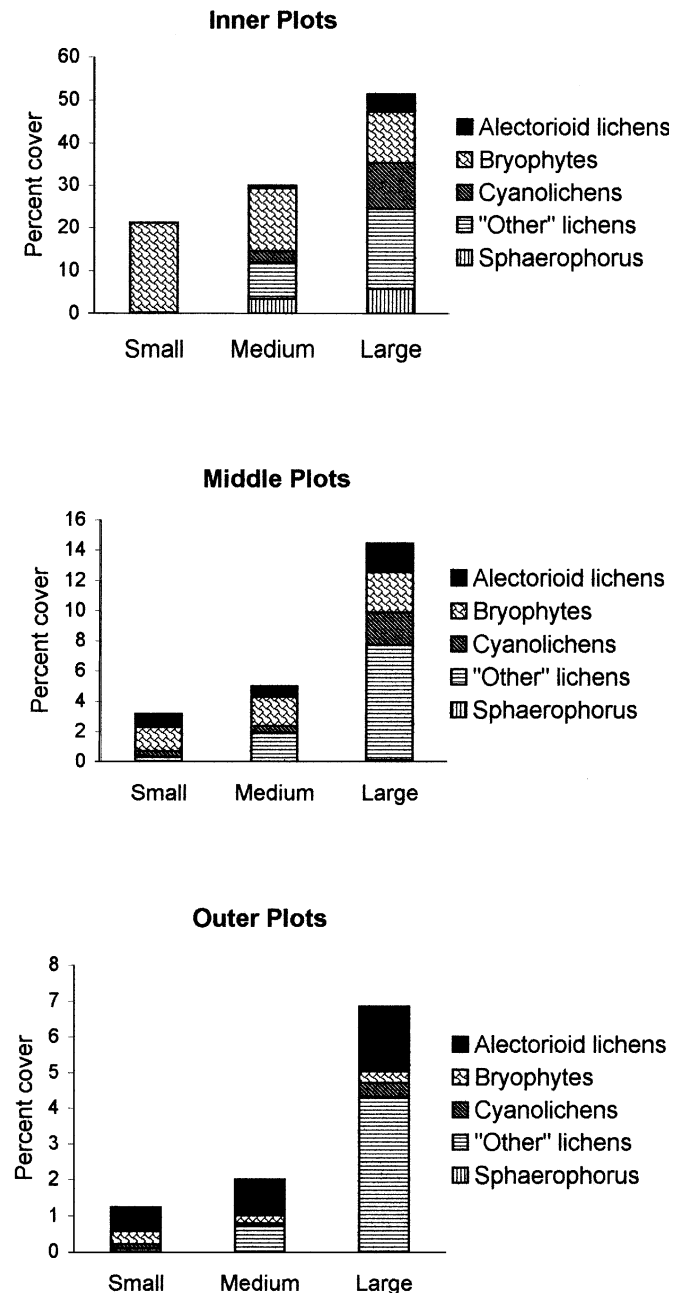


cycles become more rapid, and light increases. Accompanying this complex of environmental gradients is a mosaic of substrate types and ages upon which epiphytes are distributed. Areas closer to the tree trunk or ground probably experience a more moderate microclimate than substrates in the crown exterior. A second limitation of this study is that percent cover, rather than biomass, was used to quantify epiphyte abundance, which may have resulted in an underestimation of pendulous lichen species. However, previous studies have shown a strong relationship between epiphyte percent cover and biomass even for pendulous lichens (McCune 1990). Another limitation is that only trees growing in the more open regions of the canopy were sampled due to the need for access from the crane gondola. Therefore, data may not be representative of the stand as a whole.

Epiphyte abundance

In this forest, epiphyte cover was greatest in the upper canopy stratum, and plot height accounted for much of the variation in cover at the stand level. In contrast, epiphyte

Fig. 6. Proportional abundance of epiphyte functional groups by plot position and height class: small (1–12 m), medium (12–37 m), and large (>37 m).



biomass measured in Douglas-fir trees of Pacific Northwest forests, in old growth and younger managed stands, was greatest in the mid-canopy and lowest in the lower canopy (Pike et al. 1977; McCune 1993). Although epiphyte cover in this study was highest in the upper canopy, the total biomass is probably greatest in the mid-canopy where large branches are more abundant.

Epiphyte cover was significantly different among trees in each of the height classes even though many of the trees were similar in age. Although older trees might be expected to have a greater abundance of epiphytes than younger trees because their substrates are available for colonization for a

Table 3. Comparison of tree structural characteristics among height classes.

