

Crown structure and the distribution of epiphyte functional group biomass in old-growth *Pseudotsuga menziesii* trees¹

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Abstract: Epiphyte functional groups (alectorioid lichens, cyanolichens, other lichens, and bryophytes) were sampled in nine old-growth, canopy-emergent, *Pseudotsuga menziesii* trees along a riparian corridor in the Wind River Experimental Forest, Washington State, U.S.A., with the objective of determining epiphyte abundance and its relationship to crown structure. An additional objective was to develop a sampling design that reasonably captured the variation in epiphyte distribution so that total biomass could be estimated for an individual large tree, a design efficient enough to make description economically and logistically possible. Trees ranged in height from 51 to 66 meters and averaged 83 live and 79 dead limbs in a crown length of 40 meters. Diameter at breast height was a useful estimator of tree crown structural complexity. Epiphytes averaged 27.1 kg/tree, with alectorioid lichens (19.3 kg/tree) dominating the assemblages, followed by other lichens (3.3 kg/tree), bryophytes (2.6 kg/tree) and cyanolichens (1.9 kg/tree). The foliage region had the highest biomass of lichens (16.4 kg/tree), followed by the branches (8 kg/tree) and trunk (2.6 kg/tree). Alectorioid lichens predominated in the upper, middle and outer portions of the tree crown, whereas the lower and inner portion of the tree crowns had more equal distributions of all four functional groups. Relative height and limb size were the most significant structural attributes influencing epiphyte distribution. Limb size had a particularly strong effect on the distribution of bryophytes regardless of height. In old, canopy-emergent *P. menziesii*, the crown structural variables which determine epiphyte distribution and abundance are height, crown length, trunk surface area and exposure, distribution and abundance of small, medium and large branches, and distribution and exposure of foliated branches.

Keywords: epiphytes, biomass, lichens, bryophytes, crown structure, *Pseudotsuga menziesii*.

Résumé: Les groupes fonctionnels d'épiphytes (lichens alectorioides, cyanolichens, les autres lichens et les bryophytes) furent échantillonnées chez neuf arbres vétérans et dominants de *Pseudotsuga menziesii* le long d'un corridor riverain dans la forêt expérimentale de Wind River, dans l'état de Washington, É.U., dans le but d'en déterminer l'abondance des épiphytes en fonction de la structure des cimes. Un objectif additionnel fut de développer une stratégie d'échantillonnage qui reflète adéquatement la variation dans la distribution des épiphytes de sorte que la biomasse puisse être estimée chez un gros arbre, sans que cela ne devienne prohibitif aux plans économique et logistique. La hauteur des arbres se situait entre 51 et 66 m qui comptaient en moyenne 83 grosses branches vivantes et 79 mortes sur une longueur de cime de 40 m. Le diamètre à hauteur de poitrine s'est avéré un bon estimateur de la complexité structurale de la cime. Il y avait en moyenne 27,1 kg d'épiphyte par arbre ; les lichens alectorioides dominaient les assemblages (19,3 kg/arbre), suivis par les autres lichens (3,3 kg/arbre), les bryophytes (2,6 kg/arbre) et les cyanolichens (1,9 kg/arbre). Les parties feuillues des arbres supportaient la plus forte biomasse de lichens (16,4 kg/arbre), suivi des branches (8 kg/arbre) et du tronc (2,6 kg/arbre). Les lichens alectorioides dominaient dans les portions supérieure, intermédiaire et extérieure de la cime des arbres, tandis que les portions inférieure et intérieure de la cime des arbres présentaient une distribution plus uniforme de chacun des quatre groupes fonctionnels. La hauteur relative et la taille des grosses branches se sont avérées les attributs structuraux qui influençaient le plus la distribution des épiphytes. La taille des grosses branches a un effet particulièrement net sur la distribution des épiphytes quelque soit la hauteur. Chez les arbres vétérans et dominants de *Pseudotsuga menziesii*, les variables structurales de la cime qui déterminent la distribution et l'abondance des épiphytes sont la hauteur, la longueur de la cime, la surface terrière du tronc et son exposition, la distribution et l'abondance des branches de petite, moyenne et forte taille, ainsi que la distribution et l'exposition des branches feuillues.

Mots-clés: épiphytes, biomasse, lichens, bryophytes, structure de cime, *Pseudotsuga menziesii*.

Introduction

Epiphytes are important components of forest ecosystems where they influence forest hydrology and nutrient cycling, contribute N through nitrogen fixation, and provide wildlife food resources and habitat for vertebrates and invertebrates (Benzing, 1995; Rhoades, 1995). In the Pacific Northwest of North America, epiphytes (primarily

lichens and bryophytes) are conspicuous and abundant, exceeding 2.5 metric tons/ha dry weight in some old-growth *Pseudotsuga menziesii* (Mirbel) Franco. (Douglas-fir) dominated stands (McCune, 1993a), and fixing as much as 3-5 kg/ha/yr of nitrogen (Pike, 1978; Franklin *et al.*, 1981).

Research into epiphytic lichens and bryophytes has typically been restricted to specialists due to the difficulty of identifying species. Recently, however, McCune (1993a) proposed the use of epiphyte functional groups to help

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researchers interpret patterns of epiphyte distribution and to simplify communication with non-specialists.

McCune (1993a) divided *P. menziesii* forest macro-epiphytes (non-crustose forms) into four functional groups: cyanolichens, alectorioid lichens, "other lichens" (mainly green-algal foliose lichens), and bryophytes. Certain ecological, functional roles are shared by members of a group. A species' role in nutrient cycling, its role as forage for vertebrates, its growth form, the microhabitat it occupies, and its response to air pollutants define the group it falls into (McCune, 1993a; McCune *et al.*, 1997).

i) Cyanolichens contain a cyanobacterium as the primary photobiont, or in cephalodia. They are sensitive to air pollution, can fix nitrogen, have a foliose thallus, and are indicators of long ecological continuity (Rose, 1992; McCune, 1993a). Cyanolichens are negatively affected by high light exposure (Demmig-Adams *et al.*, 1990; Gauslaa & Solhaug, 1996) and in thalli with cyanobacteria as the primary photobiont they are physiologically activated by water, not by humid air (Lange, Kilian & Ziegler, 1986).

ii) Alectorioid lichens are fruticose lichens with a pendulous growth form that contains only green algae. They are sensitive to air pollution and are an important food source for flying squirrels, deer, and mountain caribou. Several of these species are intermediate in their tolerance to light (Gauslaa & Solhaug, 1996), and can be physiologically activated by humid air (Lange, Kilian & Ziegler, 1986).

iii) "Other lichens" contain green-algae as the photobiont, and are mainly foliose lichens, though several non-pendulous, fruticose forms are included. They do not fix nitrogen and their relationships to wildlife and pollution are not uniform. Many species can tolerate high light intensities (Demmig-Adams *et al.*, 1990; Gauslaa & Solhaug, 1996) and are physiologically activated by humid air (Lange, Kilian & Ziegler, 1986).

iv) Bryophytes are mosses and liverworts. Members of this large group are strongly influenced by water availability, humidity, and exposure, particularly in terms of vertical occurrence in a canopy (Burgaz, Fuentes & Escudero, 1994; Peck, Hong & McCune, 1995; Mazimpaka & Lara, 1995).

