

Gradients in Epiphyte Biomass in Three *Pseudotsuga-Tsuga* Forests of Different Ages in Western Oregon and Washington

BRUCE MCCUNE

Department of Botany and Plant Pathology, Cordley 2082, Oregon State University, Corvallis, OR 97331-2902

Abstract. *Epiphyte biomass on branches and trunks was estimated for 42 individual felled trees, distributed among three Pseudotsuga menziesii-Tsuga heterophylla stands aged 95, 145, and 400+ years, in the western Cascade Range of Oregon and Washington, then extrapolated to the whole stands by regression techniques. Epiphytes were sorted into four groups defined by ecological roles rather than taxonomy: cyanolichens, alectorioid lichens, other lichens, and bryophytes. In general the spatial sequence of dominance of these four groups, from upper canopy to forest floor, was: "other" lichens, alectorioid lichens, cyanolichens, and bryophytes. The zones of these functional groups of epiphytes apparently migrate upward in forests through time. For example the Hypogymnia and Platismatia that dominate throughout canopies in young forests are found primarily in the upper canopies of old forests. Similarly, bryophytes enter a stand near the forest floor and gradually expand their dominance upwards. Epiphyte biomass was greatest in the old-growth stand, with about 2.6 t/ha. In the two younger stands total epiphyte biomass was about 1 t/ha. The old-growth stand differed from the younger stands in having over 1 t/ha of cyanolichens, while this group was essentially absent from the younger stands. As a synthesis of these and previous results, a similar gradient hypothesis is proposed: epiphyte species are ordered similarly on three distinct spatial and temporal gradients: 1) vertical differences in species composition within a given stand, 2) species compositional differences among stands differing in moisture regime but of the same age, and 3) changes in species composition through time in a given stand.*

We know little about how the biomass of forest epiphytes changes through time and how it responds to various disturbances (e.g., reinvasion after clear-cutting or fire). This is partly a result of the difficulty of estimating biomass of epiphytes on a complex three-dimensional substrate (trees). Previous biomass estimates in the temperate rainforests of the Cascade Range were limited to several large trees in Oregon (Pike et al. 1972, 1977) and scattered clumps of trees on a lava flow in Washington (Rhoades 1981).

This paper reports on patterns of epiphyte distribution and abundance within and among three stands of different ages (95, 145, and > 400 years). Epiphytes were sampled on small groups of felled trees as part of development of methods for obtaining more rapid estimates of epiphyte biomass.

A second objective of this paper is to extract the commonalities in three gradients affecting epiphytes: vertical, successional, and moisture gradients. Toward this end, I propose the "similar gradient hypothesis": epiphyte species or species groups are ordered similarly along these three distinct spatial and temporal gradients.

STUDY AREA

Three forests of different ages were sampled in the Cascade Range, Oregon and Washington. The old-growth site

(age 400+ years, elevation 915 m, (44°16'N, 122°9'W) was in the H. J. Andrews Experimental Forest, east of Eugene. The younger stands (aged 95 and 145 years, elevations 550 and 500 m, 45°49'N, 121°53'W) were in Wind River Experimental Forest in southern Washington. The dominant species in all three stands was *Pseudotsuga menziesii* (Mirbel) Franco. *Tsuga heterophylla* (Raf.) Sarg., and to a lesser extent, *Thuja plicata* Donn., were the predominant understory trees. In the old-growth stand the *Pseudotsuga* trees often had broken tops and many of the *Thuja* and *Tsuga* were codominant in the canopy. The species list of epiphytes in Pike et al. (1975) is representative of the species occurring in these three stands. Although present nearby, nonparasitic vascular epiphytes (e.g., *Polypodium*) were absent in these stands.

At the Oregon site average annual temperature is 9.5°C, with January and July means of 2 and 22°C respectively (Waring et al. 1978). Average annual precipitation is 240 cm with 70% of that from November through March. At the Washington site average annual temperature is 8.8°C, with January and July means of 0 and 18°C respectively (unpublished climatological summary, Wind River Experimental Forest, 1911-1965). Average annual precipitation is 250 cm.

METHODS

Small groups of trees (to 0.5 ha) were carefully felled in fall 1990. Epiphyte biomass on branches and trunks was estimated for 42 individual felled trees, then extrapolated to the whole stands by regression techniques. Sample sizes for individual stands ranged from seven trees in a relatively uniform young stand to 22 trees of various sizes and species in the old-growth stand. Diameters at breast height

(dbh) ranged from 3 to 170 cm and heights ranged from 2 to 65 m. Trees were selected to sample the range of sizes and species, with the additional constraint that trees with the least damage in falling were preferred. This was particularly a problem with the large (1–2 m dbh, to 65 m tall) *Pseudotsuga*, whose crowns often exploded on impact. For all of the large trees, but especially for *Pseudotsuga*, loss of thick moss mats near branch bases probably resulted in underestimates of biomass of branch epiphytes. On the other hand, this problem was minimized by selecting trees and branches that suffered the least damage.