	Small	Medium	Large
Dbh			
Mean	10.5	35.6	76.6
SE	1.01	3.66	4.42
Range	7.2–16.0	20.2–56.1	50.6–93.5
Tree height			
Mean	6.9	26.2	47.3
SE	0.84	1.35	1.57
Range	4.07–11.72	17.6–30.4	37.56–51.64
Tree age			
Mean	120a	147ab	180b
SE	9.25	11.8	15.58
Range	71–177	84–207	107–229
No. of branches			
Mean	49.0	173.0	203.0
SE	9.19	11.93	18.76
Range	18–108	133–221	134–282
Branch density			
Mean	13.2	12.8	7.7
SE	1.00	1.85	0.72
Range	10.53–21.3	7.78–21.5	5.63–10.74

Note: The mean, standard error, and range are given for each combination of height class and structural variable. Structural variables include dbh (cm), tree height (m), tree age (years), the total number of branches, and branch density (branches/m). An ANOVA followed by a post-hoc Tukey test was used to examine differences in age between height classes. Significant differences between height classes ($p < 0.01$) are indicated with letters.

Table 4. Correlation matrix ($n = 30$) for tree structural variables and epiphyte functional groups.

Epiphyte functional group	Pearson's correlation coefficients		
	Tree height	Tree age	Branch density
Alectorioid	0.651**	0.497*	–0.337
Bryophyte	–0.397	–0.107	0.042
Cyanolichen	0.497**	0.205	–0.195
"Other" lichens	0.888**	0.495**	–0.337
<i>Sphaerophorus</i>	0.575**	0.448	–0.525*
Total	0.721**	0.475*	–0.380*

*The correlation is significant at the $p < 0.05$ level.

**The correlation is significant at the $p < 0.01$ level.

longer period of time, this was not the case in our study. Tree size was a better predictor of epiphyte cover than tree age, as changes in epiphyte abundance corresponded with differences in the relative position and height of a plot, regardless of tree age.

Within-tree variability in epiphyte abundance was associated with relative position (lower, middle, or upper crown) and branch size (diameter and length). The lower crown branches of all trees, which are the oldest and often the largest, had consistently higher cover than those in the corresponding middle and upper crown regions. This concurs with other epiphyte studies in the Pacific Northwest and elsewhere (Ingram and Nadkarni 1993; Hilmo 1994; Clement 1995; Esseen et al. 1996). Branch size, particularly

diameter, was an important predictor of total epiphyte abundance. Large branches, like large trees, may have more epiphytes because of increased ability to intercept propagules, nutrients, and moisture.

Within branches, plot position was the single most important determinant of epiphyte abundance. Plots closer to the trunk had higher cover than those farther out on the branch. The trend of decreasing cover toward the branch exterior detected in this study differed from a study of Douglas-fir trees at a riparian site adjacent to the WRCCRF in which epiphyte biomass was greater in the foliage than on the inner bare branch (Clement 1995). This discrepancy may have resulted from differences between host trees (host specificity and structural characteristics), habitat characteristics (riparian versus forest interior), or sampling strategy (cover versus biomass). Because the outer crowns of trees in riparian areas experience higher humidity and light levels, they may have a greater abundance of epiphytes than the outer crowns of trees in drier, non-riparian forests.

Community composition

The distribution of alectorioids at the stand and tree level in this and other studies suggests a relationship with plot exposure and substrate age (Stone 1989; Hilmo 1994; Clement 1995). In this study, alectorioids were proportionally more abundant in the upper tree crowns and outer branch regions of all sampled trees, but they were abundant in absolute terms only in the upper tree crowns of large trees. Other studies that relied on biomass estimates reported more alectorioids in the epiphyte community than reported here (Clement 1995; McCune et al. 1997). Possible explanations for this are that alectorioids are more abundant in large Douglas-fir tree crowns than in western hemlock or that alectorioid lichens were underestimated in this study by the use of percent cover rather than biomass.

The high cover of bryophytes within the lower forest canopy and on small trees suggests that plot height has a strong influence on bryophyte abundance at the stand level, probably because of the relationship between canopy height and humidity. However, bryophytes were found on large trees in plots as high as 40 m above the forest floor. The dense, drooping foliage of large western hemlock crowns may create an internal microclimate similar to that in the lower canopy where bryophytes are most abundant.