Factors controlling the distribution of epiphytes in the Pacific Northwest of North America are logically organized in McCune's (1993a) Similar Gradient Hypothesis, which states that three dominant gradients affect epiphytic communities: *i*) time (succession, stand age), *ii*) vertical forest stand factors (canopy structure, microclimate), and *iii*) climatic moisture gradients across the landscape. Within *P. menziesii* forests, stand age has a profound influence on epiphyte development; other lichens tend to dominate young stands, alectorioids move in after 100 years or so, and cyanolichens and bryophytes follow after about 200 years. These four groups are vertically organized in older forests, with other lichens dominating the most exposed conditions of the upper canopy, alectorioids occurring with other lichens in the middle to upper canopy, cyanolichens dominating the middle to lower canopy, and mosses dominating the lower canopy. The regional climatic regime influences the abundance and relative height zone each functional group will occupy for a stand of a given age. The wetter the

forest, the sooner it will be colonized by cyanolichens and bryophytes, and the higher up into the canopy they will eventually occur (Peck, Hong & McCune, 1995). On a local scale, bryophytes and cyanolichens are best developed near riparian areas (Sillett & Neitlich, 1996).

The distribution of epiphytes within an individual tree crown is controlled by a number of factors (Barkman, 1958). Within *P. menziesii*, Sillett (1995) sampled the branches (limbs > 7 cm diameter, excluding branchlets) which constituted the "inner crown" of four 700-year-old trees in Oregon. Two trees were located on a clearcut edge and two within a forest. The dominant gradient affecting species occurrence was height, but there was an additional factor associated with exposure, *i.e.*, the most exposed sites were dominated by high lichen cover and low bryophyte cover, and the most sheltered sites were dominated by bryophytes. McCune (1993a) and McCune *et al.* (1997) have also described the vertical gradient within tree crowns. Pike, Rydell & Denison (1977) described the importance of branchlets (systems of twigs together with attached needles) as a structural feature, with more than 50% of the epiphytic biomass occurring on them.

The problems and techniques associated with sampling epiphytic lichen biomass have been reviewed by Boucher & Stone (1992). A general approach has emerged, based on Pike, Rydell & Denison (1977), that first describes and measures the structural attributes of a tree and then subsamples these structures. Total tree epiphyte biomass is then estimated by scaling up from known sample areas using ratio estimators. There have been very few studies that have quantified epiphytic lichen and moss biomass due to the large logistical problems, particularly in tall stature forests of the Pacific Northwest. Pike, Rydell & Denison (1977), using tree climbing techniques, and McCune (1993a), using felled trees, estimated that individual old-growth *P. menziesii* tree crowns have from 1.7 kg to 17.8 kg of epiphytes.

Current forest management within the Pacific Northwest will require more estimates of stand- and tree-level epiphytic biomass if forest manipulations designed to maintain or enhance epiphyte ecological functioning are to be monitored (Rosentreter, 1995). Developing a sampling technique that is both feasible and suitable for describing epiphyte biomass is challenging, but possible (Van Daele & Johnson, 1983).

The purpose of this research was: *i*) to develop a sampling design for estimating epiphyte biomass within the entire tree, a method that would also be feasible as a field technique applied to sampling many forests and trees, and *ii*) to determine if structural features of a tree control the distribution of epiphyte functional groups. Our null hypothesis was that tree structure does not influence epiphyte functional group distribution except for the known vertical organization of epiphytes.

It is important to know whether structural features of a tree crown influence the organization of biodiversity, because it is precisely forest and tree structures which can be preserved in forest management (Kolm & Franklin, 1997). Structural features of tree crowns can then be used to help in the preservation of biodiversity in the managed land-

scape. We chose to sample old-growth (450 year +) canopy-emergent, riparian *P. menziesii* trees because they have long crowns and complex structure, and because the lack of shading by other trees would minimize the confounding effect of stand structure on the epiphyte communities.

Material and methods

STUDY SITE

This study took place in the 4380 ha Wind River Experimental Forest in southern Washington State, U.S.A. (45° 49' N, 121° 58' W). The average annual temperature is 8.7°C with a July mean of 17.5°C and a January mean of 0°C. The average annual precipitation is 250 cm and is seasonal with summer having a low rainfall (Franklin, 1972). Nine large *P. menziesii* trees were sampled in an old-growth riparian stand along a 1.5 km reach of Trout Creek. The stand (elevation 350 m) is approximately 450-500 years in age (Franklin & DeBell, 1988). Dominant tree species are *P. menziesii*, *Tsuga heterophylla* (Raf.) Sarg. (western hemlock), and *Thuja plicata* Donn. (western red cedar). Other conifer species in the stand are *Abies amabilis* (Dougl.) Forbes (Pacific silver fir), *Abies grandis* (Dougl.) Forbes (grand fir), and *Pinus monticola* Dougl. (western white pine). Deciduous species in this riparian site include *Acer macrophyllum* Pursh (bigleaf maple), *Alnus rubra* Bong. (red alder), and *Populus trichocarpa* Torr. & Gray (black cottonwood).

TREE SELECTION AND CROWN ACCESS

Using Trout Creek as a "meandering transect", we selected nine canopy-dominant *P. menziesii* trees within 40 m of the creek. Trees were selected based upon the following criteria, in descending order of importance: safety, emergent status, and apparent structural complexity. Trees were deemed safe if they could be climbed without undue risk to the researchers (e.g., trees with excessive rot and "leaners" were avoided). Emergent individuals (large trees which are taller than the surrounding canopy) were selected to minimize the influence of the surrounding canopy upon microclimate and structural variability. Trees of different structural form were selected in order to encompass a wide range of structural variation.

Trees were accessed by using a crossbow to fire a line over a strong lower limb and hauling a climbing rope into place. The rope was climbed using ascenders developed for mountain climbing and rescue (Perry, 1978). Once into the crown, the remaining portion of the tree was climbed and the rope fastened at a safe location within 5 m of the top. Arborist rope techniques enabled extensive vertical and horizontal movement throughout the crown to make measurements and take samples. An aluminum hook-and-loop pole was used to bring outer branch tips within reach. These access techniques were non-destructive and provided access to virtually any part of the crown.

PRELIMINARY SAMPLING

Tree diameter at breast height (dbh) was measured and each limb was numbered, characterized by height and base diameter, and classified into one of three size classes: small

(3-10 cm), medium (10.1-20 cm), and large (> 20 cm). For each tree, ten percent of the living limbs from each size class and ten percent of all dead limbs were selected randomly for more intensive measurements.

