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Vertical Profile of Epiphytes in a Pacific Northwest Old-growth Forest

Abstract

The vertical stratification of epiphytes is a striking feature of Northwestern forests that surely influences the distribution of other organisms in the canopy. We are just now learning how and why the stratification varies from place to place. Functional groups of epiphytes were stratified with height in an old-growth *Pseudotsuga-Tsuga* forest in the following order, from the ground up: bryophytes, cyanolichens, and alectorioid lichens. Other macrolichens (mainly green-algal foliose) were found throughout the vertical profile, but their relative abundance peaked in the middle to upper canopy. Cyanolichens (mainly *Lobaria oregana*) were concentrated in the "light transition zone." The light transition zone is the range of heights in which we found abrupt transitions in light transmittance by the canopy. This zone extends from about 13 to 37 m in height, in an overall canopy height of 50-60 m. Bryophytes were concentrated between the ground and the middle of the light transition zone. The biomass of epiphytic macrolichens was about 1.3 metric tons/ha, composed of approximately 42% cyanolichens, 28% alectorioid lichens, and 30% other lichens.

We draw the following methodological conclusions. Using quadrats as windows from a suspended gondola overestimates the relative abundance of alectorioid lichens and underestimates cyanolichens and other lichens. Using 14, 2-m radius lichen litter plots is barely adequate to represent the epiphytic macrolichens of an old-growth stand. Ground-based canopy density measurements (photographic and densiometer) are insufficient to characterize the openness of a vertical transect, because of interference from understory vegetation.

Introduction

Communities of canopy epiphytes change conspicuously with height in the conifer forests of the Pacific Northwest (Pike et al. 1975, McCune 1993, Sillett 1995). The sequence of dominance with increasing height is fairly constant in different areas of the Pacific Northwest. Bryophytes dominate near the ground, then cyanolichens, alectorioid lichens, and other macrolichens (mainly green algal foliose lichens) dominate progressively higher zones in the canopy. The depth of these zones varies with climate and forest age. McCune (1993) hypothesized that the zones shift upward in wetter climates or as forests age, but that the basic sequence of dominance remains the same. So few stands have been profiled, however, that this hypothesis remains unsubstantiated.

The goal of this study was to characterize the profile at a new site and to compare the vertical profile of epiphytes with the vertical profile in light transmittance. Would the vertical profile of epiphytes shift downward in more open parts of the canopy?

The canopy crane at the Wind River Experimental Forest provided us with an opportunity to meet these objectives. Studying the forest from a suspended gondola created a need for a new method for non-destructive sampling of the vertical profile in epiphyte communities, subject to a constraint that we would often be beyond reach of the substrates we were sampling. We also collected lichen litter data to estimate the absolute and relative abundance of three functional groups of epiphytic lichens. These litter data allowed estimates of canopy lichen biomass and provided an independent check on data quality from the sampling via the gondola.

Study Area

We studied the forest of the Wind River Canopy Crane Research Facility in the southern Washington Cascades. The canopy crane is a large construction crane on a fixed platform, providing 3-dimensional access to a 2.3 hectare circular area of old-growth *Pseudotsuga menziesii* - *Tsuga heterophylla* forest (Franklin & DeBell 1988;

nomenclature of vascular plants after Hitchcock and Cronquist 1973). The oldest trees in the forest are about 400-500 years old. The crane is located in the T. T. Munger Research Natural Area at the Wind River Experimental Forest (45°49'N 121°57'W) at an elevation of 355 m. Average annual temperature is 8.8°C, with January and July means of 0°C and 18°C respectively (unpublished climatological summary, Wind River Experimental Forest, 1911-1965). Average annual precipitation is 250 cm.

Methods

At seven locations within the crane circle we sampled canopy density from the ground, vertical transects of epiphytes, and lichen litter. Locations were chosen to represent a range of canopy openness up to medium-sized canopy gaps formed by several large dead trees. Light profiles were collected as a separate data set and thus were not co-located with the vertical transects of epiphytes.