In this and previous studies, cyanolichens were most abundant in the mid-canopy stratum and on limbs of large trees (Lesica et al. 1991; Sillett 1995; Sillett and Neitlich 1996). Cyanolichens were nearly absent from small understory trees in this study. The frequency and rapidity of wetting and drying are important for the growth of cyanolichens (Shirazi et al. 1996) so the lack of environmental variability within the lower canopy may contribute to the low abundance of cyanolichens observed there. Field experiments using transplanted thalli of two old-growth associated cyanolichens (*Lobaria oregana* and *Pseudocyphellaria rainierensis*) demonstrated that cyanolichens can grow as well in young forest as in older forests (Sillett and McCune 1998), suggesting that forest microclimate may not be as important for cyanolichen growth as previously thought. However, the transplanted thalli in the old-growth forest were placed in the upper crowns of large trees (approximately 50 m), so no

Table 5. Correlation matrix for epiphyte abundance with branch structural variables (length, diameter, and height).

Epiphyte functional group	Spearman correlation coefficients		
	Branch length (<i>n</i> = 958)	Branch diameter (<i>n</i> = 953)	Branch height (<i>n</i> = 958)
Alectorioid	0.2**	0.26**	0.53**
Bryophyte	0.3**	0.25**	−0.42**
Cyanolichen	0.39**	0.37**	0.04
“Other” lichens	0.61**	0.65**	0.77**
<i>Sphaerophorus</i>	0.52**	0.52**	0.28**
Total Cover	0.7**	0.72**	0.34**

Note: Sample size for this analysis is less than the number of sampled branches (961) owing to missing branch data.

**The correlation is significant at the $p < 0.01$ level (2-tailed).

conclusions could be made about the effect of microclimate or canopy position on cyanolichen abundance within the lower canopy or understory of an old-growth forest.

The peak cyanolichen cover in this study (27–33 m) was higher than that recorded for all species of trees at the same site (McCune et al. 1997). Cyanolichens may peak higher in the crowns of shade-tolerant western hemlock trees than in other tree species because the dense foliage characteristic of shade tolerant western hemlock may limit light lower in the tree crowns. Within both the middle and lower strata, cyanolichens were more abundant on branches from large trees than on branches from medium trees even though these trees were not significantly different in age. This pattern could be the result of differences in substrate characteristics (e.g., branch size, age, bark roughness). However, a recent study on the dispersal of cyanolichens found that bark roughness did not significantly affect colonization or establishment rates of cyanolichens (Sillett et al. 1999), and cyanolichens were only weakly correlated with branch size in this study.

Tree height class was a good indicator of “other” lichen abundance at the stand level. The abrupt change in frequency of “other” lichens between small trees (10%) and medium and large trees (31 and 59%, respectively), which corresponds to a shift out of the low light zone, implies low light may affect “other” lichen abundance. In this study, “other” lichens comprised a greater proportion of the total lichen cover and peaked in abundance at a greater height in the canopy (54 m) than reported by McCune et al. (1997) (30–45 m) at the same site. The differences in peak height of “other” lichens may be a result of differences in the methods of estimating percent cover. In this study, quadrat frames were placed horizontally on individual branches, while McCune et al. (1997) held up quadrat frames vertically and estimated percent cover by peering through the quadrat like a window. The “window” method may have underestimated the cover of “other” lichens, which grow close to the branch surface and are often obscured by the foliage in the upper crowns of large western hemlock trees.

Canopy structure and epiphyte diversity

Relative position and branch size were important determinants of total epiphyte cover within individual tree crowns, but height in the canopy was a more important factor in determining the vertical distribution and abundance of specific epiphyte functional groups. Individual structure vari-

ables only partially explained the variability in epiphyte cover. A possible explanation for the low correlation among individual structural elements and epiphyte abundance is that structural and positional variables do not directly influence epiphytes but rather serve as partial surrogates for other environmental variables that directly influence epiphyte abundance such as temperature, light, and humidity (Parker 1995).

Stand age has been shown to be a major positive influence on epiphyte abundance and diversity (Lesica et al. 1991; McCune 1993; Neitlich 1993; Esseen et al. 1996). Possible reasons cited for the decreased abundance in young stands include dispersal limitations, unsuitable substrates, and unsuitable canopy microclimate (Sillett and Neitlich 1996). In contrast, a recent study of epiphyte abundance in the Gifford Pinchot National Forest found forest age to be less important than structure in explaining patterns of epiphyte abundance (Pipp 1998).