The sampling protocol did not designate the irregular fan-shaped branch systems in the lower crown as distinct structural components. In these trees, the small limbs that comprised this phenomenon were separate units that were infrequently appressed to each other enough to provide a distinct structural habitat. To simplify the sampling protocol and maintain consistency in limb categories, these clusters of small limbs in the lower crown were considered a sum of their parts, and each limb was treated as a distinct unit. This is a departure from the protocol of previous studies (Pike, Rydell & Denison, 1977).

INTENSIVE SAMPLING

TRUNK

For each tree, the diameter of the trunk was measured at the highest safe point (generally within 2 m of the top) and at 10 m intervals to the ground. To assess trunk epiphytes, sample units (cylindrat), each one consisting of the cylindrical surface of a 0.5 section of trunk, were stripped of epiphytes at 10 m intervals along the trunk. The sampling was begun at a randomly selected point within the upper 10 m of trunk and repeated at 10 m intervals to the ground. Diameter and height at the center of each sample plot were recorded.

DEAD LIMBS

Length and the diameter at the terminal end were recorded for the subsampled dead limbs.

LIVE LIMBS

Azimuth and total length of limb were recorded. Stem and foliage of the branch system were sampled separately as follows:

The length of the primary stem (unbranched main axis of the branch system) was measured. For each meter of length, one 10 cm cylindrat was stripped of lichens and mosses. The plot was located at the mid-point of each meter measured from the bole. Diameter, slope (using a clinometer), and percent cover of epiphytes were recorded for each sample plot.

"Foliage units", i.e., units of foliated branch tips 0.75 m long and 1-2 cm diameter at base (equivalent to branchlets of Pike, Rydell & Denison, 1977), were counted for each subsampled limb system. Ten percent or a minimum of three were selected from different areas of the branch system and either removed and stripped of all lichens and mosses or were sampled in place. Foliage volume was also estimated by measuring length, width, and approximate depth of the foliated portion of the limb.

All samples taken from the trees were collected in separate paper bags and transported to the lab for sorting. Once in the lab, the biomass samples were cleaned of all non-epiphytic matter and sorted into four functional groups; cyanolichens, alectorioid lichens, other lichens, and bryophytes. Each sorted sample was oven-dried (60° C for 24 hours) and weighed to the nearest 0.001 g.

DATA ANALYSES

STRUCTURE

Frequency distributions and descriptive statistics were used to reveal trends in the structural data. Foliage volume was calculated using field measurements, as was dead limb volume, which was based on the volume of the frustum of a right cone:

$$V = 1/3\pi h(R^2 + r^2 + Rr) \quad [1]$$

Where h represents height, R is radius of the base and r the radius of the upper base. Depth of crown for each tree was calculated as the height of the tree minus the height of the lowest live limb. This distance was divided into three equal segments to provide the categorical variable "height zone", *i.e.*, the designation of upper, middle, or lower crown for each tree. A correlation matrix for individual tree parameters was generated by SPSS PC+ (Norusis, 1991). This matrix included tree height, dbh, number of large limbs, crown depth, density of live limbs, total limb density, diameter of largest limb, and mean diameter of live limbs as variables. The categories were the number of small limbs, medium limbs, and large limbs per tree.

The surface area for each trunk and limb sample unit was calculated as for a cylinder. The surface area for the foliage sample units was later estimated from the mean surface area for a subsample of 35 foliage units selected from one of the study trees. The surface area of the main stem of each unit was measured as the surface area for the frustum of a right cone (one half the sum of the perimeters of the two bases times the slant height). Smaller twigs were measured as cones using the base diameter of the twig. Needle surface area was not calculated.

Total surface areas for the three substrate types were extrapolated to determine the distribution of available substrate among trunk, limbs, and foliage twigs. The total trunk surface area per tree was calculated as the surface area for the frustum of a right cone. Surface area for each sampled limb was determined as the sum of a series of stacked cylinders of known diameter. This factor was multiplied by 10 (10% of limbs had been sampled) to provide total limb surface area per tree. The calculated surface area for each foliage unit was multiplied by ten times the number of units in the branch system (10% of systems had been sampled) to obtain total foliage twig surface area.

To visualize the comparative structural properties of the study trees, graphic representations of each tree were created using Quattro Pro (Quattro Pro, 1993). Representations of small, medium, and large limbs were drawn and placed on trunks according to field measurements. The relative volume of the different limb sizes could not be maintained due to the two-dimensional nature of the image, *e.g.*, large limb systems represent far more volume relative to small and medium limbs than is apparent in these images. These representations were arranged according the Shannon-Weiner Diversity Index value for each tree to compare structural variability among the trees. The Shannon-Weiner Index (H') is based on the equation:

$$H' = -\sum p_i \ln p_i \quad [2]$$

where p_i is the proportion of individuals found in the i^{th} category (Magurran, 1988). The categories used were the number of small, medium, and large limbs per tree.

EPIPHYTES

We extrapolated the mean proportion of each functional group present in different zones of each tree and computed the total abundance and distribution of epiphytes. The trunk epiphyte biomass samples (taken from 5% of the total trunk surface area) were multiplied by 20; the foliage and limb biomass samples (taken from 10% of the area of 10% of the limbs) were each multiplied by 100. The biomass was estimated for each tree, and then mean biomass values were determined for an idealized tree with the proportional distribution of epiphytes among trunk, limbs, and foliage (standard deviations based on $n = 9$). The trunk and limb samples were lumped separately from foliage samples to provide "inner crown" *versus* "outer crown" comparisons.

For statistical analyses, it was necessary to standardize the biomass values per unit surface area. As with most heterogeneous community data, the standardized biomass values were not normally distributed. In order to transform the data closer to a normal distribution, the square-root transformation was used (McCune, 1993b).

To evaluate the importance of the height and limb diameter variables and investigate the interactions between them, a two-way analysis of variance procedure for each functional group was run using the SPSS PC+ two-way ANOVA procedure (Norusis, 1991). The dependent variables in the analysis of variance were the square-root transformed biomass values for each functional group. Trunk plots were excluded to avoid confusion in the use of the "limb diameter" variable. The independent variables were categorical representations of canopy height zone ("zone": upper, middle, and lower), limb diameter class ("size": small, medium, and large), and their interaction.

We discovered additional indications of the strength of limb size in the distribution of these epiphytes by plotting the square root-transformed epiphyte functional group biomass per limb (y axis) *versus* limb diameter (x axis).

Results

STRUCTURE

Average tree height for the nine sample trees was 59 m and average dbh was 166 cm (Table I). Crown depth (length) averaged 40 m with 83 live limbs and 79 dead limbs, averaging 4.1 limbs/m of crown. Dead limbs were common within the tree crown, but they accounted for only 0.4 m³/tree of wood volume or 4% of the total limb wood volume/tree (Table II). Small limbs were concentrated in the upper third of the tree, whereas medium and large limbs were well distributed throughout the crown (Figures 1 and 2).

Variation of individual limb foliage volume was great, ranging between 0.01 m³ to 44.0 m³. Large limbs accounted for 75% of the foliage volume and 50% of the limb surface area per crown (Table II).