Canopy density

We measured canopy density as viewed from the ground at the base of each vertical transect. Sixteen spherical densiometer readings, four at each of four locations near the perimeter of a 2-m radius circle, were averaged to estimate percent canopy closure. A vertical photograph with a wide-angle (38 mm) lens supplemented the densiometer readings. The photographs were scored for percent canopy cover and provided a view of each vertical profile from the ground.

Light profiles

Photosynthetically active radiation (PAR) light profiles were taken along sixteen vertical transects. These were chosen to be spatially dispersed, representing a range of canopy closure. Several of the profiles extended through gaps in the upper canopy caused by the death of several large trees. Details of our PAR sampling are given in Parker (1997). PAR was measured at high sun angles in clear weather.

Epiphyte profiles

The vertical profile of epiphytes was determined at 7 locations. At each location two observers simultaneously completed vertical transects from the crane gondola, with one observer facing north-

east and the other facing southwest, for a total of 14 vertical transects. Each observer estimated percent cover of each functional group at 5 m intervals beginning 5 m from the ground. Transects continued through the highest 5 m mark with visible epiphytes (55-60 m above ground level). A 50 cm X 10 cm quadrat held horizontally at eye level and arm's length was used to estimate cover in the two-dimensional view.

Definition of functional groups (bryophytes, cyanolichens, alectorioid lichens, and "other" macrolichens) follows McCune (1993). The groups are functional, as opposed to taxonomic, because the members of a group share ecological, functional roles more than do members of different groups. Their ecological roles include nutrient cycling, who eats them, microhabitats occupied, and responses to air pollutants.

"Cyanolichens" include all macrolichens with a cyanobacterium as a primary or secondary photobiont. At the crane site cyanolichens are mainly *Lobaria oregana*, with smaller amounts of other *Lobaria* species, *Nephroma*, *Peltigera*, and *Pseudocyphellaria* (nomenclature of lichens follows Esslinger and Egan 1995). Functionally these genera are related by their N-fixation and their sensitivity to air pollution (e.g., Richardson 1988).

"Alectorioid" lichens include all pendulous species in *Alectoria*, *Bryoria*, and *Usnea*; in this case, mainly *Alectoria sarmentosa*. In addition to having similar growth forms, *Alectoria* and *Bryoria* tend to be preferred food species for flying squirrels (C. Maser et al. 1986, Z. Maser et al. 1985), deer (Stevenson 1978), and mountain caribou (Edwards et al. 1960, Rominger and Oldemeyer 1989, Servheen and Lyon 1989).

The group "other lichens" includes all remaining macrolichens, mainly *Platismatia* and *Hypogymnia* species. These species do not fix nitrogen, they have less well documented relationships to wildlife, and they have varied sensitivities to air pollutants. In this case, most species are foliose, light-colored above, and contain atranorin in the cortex.

"Bryophytes" includes all bryophytes, but probably overlooking some small leafy liverworts and pleurocarpous mosses that contribute little to the total biomass. Although there is certainly ecological diversity within bryophytes (During 1992, Grime et al. 1990), in general the epiphytic species are ecologically more similar to each other

than they are to lichens, as shown by their tendency to cluster together in analyses that include both bryophytes and lichens (e.g. McCune and Antos 1982). The predominant bryophytes in this study were *Antitrichia curtipendula*, *Dicranum fuscescens*, *Hypnum circinale*, and *Isoetecium myosuroides*, (nomenclature of mosses follows Anderson et al. 1990).

To reduce variability among observers, we practiced evaluating cover with a simulated canopy "scene" of epiphyte-covered branches. Although there was considerable variation in the absolute cover values recorded for each functional group, relative values were fairly consistent between observers.

Percent cover values from each transect were converted to relative cover of each functional group at each height. This conversion allowed comparisons between transects made at varying distances from the trees and reduced between-observer differences in cover estimates. To represent the general distribution of epiphytes within the stand, the "overall average" relative covers for each group were calculated as the average relative cover over all transects at each height.