FUNCTIONAL GROUPS

To reduce the extremely labor-intensive task of sorting epiphytes by species, they were instead sorted into four functional groups. 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, what eats them, microhabitats occupied, and responses to air pollutants.

“Cyanolichens” include all macrolichens with a cyanobacterium as a primary or secondary photobiont [in this case mainly *Lobaria oregana* (Tuck.) Mull. Arg. with smaller amounts of other *Lobaria* species, *Nephroma*, *Peltigera*, *Pseudocyphellaria*, and *Stictia*]. 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 *A. sarmentosa* (Ach.) Ach. 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 & Oldemeyer 1989; Servheen & Lyon 1989).

The group “other lichens” includes all remaining macrolichens, mainly *Platismatia* and *Hypogymnia* species. These species do not fix nitrogen, have less well documented relationships to wildlife, and 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, in this case excluding some small leafy liverworts and pleurocarpous mosses that were very tedious to remove from the bark. 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 & Antos 1982). The predominant bryophytes in this study were *Antitrichia curtipendula* (Hedw.) Brid., *Dicranum fuscescens* Turn., *Isoetes myosuroides* Brid., *Metaneckera menziesii* (Drumm.) Steere, and *Porella navicularis* (Lehm. & Lindenb.) Lindb.

ESTIMATING BIOMASS ON INDIVIDUAL TREES

All biomass results are based on oven-dry (24 hr. at 60°C) weights, recorded to the nearest 0.001 g. Separate estimates for each functional group were made for branches and the main trunk on each tree. Several small trees (<5 m tall) in each stand were stripped completely rather than subsampled. Larger trees were systematically subsampled using three-stage hierarchical sampling as described below. The 527 sample units (quadrats, cylinders, and branch segments) were collected from throughout the trees.

Biomass on trunks was estimated by stripping epiphytes from opposing 0.5 x 0.2 m quadrats at 4–6 m intervals up the trunks, or using 0.5 m cylinders when trunk diameters were less than 20 cm. An appropriate multiplier was then used to bring biomass up to a g/m basis. To estimate total epiphyte biomass on the trunk, these values were then numerically integrated along the length of the trunk, using straight-line segments to approximate biomass density between sample points. Integration using spline functions was also tried but gave unsatisfactory results for the abrupt spatial discontinuities that are frequently found in biomass distributions.

Branch density (branches/m) and epiphytes on branches were sampled at intervals along the trunks. Small branches were stripped completely; branches > 1.5 m long were subsampled by stripping epiphytes within four evenly-spaced 0.5 m-wide concentric arcs (subsamples), using a measuring tape nailed to the base of the branch. Biomass on each subsampled branch was estimated by numerical integration along the branch. Individual branch estimates were then aggregated to the whole tree by first multiplying branch density by epiphyte biomass along the length of the trunk, then numerically integrating the resultant epiphyte biomass values along the whole trunk.

The series of steps of integration was accomplished with program BIOMASS (McCune, unpubl.), resulting in estimates of biomass by functional group for trunks and branches as well as graphs of vertical and horizontal distributions of epiphyte biomass on individual trees.

AGGREGATING FROM TREE LEVEL TO STAND LEVEL

Stand-level biomass of each functional group of epiphytes was calculated by using the stand-specific regression equations relating epiphyte biomass to tree dbh and species. The regression equations were then applied to extensive tree dbh data for the stand (Easter & Spies 1993) to estimate epiphyte biomass on trees not included in the direct sample.

The fit between tree dbh and epiphyte biomass was closest when epiphyte biomass was log-transformed and tree dbh was transformed by the square root of the log. A simple log transform of tree dbh gave nearly as good a fit, but taking the square root of the log is more conservative because trees with dbh somewhat larger than the largest tree sampled for epiphytes (i.e., extrapolated beyond the calibration region of the regression equation) show a relatively strong exponential increase in back-transformed biomass. On biological grounds it seemed more prudent to assume that epiphyte biomass should not increase rapidly with small diameter increments to large trees. (For example, large portions of the tops often break out of old trees.) The biomass of individual functional groups of lichens in individual stands was strongly related to tree dbh, with $0.68 < r^2 < 0.97$ and all but two r^2 values > 0.8 . The quality of these fits allowed biomass estimates for trees not sampled for epiphytes.

In contrast to lichens, biomass of bryophytes showed little relationship to tree size in the younger stands. Bryophytes in these stands were, therefore, rather evenly distributed on a biomass basis between small suppressed trees and the bases of larger trees. Biomass of bryophytes showed a fairly strong relationship to tree dbh in the old growth stand ($r^2 = 0.57$). Binary variables indicating tree species were allowed to enter these equations, but in only three cases did including a tree-species variable provide a significant improvement in fit of the equations.