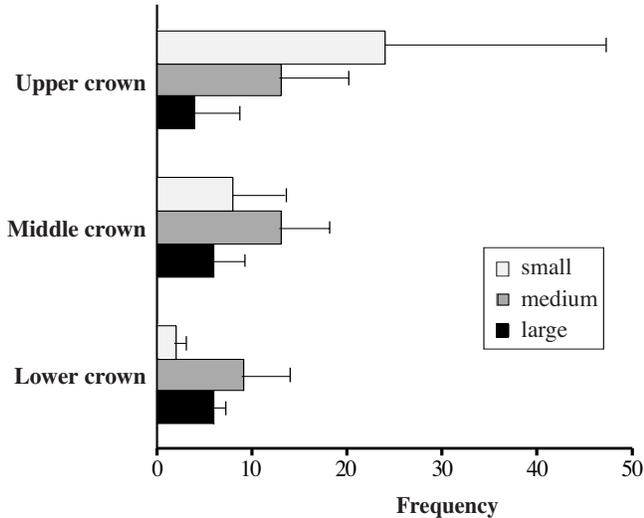


FIGURE 1. Distribution of branches in the lower third, middle third, and upper third of the tree crown. Bars indicate standard deviation.

The Shannon-Weiner Diversity Index, used to rank the trees according to structural diversity, provided a relative understanding of the range of diversity within the sample trees (Figure 2) and indicated the importance of large limbs. Diameter at breast height (dbh) is a good predictor of the size and abundance of large limbs and thus structural diver-

TABLE I. Structural variables for the nine sample trees

	Mean	SD	Min.	Max.
height (m)	59	4.8	51	66
dbh (cm)	166	20	137	204
crown depth (m)	40	7.3	23	51
# live limbs	83	32	36	131
# dead limbs	79	25	48	131
limbs per meter	4.1	0.8	2.6	5.3
largest limb diameter (cm)	39	13	23	61
foliage volume (m ³)	690	244	233	1145

sity in this case. This is shown by the correlation between dbh and number of large limbs ($r = 0.863, p = 0.003$); dbh and mean limb diameter ($r = 0.930, p = 0.000$); dbh and largest limb diameter ($r = 0.731, p = 0.025$); mean limb diameter and limb density ($r = -0.794, p = 0.011$).

EPIPHYTES

The alectorioid lichens were dominated by *Alectoria sarmentosa*, *Usnea filipendula* group (*sensu* McCune & Geiser, 1997), and included five *Bryoria* species. Cyanolichens were mostly *Lobaria oregana*, but included *Pseudocyphellaria anthraxis* and *Sticta fuliginosa*. Other lichens had the highest species diversity of all four groups, and were dominated by *Platismatia glauca* and *P. herrei*, *Hypogymnia*, especially *H. apinnata*, *H. enteromorpha*, *H. inactiva*, and *H. imshaugii*, and *Sphaerophorus globosus*. The bryophytes were dominated by the mosses *Antitrichia*

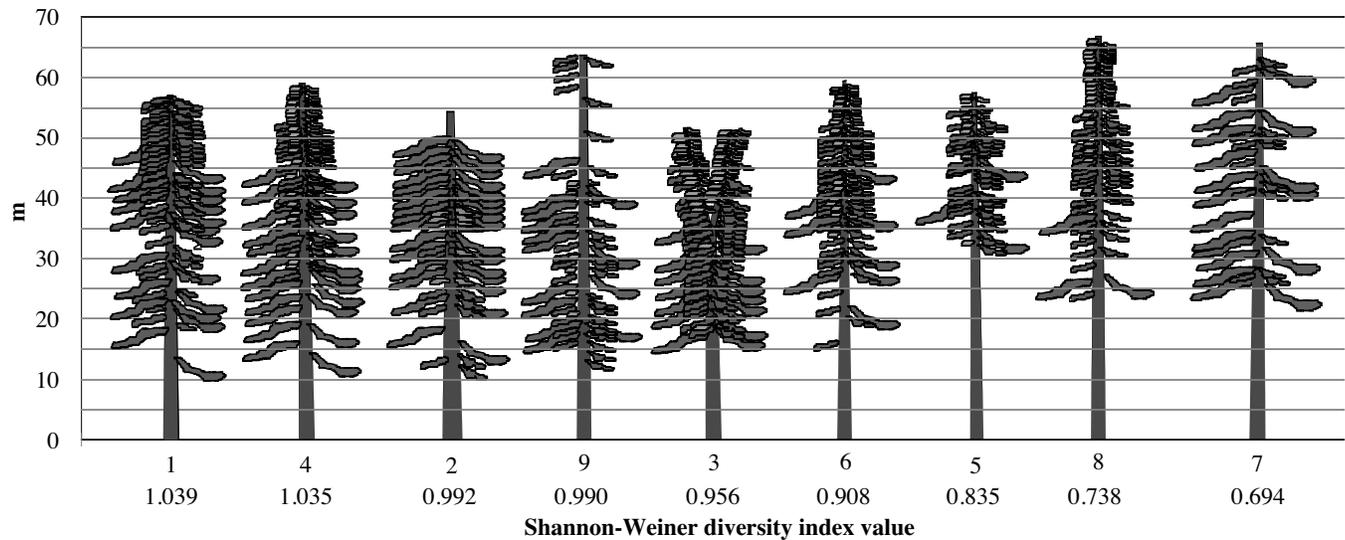


FIGURE 2. Diagrammatic representation of structural features of nine sampled trees. Branch size classes: small (2.0-10.0 cm diameter), medium (10.1-20.0 cm diameter), and large (≥ 20.1 cm diameter). Trees are ranked according to the Shannon-Weiner Diversity Index.

TABLE II. Mean dimensions for limbs in the nine sampled *Pseudotsuga menziesii* tree crowns. n/a means that data were not available

	Large limbs	Medium limbs	Small limbs	Dead limbs
length (m)	7.00 (2.46)*	4.83 (2.64)	2.17 (1.43)	0.89 (0.85)
height (m)	34 (5.00)	39 (6.30)	47 (8.40)	37 (3.40)
diameter (cm)	27.5 (3.70)	14.4 (0.90)	6.6 (0.50)	9.6 (1.50)
surface area (m ² **)	4.6 (0.74)	2.8 (0.48)	1.4 (0.10)	0.4 (0.25)
foliage volume (m ³)	25 (8.50)	7 (3.80)	1 (0.70)	n/a
# per tree	15 (9.59)	34 (10.60)	34 (27.90)	79 (26.92)

* Standard deviation in parentheses

** Does not include needle surface area.

curtipendula, *Isothecium stoloniferum*, *Dicranum fuscescens* and *D. tauricum*.