To compare vertical distributions of epiphytes with canopy density and PAR profiles, we calculated "95% distribution limits" for each functional group in each transect. These limits define the portion of the vertical profile that includes 95% of the relative cover of a functional group. We used this method, rather than the total range of a functional group, to reduce the statistical influence of any small, outlying patches of a given functional group. To calculate the limits, we treated the relative cover values of each functional group as histograms with bars centered at 5 m intervals; 2.5% of the total area represented by a given histogram was then subtracted from each end of the distribution, yielding height cutoffs for the middle 95% of the "total relative cover" of each functional group. The analysis was limited to heights between 5 and 55 m (the heights surveyed by all observers).

Epiphyte litter

Epiphytic lichen litter was collected in April 1996 from the forest floor at the base of the seven vertical transects. The purpose of these data was not to estimate total annual litterfall, but rather to estimate in-situ epiphyte biomass. Besides providing a basic description of canopy lichens, we

used the relative abundance of functional groups as a check on data quality obtained from the crane. Two, 2-m radius plots were sampled at each site using the method of McCune (1994). Bryophytes were not included because of problems described by McCune (1994). Litter was sorted by functional group during collecting. Samples were oven dried at 60°C for over 24 hours, then weighed to the nearest milligram.

A previous litter sample in August 1994 included 15 plots at 40 m spacings on transects through the crane circle. Processing was similar to the samples below the vertical transects.

Results and Discussion

Canopy density

Canopy density varied over a narrow range, from 81-93% canopy closure. The estimates of canopy density for each transect site were reliable, based on an observed standard error of only 2-6% of the mean. Canopy density was not, however, correlated with the variation in the vertical profile of epiphytes.

Ground-based canopy density measurements were insufficient to characterize the openness of the vertical transects, because of interference from understory vegetation. Most of the gaps, when viewed from above, were carpeted with an understory of *Tsuga* and shrubs, so that even though there might be a large cylindrical opening in the canopy, it would not be reliably detected from the ground.

Light profiles

Transmittance profiles of photosynthetically active radiation (Parker 1997) showed abrupt transitions from bright (over 75% transmittance) to dark (typically less than 25% transmittance) between 13 and 37 m above the ground at 16 sites throughout the study area. The height at which light levels declined below 50% transmittance was generally found in this mid-canopy region. The breadth of this light transition zone (Figure 1A) aptly describes the uneven filling of the mid to upper canopy.

Epiphyte profiles

The relative abundance of bryophytes, cyanolichens, alectorioid lichens and other lichens was