In this study, tree size was a more important factor than tree age for predicting epiphyte abundance. Tree age was only weakly correlated with epiphyte abundance (Table 3) so increased exposure time alone does not ensure a more abundant or diverse epiphyte community. As stands age and trees grow, the heterogeneity of substrates and microclimate increases creating more specialized niches and microhabitats for species inhabiting the forest canopy. Our results also suggest new branch segments of small trees and outer branch plots are colonized more slowly than new branch segments on large trees and areas closer to the tree trunk.

Epiphyte succession

Initially, height classes were intended to represent age classes and used to examine succession of epiphytes on trees of increasing age, but the weak relationship between tree age and height precluded use of the height classes as a chronosequence of age. Instead, height classes were used to represent a chronosequence of environmental extremes. The study trees ranged in age from 71 to 229 years, while the stand is estimated to be nearly 500 years old. Therefore, all of these trees must have originated in the understory. Some trees were able to grow out of the more humid, low light zone and into the drier, brighter upper canopy, while other trees remained suppressed in the understory.

The distribution of epiphytes found in this study suggests that the sequence of epiphyte colonization within individual trees and branches does not consistently follow the sequence of colonization observed in a series of stand ages. Comparative analyses of epiphyte communities in multiple stand age classes has shown that trees growing in the exposed conditions of a young stand are initially colonized by "other" lichens, followed by alectorioid lichens. As stand age increases and canopy closure occurs, bryophytes and cyanolichens begin to colonize new growth in the upper and outer canopy (Lesica et al. 1991; McCune 1993; Sillett and Neitlich 1996). However, epiphyte succession on trees originating in the understory of this old-growth forest seems to follow a different pattern. Small understory trees were colonized first and almost exclusively by bryophytes and were nearly devoid of "other" lichens, the primary colonists of young trees in young stands. Alectorioid lichens, while proportionally abundant in the upper crown and outer branch

plots of small trees, were sparse in terms of total cover (0.8 and 0.7%, respectively). With the exception of these tiny fragments of alectorioid lichens, the outer plots of small trees were not colonized.

Although epiphyte succession was not observed directly, information on the distribution of epiphytes from this study can be used to pose hypotheses on within-stand patterns of epiphyte succession. Since all study trees originated in the understory, the vertical distribution of epiphytes on the medium and large trees reflect the probable sequence of epiphyte colonization that will occur as understory trees grow and move progressively upward in the canopy of an old-growth forest. We hypothesize that as understory trees in old-growth forests grow out of the low-light zone into the mid-upper canopy, those species more common on medium and large trees, alectorioid and "other" lichens, will increase in abundance. In this forest, abundance of these functional groups increased with height in the canopy. Epiphyte communities on small trees that remain suppressed in the understory, are unlikely to have such a shift. New growth in the relatively younger, upper and outer canopy of medium and large trees was colonized primarily by chlorolichens (lichens with green algal symbionts including alectorioids and "other" lichens). Cyanolichens and *Sphaerophorus*, which are generally considered late colonists in the sequence of stand development, also appear to be later colonists of trees originating in the understory. Cyanolichens and *Sphaerophorus* were found on the relatively older lower branches and inner branch regions.

Suggestions for future work include (i) direct comparisons of epiphyte abundance in trees of known ages in young versus old stands, (ii) examination of epiphyte abundance and community composition on branches of known age in different regions of the canopy, (iii) coupled measurements of canopy microclimate and epiphyte abundance, and (iv) experiments that involve placing transplants in different positions within a single forest and measuring their growth and mortality. These types of studies could provide needed information on the interactions between stand or tree age, canopy position, and microclimate and their effects on epiphyte abundance and distribution.

Summary

Epiphytes of western hemlock in this old-growth forest stand are differentially distributed across substrate types. They vary with height class, absolute position within the canopy, and relative position within individual trees and branches. The structural variables most important for predicting epiphyte abundance are tree height, branch diameter, and plot position. Models of epiphyte succession based on chronosequences of stand ages are useful to gauge differences among stands and explain broad patterns in epiphyte distribution, but they may not explain variability at finer spatial scales, particularly within stands with multiple age and size classes of trees. Shade tolerant species such as western hemlock, which grow in the understory, may have a different sequence of epiphyte colonization than reported for Douglas-fir. The succession of epiphyte functional groups on western hemlock trees appears to depend less on tree age than on tree size and relative canopy position. Small un-

derstory trees in this old-growth forest are colonized first by bryophytes, not by alectoroid and "other" lichens, which are the primarily colonists of trees in young stands.

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