Total biomass for the nine sample trees averaged 27.1 kg/tree (dry matter) with tree 2 having the least biomass (12.9 kg/tree) and tree 6 having the most (41.2 kg/tree). Alectorioid lichens dominated the epiphyte assemblage, averaging 19.3 kg/tree and accounting for almost 75% of total epiphyte biomass (Figure 3). Other lichens and bryophytes averaged 3.3 kg/tree and 2.6 kg/tree respectively, whereas cyanolichens were least abundant with 1.9 kg/tree. Total epiphyte biomass was distributed unevenly among foliage, limbs and the trunk, averaging 16.4, 8.0, and 2.6 kg/tree respectively (Table III). The upper and middle crown was dominated by alectorioid lichens, whereas the lower crown was represented by all groups, but much less total biomass (Figure 4). There was a clear difference between inner (trunk, limbs) and outer (foliage, twigs) crown, with the inner portion exhibiting greater inter-group diversity and the outer totally dominated by alectorioids (Figure 5). Large limbs also supported greater inter-group diversity than the medium or small limbs (Figure 6). There was no indication that limb slope had any effect on epiphyte distribution.

The following summarizes the distribution of each functional group:

ALECTORIOIDS

This group dominated all regions of the crown except the lower, inner region. These pendulous lichens were most dominant in the foliage but not restricted to that outer region. Alectorioids represented over 30% of the inner crown epiphytic biomass, coating the limbs and trunk throughout the upper crown. As height decreased so did relative biomass, most dramatically in the inner crown where

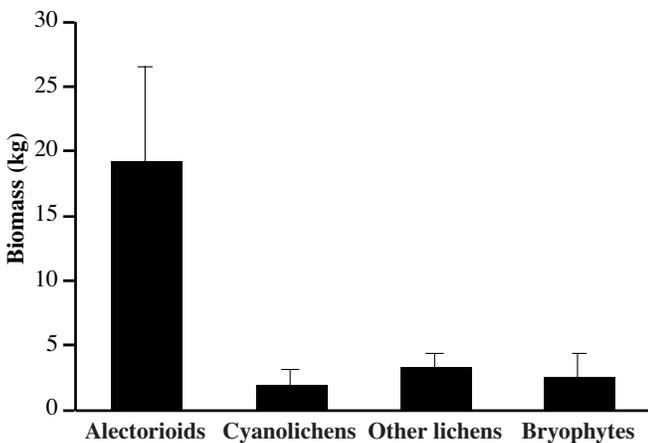


FIGURE 3. Average biomass (dry matter) of each functional group per tree. Total biomass per tree averaged 27.1 kg. Bars indicate standard deviation.

Alectorioids represented only 15% of the epiphytic biomass in the lower region.

CYANOLICHENS

These species tended to thrive in greater abundance in the middle to lower crown. They were most often found in limb samples, were absent from the trunk, and found only in trace amounts in foliage samples.

OTHER LICHENS

As with all the groups except alectorioids, the “others” were more abundant in the inner crown. They were particu-

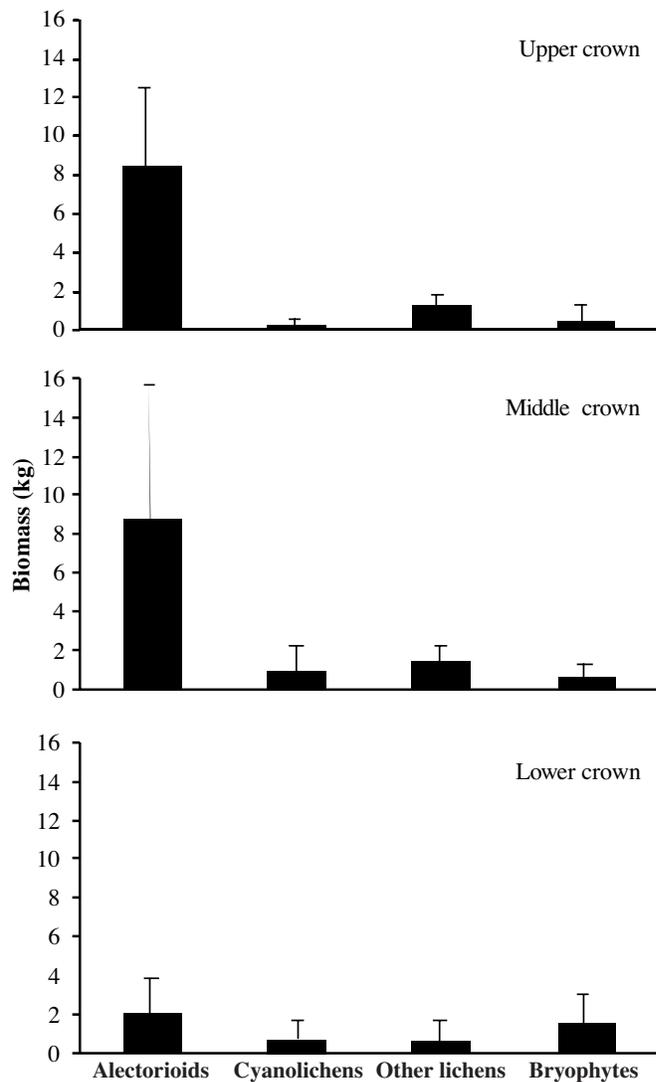


FIGURE 4. Average distribution of epiphyte functional groups in the upper, middle, and lower crown. Bars indicate standard deviation.

TABLE III. Mean biomass (kg/tree dry weight) of epiphyte functional groups on trunk, limbs, and foliage regions

Structure	Alectorioids	Cyanolichens	Other lichens	Bryophytes	Total
Trunk	1.17 (0.07)*	0.00 (0.00)	0.68 (0.06)	0.77 (0.09)	2.62 (0.11)
Limbs	2.18 (0.18)	1.88 (0.19)	2.18 (0.10)	1.80 (0.14)	8.05 (0.38)
Foliage	15.94 (0.73)	0.00 (0.00)	0.46 (0.04)	0.01 (0.00)	16.41 (0.74)

* standard deviation in parentheses

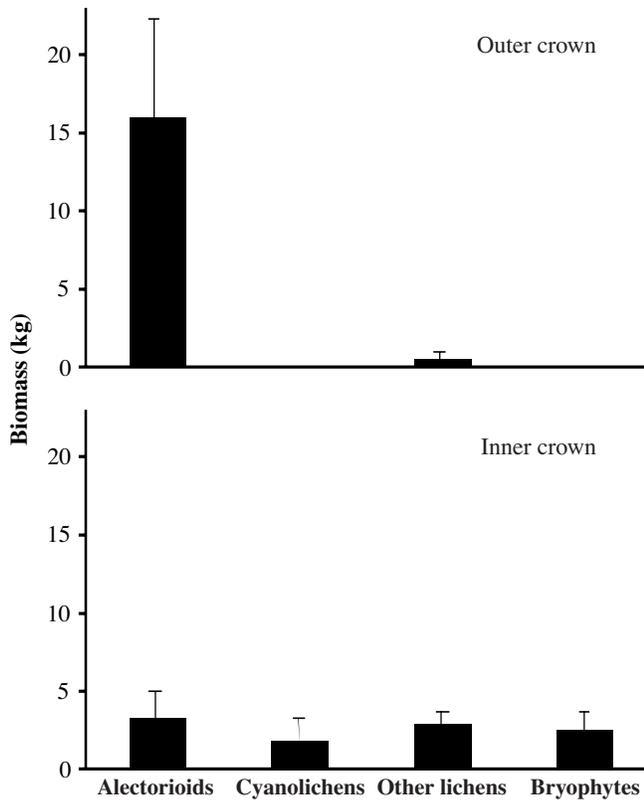


FIGURE 5. Average distribution of epiphyte functional groups in the inner and outer crown. Bars indicate standard deviation.

larly dense on the upper trunk. According to data from six of the sample trees, *Sphaerophorus globosus* biomass tended to increase with decreasing height at this site; removing this genus from the “others” group reveals a stronger, more characteristic vertical gradient. This may suggest that the *Sphaerophorus* genus belongs in a separate functional group for this site.