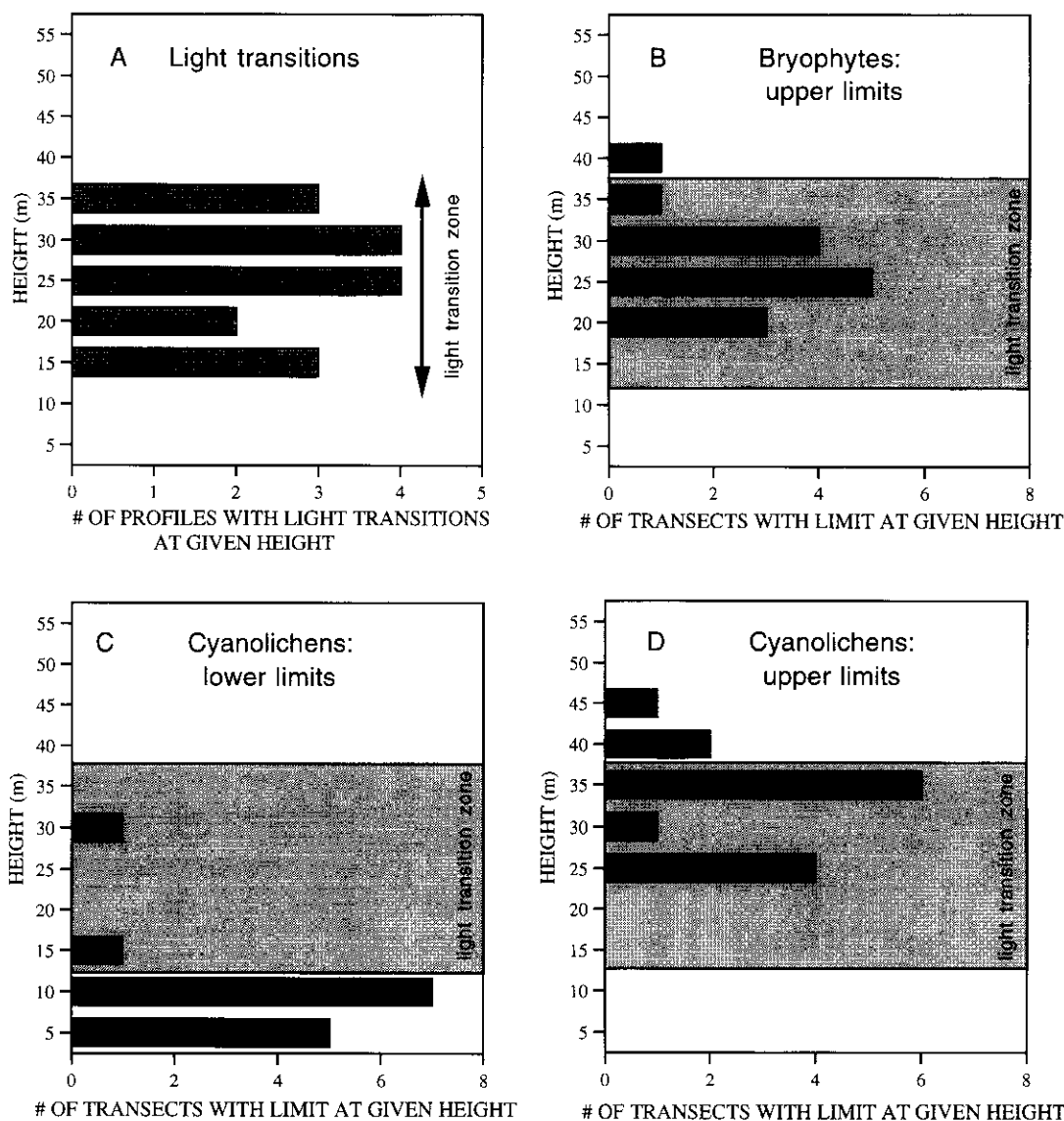


Figure 1. Comparison of the locations of the light transition zone and the upper and lower limits of epiphytes. A. Frequency distribution of the height at which light declined below 50% ($n=16$ transects) with the light transition zone indicated. B-D. Distribution limits of epiphytes ($n=14$ transects for each graph) compared to the light transition zone. B. Upper limits of bryophytes. C. Lower limits of cyanolichens. D. Upper limits of cyanolichens.

clearly stratified by height. The stratification was apparent in both the individual transect profiles and in the profile of the combined transect data (Figure 2). The pattern was generally comparable with what has been reported previously for other areas (McCune 1993). However, unlike those results, cyanolichens (mainly *Lobaria oregana*) never quite achieved dominance over other groups.

"Other lichens" were spread throughout the vertical gradient and were highly variable in total abundance, with less of a distinct peak as compared with other functional groups. At lower levels, *Sphaerophorus* contributed most of the "other" biomass while green-algal foliose genera such as *Hypogymnia* and *Platismatia* comprised most of the "other" biomass at higher points. Better reso-