BRYOPHYTES

The mosses and liverworts were very sparse in the upper canopy, virtually absent from foliage samples, and abundant in the lower canopy. However, isolated pockets were found in the tops of the tallest sample trees. They dominated the lower trunk and could be found as far as 5 m from the trunk on the large limbs. They were noticeably abundant on larger limbs regardless of height.

Height and limb diameter are the most likely structural variables to influence epiphyte distribution. To assess the importance of each of these variables, the means were compared in a two-way analysis of variance (Table IV). These results demonstrate that: *i*) the height and limb size variables interact and are therefore confounded for the alectorioids and the cyanolichens, *ii*) the distribution of other lichens is strongly and independently affected by height, and *iii*) the distribution of bryophytes is strongly and independently affected by limb size.

Increasing biomass with increasing branch size is generally true for bryophytes ($r = 0.740$), and other lichens

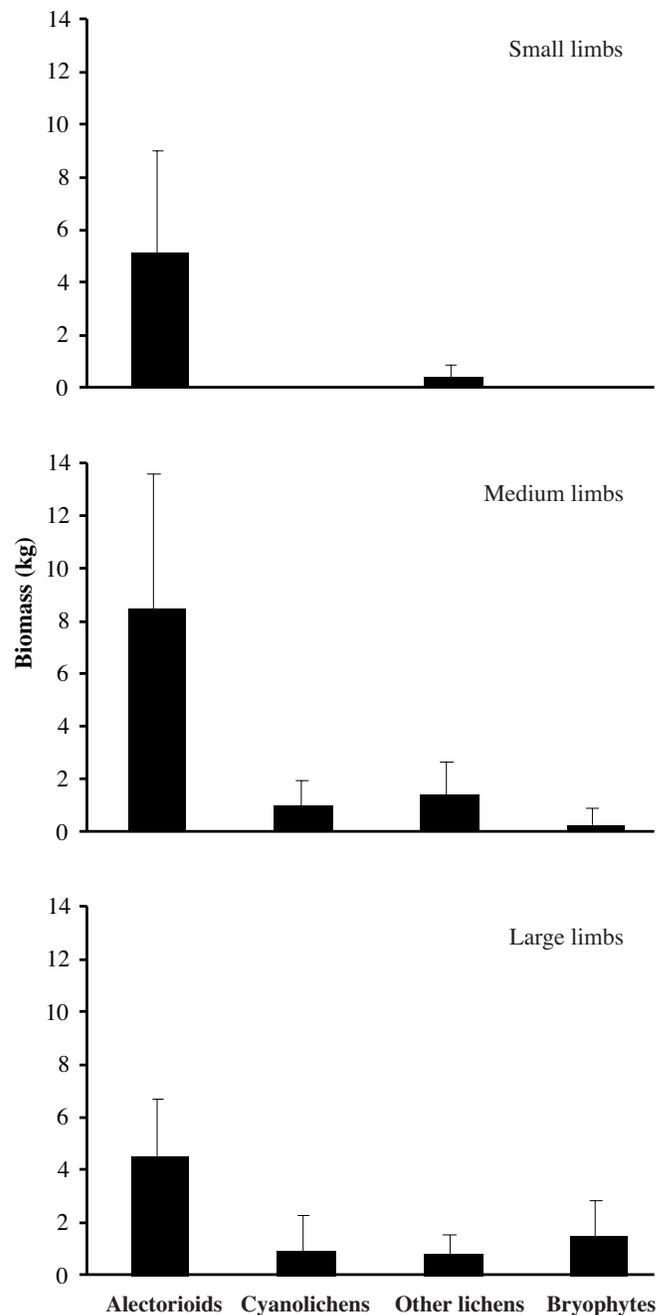


FIGURE 6. Average distribution of epiphyte functional groups on small (2.0-10.0 cm diameter), medium (10.1-20.0 cm diameter), and large (≥ 20.1 cm diameter) limbs. Bars indicate standard deviation.

($r = 0.501$), whereas it is less pronounced with cyanolichens ($r = 0.338$) and alectorioids ($r = 0.230$; Figure 7).

Discussion

SAMPLING TECHNIQUE

The sampling technique described in this paper required two days in order to rig and structurally describe a tree, two days to sample biomass and de-rig the tree, and one week for a team of student workers to clean, sort, dry,

TABLE IV. Analysis of variance comparing effect of height zone, limb diameter, and their interaction for epiphyte functional group biomass

Group	Effect	df	Mean square error	F	P
Alectorioids	height zone	2	284.11	18.2	< 0.001
	diameter	2	74.60	4.8	0.009
	interaction	4	45.75	2.9	0.021
Cyanolichens	height zone	2	15.69	1.7	0.184
	diameter	2	21.32	2.3	0.1
	interaction	4	43.54	4.7	0.001
Other lichens	height zone	2	51.81	6.3	0.002
	diameter	2	15.72	1.9	0.151
	interaction	4	7.16	0.9	*0.484
Bryophytes	height zone	2	19.05	3.2	0.04
	diameter	2	84.09	14.3	< 0.001
	interaction	4	11.43	2.0	*0.102

* indicates an absence of confounding interaction

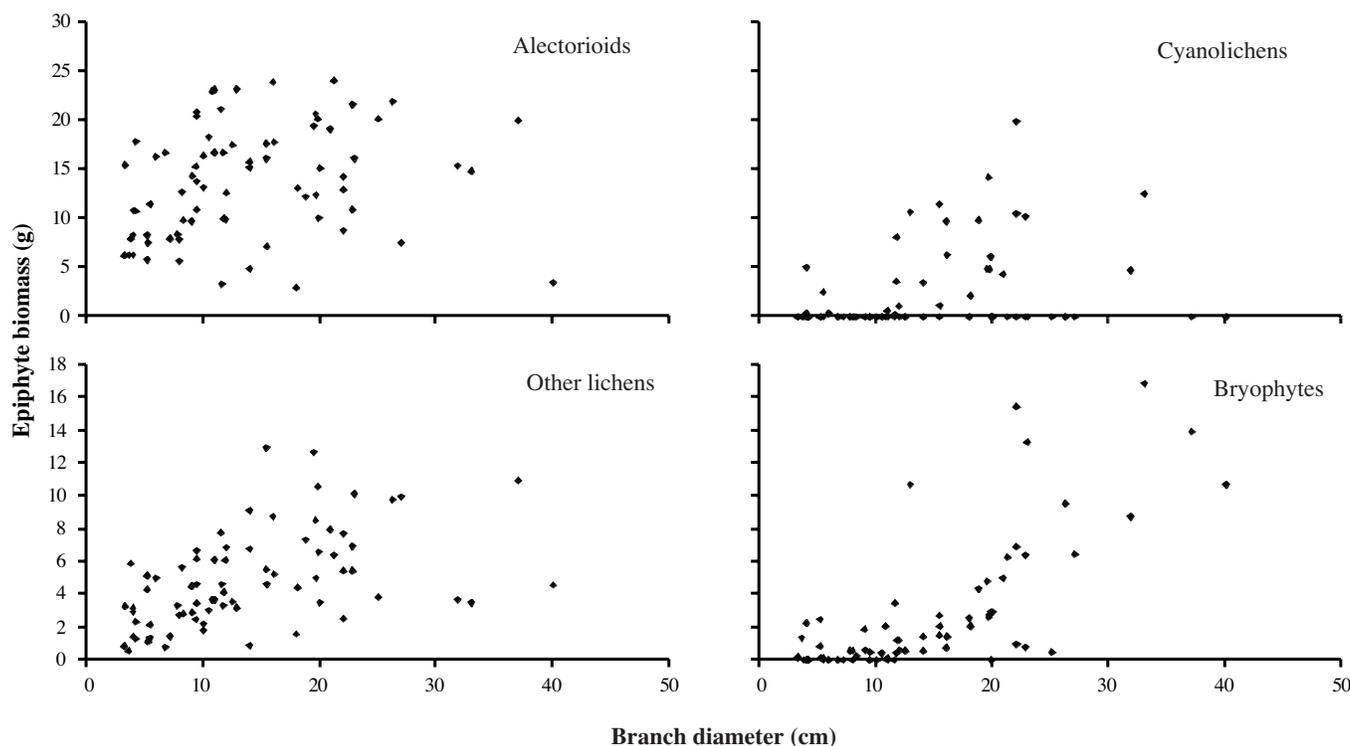


FIGURE 7. Distribution of epiphyte functional group biomass (square root transformed) versus branch diameter.

and weigh epiphyte functional groups for one old-growth *P. menziesii* tree. All nine trees were sampled in nine weeks of field work followed by a similar amount of time for lab work. This is a reasonably efficient field method to quantify general tree structure and biomass, and the lab work is particularly efficient because epiphyte functional groups were used. Although the technique used by Pike, Rydell & Denison (1977) will provide more accurate data, it is impractical to use such a method on a large scale because of time constraints.

The techniques described in this study may still be too intensive to be utilized on a landscape scale or in many forest stands. Finding a way to scale back the amount of biomass collection per tree, such as done by Van Daele & Johnson (1983), may be necessary. For a whole stand estimate of lichen diversity and biomass, we recommend a variety of techniques as described by Boucher & Stone (1992),

McCune & Lesica (1992), and McCune (1994), with tree climbing and individual tree biomass contributions forming the backbone of the estimates. Using these techniques, perhaps half the effort (5% of the limbs/foilage, 2.5% of the trunk) we presented would be necessary. Another approach would be to combine biomass collections and percent cover estimates of plots within an individual tree crown (Boucher & Stone, 1992).

ABUNDANCE

Epiphyte biomass averaged 27.1 kg/tree in these old-growth canopy-emergent trees. We estimate that between five and ten trees of this type are present in each hectare along the riparian forest of Trout Creek. Therefore, the biomass contribution to the standing crop of epiphytes is between 132 and 271 kg/ha, with lichens representing between 122 and 245 kg/ha. The nearby Wind River

Canopy Crane Research Facility forest has been estimated to contain 1 300 kg/ha of lichen epiphytes (McCune *et al.*, 1997), indicating the potential of this tree type for contributing between 9% and 19% of the standing crop of lichens.

Individual old-growth tree epiphyte biomass reported for *P. menziesii* ranges between 1.7 kg (McCune, 1993a) to 17.8 kg (Pike, Rydell & Denison, 1977), with cyanolichens (58%, Pike, Rydell & Denison, 1977; 65%, McCune, 1993a) and bryophytes (26%, Pike, Rydell & Denison, 1977; 29% McCune, 1993a) dominating over the alectorioid and other lichen groups (combined total: 16% Pike, Rydell & Denison, 1977; 9% McCune, 1993a). The Trout Creek trees averaged 27.1 kg/tree with cyanolichens (7%) and bryophytes (10%) being dominated by alectorioid (71%) and other (12%) lichens (combined = 83%). This shift in dominance of cyanolichens and mosses to alectorioid and other lichens can be explained by the similar gradient hypothesis (McCune, 1993a), which predicts a decrease in cyanolichens and mosses as climate becomes more continental. The trees of the Pike and McCune studies were both located in the H. J. Andrews Experimental Forest on the west slope of the Cascade Mountain range of central Oregon (44° 16'N, 122° 9'W), which has a more maritime climate than the Wind River Experimental Forest (McCune *et al.*, 1997).

The dominance of alectorioid lichens, and their overall contribution to greater epiphyte biomass/tree, could also be favored by our choice of canopy-emergent, dominant trees in this riparian zone. We intentionally sampled individualistic trees with exposed crowns in hopes of minimizing the amount of variation caused by the surrounding canopy. Alectorioid lichens are known to be more abundant in the upper forest canopy (McCune, 1993a; McCune *et al.*, 1997) and we have shown their abundance in the outer crown, upper crown, and foliage areas at Trout Creek. Our choice of exposed, dominant trees may have selected for high alectorioid abundance.

VERTICAL PATTERNS

The vertical patterning of epiphytic lichens and bryophytes within forests is well-documented (Hale, 1952; 1965) and involves a response to the wide range of microenvironmental conditions compressed into the length of an individual tree (Hale, 1974). Our results were similar to Pike *et al.* (1975), McCune (1993a), Sillett (1995), and McCune *et al.* (1997) for old-growth *P. menziesii*. Bryophytes dominated the lower crown, cyanolichens occupied a zone just above and intermixed with bryophytes, and green algal lichens, exclusive of *Sphaerophorus*, occupied the middle, upper and outer crown. However, the relative height of bryophytes and cyanolichens was much lower in the Trout Creek trees than at the H. J. Andrews Experimental Forest and Santiam River sites sampled in the previous studies, reflecting the more continental climate of the Wind River Experimental Forest.

Interestingly, large limbs, which occur throughout the crown (Figure 1), appeared to carry cyanolichens and bryophytes high into the canopy (Figures 6 and 7). A general upward migration of bryophytes and cyanolichens with

time has been described by McCune (1993a) and Sillett & Neitlich (1996). It is possible that a successional sequence is occurring which, although complex, involves the eventual co-occurrence of all four functional groups on a large, old branch.