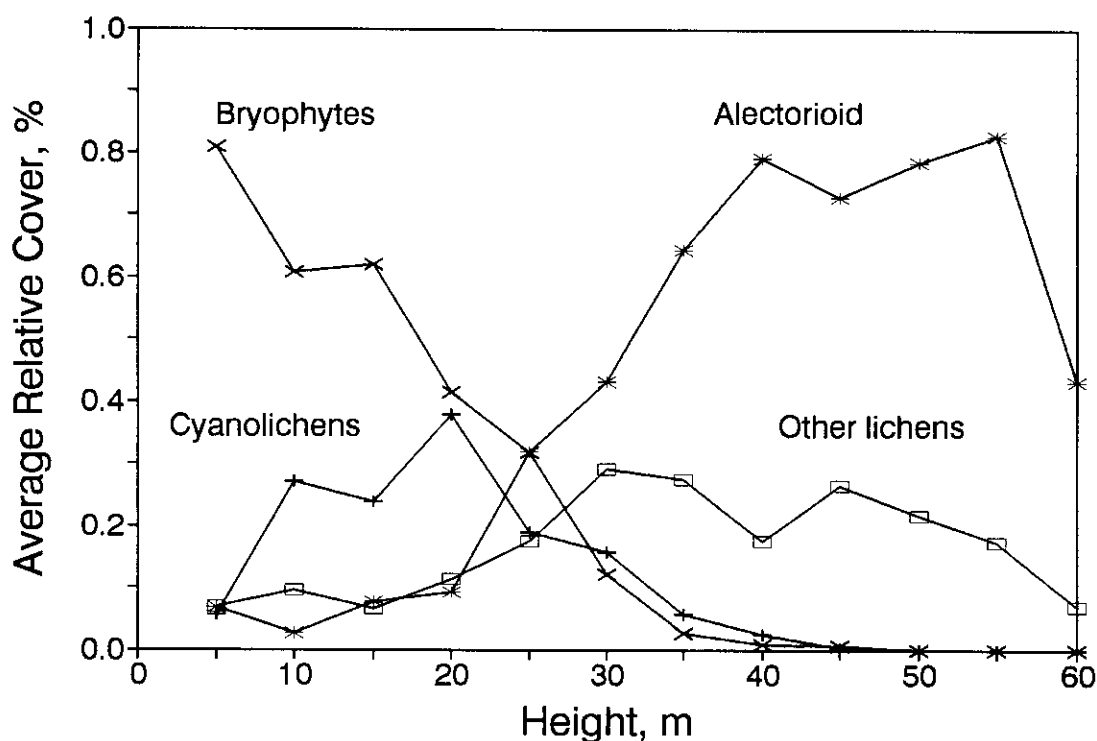


Figure 2. Average relative cover as a function of height in the forest canopy. Relative cover was averaged across all transects for a given height (n=14 transects).

lution of the vertical distribution of "other" lichens might be obtained by dividing this group into two more ecologically similar groups: tufted fruticose (*Sphaerophorus* and *Cladonia*) in contrast to green-algal foliose lichens (*Hypogymnia* and *Platismatia*).

The location of the light transition zone was related to the distribution limits of at least two of the functional groups. The upper limits of the bryophytes (mainly *Isoetecium myosuroides* and *Antitrichia curtipendula*) usually fell in the middle of the light transition zone (Figure 1). The upper limits of the cyanolichens straddled the upper end of the light transition zone, and the lower limits of cyanolichens fell on or just below the light transition zone (Figure 1). In other words, cyanolichens were concentrated in the light transition zone, and bryophytes were concentrated below the middle of the light transition zone.

No consistent difference between northeast and southwest facing transects could be discerned. Furthermore, we found no obvious differences in the vertical gradient between dense and more open areas. To examine this point adequately,

however, we need canopy closure data from above the ground (see "canopy density" above), preferably a series of observations along the length of each transect.

There were numerous sources of variation in our sampling. Some resulted from the use of different observers for each transect. Variation in the distance between the observer and the trees also introduced a bias, depending on visibility of functional groups. As distance of observation increased, "other" lichens and cyanolichens became more difficult to see than alectorioid lichens.

To minimize these problems, we suggest that future studies use a larger number of transects and a single observer. Using a consistent distance between observers and the trees might also reduce variation between transects.

Epiphyte litter

The total biomass of epiphytic macrolichens was about 1.3 tons/ha (dry mass). The result was based on the August litter sample, using a 100:1 ratio for in-situ:litter biomass (McCune 1994). That

ratio was developed based on a late-summer litter sampling. Lichen litter is typically maximal following winter storms but declines through the summer (Esseen 1985, Stevenson & Rochelle 1984). Had we used the April litter sample our estimate would have been 3.3 tons/ha, about 2-3X too high.

The biomass of epiphytic macrolichens based on the April sample was approximately 42% cyanolichens, 28% alectorioid lichens, and 30% other lichens (Table 1). Because the adequacy of the April sample was considerably better than the August sample (see ratio of standard error to mean in Table 1), these percentages are probably more reliable than those based on the August sample. A ratio of standard error to mean of 10-20% is often used as a rule-of-thumb for sample adequacy in describing ecological quantities (McCune and Menges 1986).