The vertical pattern of lichens in these *P. menziesii* trees is also similar to accounts of phytosocial groups described for northern Europe by James, Hawksworth & Rose (1977), Rose (1988), and Gauslaa & Solhaug (1996) where *Lobarion*, dominated by cyanolichens, occupies boles and main branches of the lower canopy, *Usneion*, dominated by alectorioid lichens, occupies branches higher in the canopy, and *Parmelion*, dominated by other lichens, is generally ubiquitous.

The occurrence of cyanolichens in the lower to middle canopy is related to a number of factors including a negative response to high light that causes photoinhibition (Demmig-Adams *et al.*, 1990; Gauslaa & Solhaug, 1996) and the need for water, rather than humid air, for physiological reactivation of the thallus (Lange, Kilian & Ziegler, 1986). *Lobaria oregana*, the dominant cyanolichen at this site, does not have cyanobacteria as the primary photobiont and therefore may not require liquid water. However, *L. oregana* grew significantly less along a forest edge compared to the forest interior when transplanted to these microhabitats in an old-growth, tall stature forest, which indicates the negative effect of a sunnier, more desiccated microenvironment (Sillett, 1994). Many green algal lichens tolerate high light and can reactivate by absorbing water from the atmosphere making them much more capable of life in the sunny, desiccated upper canopy.

Water availability, humidity, and exposure appear to be driving factors influencing the vertical distribution of bryophytes (Burgaz, Fuentes & Escudero, 1994; Peck, Hong & McCune, 1995; Mazimpaka & Lara, 1995) and this need for a mesic environment keeps them in the lower canopy of tall stature forests. The importance of water as the primary factor influencing bryophyte distribution is elucidated by the higher vertical occurrence of bryophytes with a shift from xeric to mesic regional climates (Peck, Hong & McCune, 1995) or a shift on a local scale from exposed ridge tops to mesic valley floor (Pike *et al.*, 1975).

INFLUENCE OF CROWN STRUCTURE

Tree and crown structure profoundly influence the distribution of epiphyte functional groups within large *P. menziesii* trees. Tree height, crown length, distribution of small, medium and large limbs, and the basic structures of trunk, limbs (axes), and foliage area (branchlets) all influence epiphyte distributions. Tree height determines the relative position of the basic substrates within the forest as a whole, which in turn determines the relative microclimatic conditions these substrates will be exposed to. The trees at Trout Creek were tall, dominant, canopy-emergent trees with exposed crowns. The predominance of alectorioid and other lichens reflects this exposure.

Crown length influences the relative length of the bole affected by inner and outer crown conditions (Sillett, 1995;

Figure 5). The shaded inner portion of the crown has more cyanolichens and bryophytes than the exposed outer crown area. The crown also provides the basic substrate of limbs (axes) and foliage area (branchlets), and therefore the relative length of the crown will profoundly influence the biomass of all epiphyte functional groups.

The basic substrates, trunk, limbs (axes), and foliage regions (branchlets) define the available substrates within the tree. Tree height and crown length then combine with these substrates to characterize the potential physical variables controlling epiphyte functional group distribution. Barkman (1958) and Hale (1974) reviewed these variables and found that water availability and humidity, exposure to wind desiccation, and light stand out as primary factors.

The abundance and distribution of small, medium, and large limbs within the tree crown also have a profound and independent influence on the distribution of epiphyte functional groups within Douglas-fir tree crowns (Figure 6; Table IV). Large limb systems accounted for over 50% of the limb substrate surface area within the crown (excluding needles) and encompassed over 75% of the foliage volume. The distribution of large limbs throughout the crown defines its irregular shape and horizontal boundaries (Figure 2), its "ecological space" (Spies & Cohen, 1991). Well-distributed large limbs "break up" the deep crown vertically into the characteristic heterogeneous and asymmetrical form which provides a diverse range of habitats and is extremely effective at capturing nutrients and moisture from the atmosphere (Franklin *et al.*, 1981). The large limb itself represents a long microclimatic and structural habitat gradient from the large, shaded limb substrate near the trunk to the well-lit, exposed twigs and branchlets at its outer tip (Silllett, 1995).

The structural data indicated the architectural dominance of large limbs, while the analysis of the distribution of epiphyte functional groups demonstrated that these large limbs play a functional role by influencing the diversity of epiphytes, especially bryophyte distribution, and therefore affects the diversity of epiphyte groups found throughout the tree. Esseen, Renhorn & Pettersson (1996) demonstrated that increasing limb size and age were correlated to increased lichen biomass in Norway spruce (*Picea abies* L. [Karst.]) in Sweden.

The role of succession as a confounding variable in the effect of crown structure on epiphytic lichen and bryophyte communities should not be ignored (Hale, 1974; Hilmo, 1994), but is very difficult to determine (Kantvilas & Minchin, 1989; Arseneau, Sirois & Ouellet, 1997). In this case, limb size has been used as a surrogate for limb age, and implies that succession involves the growth of large limbs with well-developed communities of each functional group.

The direct relationship between large, old structures and structural diversity has been documented by ecologists classifying the structural diversity of old-growth stands at the landscape level (Franklin & Spies, 1991b; Spies & Franklin, 1991). The large, emergent trees appeared to dominate and define the structural composition of the forest; they provided a greater range of microclimates and habitats, affected a broader spectrum of organisms, and

influenced more volume within the forest. Multivariate analysis demonstrated that variables associated with the number and spread of large trees were indeed the most useful tools for categorizing old-growth stands (Franklin & Spies, 1991a; Spies & Franklin, 1991; Spies & Cohen, 1991). Large limbs appear to play this role in individual tree crowns of *P. menziesii*.

Conclusions

The tree structural variables of height, crown length, trunk, limb and foliage regions, as well as the abundance and distribution of small, medium, and large limbs, play an important role in the abundance and vertical occurrence of epiphyte functional groups within old-growth *P. menziesii* trees. Large limbs in particular influence the distribution of epiphyte functional groups within an individual old-growth tree crown. This general knowledge of the relationship of structural attributes to epiphyte distribution and abundance can be utilized when choosing trees for green tree retention (Franklin, 1989) during forest management. In particular, tall, structurally diverse old-growth trees with well-distributed large limbs and long crowns will enhance biodiversity of the affected lands. We found that dbh is a useful surrogate measure for structural complexity. In addition, increasing tree diameter is known to be associated with increased epiphyte biomass (McCune, 1993a; Arseneau, Sirois & Ouellet, 1997).

This study highlights the need to thoroughly sample entire crowns. McCune (1990) pointed out that although very few studies have assessed epiphytes on branches, it is important to "sample where the epiphytes are" rather than depend on assessments of communities such as trunk-based epiphytes which may not be representative of epiphyte communities in general. Foliage samples were particularly important, dominating the total epiphyte biomass collected from these trees (59%). Available substrate surface area on foliage twigs alone was greater than that of the massive trunks, indicating that this important region of the tree should be included in any sampling effort.

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