The fairly high percentage of cyanolichens in both the August and April samples was somewhat surprising, since alectorioid lichens are the most conspicuous group of epiphytes at the crane site. Cyanolichens are, however, considerably heavier per unit volume of thallus than alectorioid lichens.

Comparison with other vertical profiles

The forest at the crane site has a vertical profile of epiphytes typical of old-growth *Pseudotsuga-Tsuga* forests at low to mid elevations in the Cas-

cades. Cyanolichens are, however, less abundant at the crane site than in similar-aged stands at the H. J. Andrews Experimental Forest in the Oregon Cascades (McCune 1993, Pike et al. 1975). At the Andrews Forest the biomass of cyanolichens is four times that of alectorioid lichens (McCune 1993), while at the crane site, the biomass of cyanolichens is only 1-1.5 times the biomass of alectorioid lichens (Table 1). The upper limit of cyanolichens is also somewhat lower than in comparable aged stands at the Andrews Forest, reflecting the somewhat drier character of the vegetation at the canopy crane site. Despite slightly higher precipitation at the crane site than at the Andrews Forest, the valley has an overall south-facing aspect and is subject to more frequent penetration of dry air masses from east of the Cascades, owing to the proximity of the crane to the Columbia Gorge (J. Franklin, pers. comm., 1996).

The forest in the Middle Fork of the Santiam Wilderness that Sillett (1994, 1995) studied is both older and wetter than forests at both the Andrews and Wind River Experimental Forests. In keeping with the "similar gradient hypothesis" (McCune 1993), the very old, wet, Santiam forest has a larger total biomass of cyanolichens than at the crane site, and cyanolichens dominate almost to the tops of the trees. Bryophytes are likewise well developed and form large cushions very high in the trees. The very old age and high precipitation

TABLE 1. Proportionate contributions of functional groups of epiphytes to biomass and cover, based on litterfall and vertical profile sampling. "Top" means that the group is abundant at the top of the profile, the actual height varying with the height of the canopy. "Base" means that the group is abundant to the base of the profile, even though sampling stopped at 5 m.

	Bryophytes	Cyanolichens	Alectorioid lichens	Other lichens
LITTERFALL				
Estimated biomass in canopy, kg/ha ¹	no data	1401	934	981
Percent of lichen biomass, April	—	42	28	30
Percent of lichen biomass, August	—	33	33	34
Standard Error/Mean, April, %	—	22	14	11
Standard Error/Mean, August, %	—	29	30	14
CRITICAL HEIGHTS				
Upper limit, average (st. dev.), m	28 (6)	34 (6)	top	top
Lower limit, average (st. dev.), m	base	9 (6)	22 (11)	13 (9)
AVERAGE RELATIVE COVER, %	27 (13)	17 (3)	58 (8)	25 (10)

¹Based on August sample

allowed epiphytes to advance to the point where functional groups typically found low in the profile have successfully invaded the upper canopy.

We still have large gaps in our knowledge of how the vertical profile varies across the landscape. The vertical gradients in coastal *Picea* and *Pseudotsuga* forests have not been studied systematically. The conspicuous elevational gradient in the abundance of cyanolichens and alectorioid lichens has also not been documented, much less how the vertical profile changes with elevation. We also have limited understanding of how the change in epiphyte environment (temperature, relative humidity, heat load, potential evapotranspiration) change with forest age and site conditions.

Furthermore, we still need to understand the within-stand variation in vertical profiles. Specifically we need to explore how the vertical profile in the distribution of species expands or compresses depending on forest structure. Forest management under the Northwest Forest Plan will pro-

duce variable spacing of remnant trees. This spacing is expected to influence development of canopy epiphytes. Two ways to anticipate the result of different spacings among remnant trees are (1) to document how the vertical stratification of epiphytes differs between vertical transects through different local canopy densities and (2) to examine environmental and community changes in canopy remnants after different patterns of logging.

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