Log(biomass) of each functional group was thus cal-

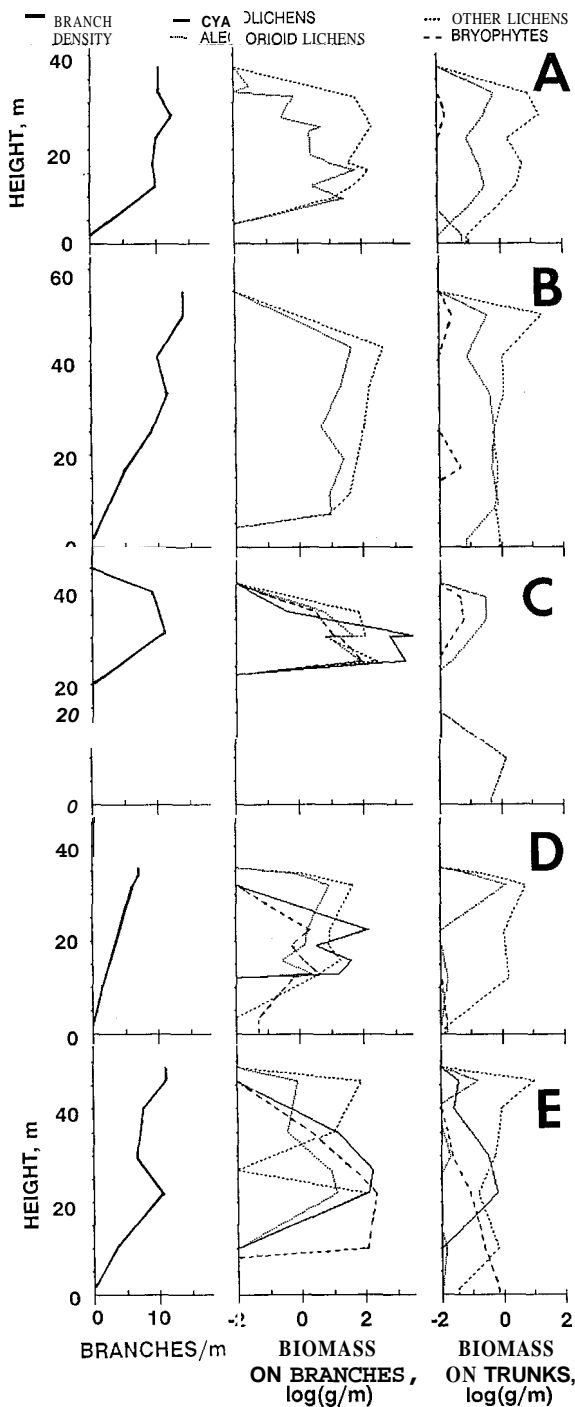


FIGURE 1. Vertical distribution of epiphytes in selected trees from three forests of different ages in the Cascade Range, Oregon and Washington. A. 50 cm dbh, 37 m tall *Pseudotsuga* from a stand 95 years old, B. 96 cm dbh, 55 m tall *Pseudotsuga* from a stand 145 years old, C. 107 cm dbh, 48 m tall (broken top) *Pseudotsuga* from a stand 400+ years old, D. 42 cm dbh, 35 m tall, understory *Tsugu heterophylla* from a stand 400+ years old, E. 109 cm dbh, 49 m tall *Thuja plicata* from a stand 400+ years old. Total biomass values for each functional group on each of these trees are given in Table 1.

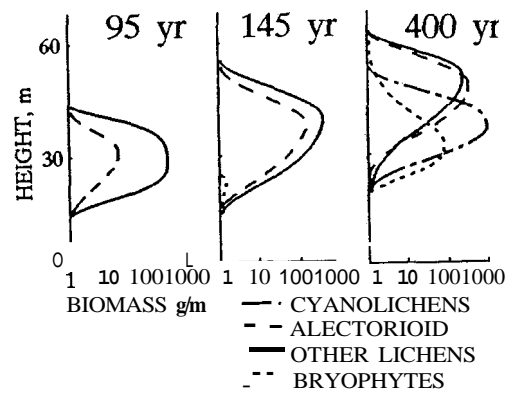


FIGURE 2. Summary curves for vertical distribution of epiphytes in three *Pseudotsuga-Tsuga* forests of the western Cascades.

culated for each of 600–800 trees in each of the three stands (tree data from Easter & Spies 1993). These values were back-transformed and then summed to provide stand-level biomass estimates. Back-transforming from a regression line introduces a downward bias (Baskerville 1972), but this effect was eliminated by reintroducing the original error variance into the predicted biomass. This was done by adding to each individual tree's biomass estimate a random number taken from a normal distribution having a mean of zero and a standard deviation based on the error sums of squares of the regression equations. Because of the large number of trees, the consequences of choosing a particular sequence of random numbers were minimal.

RESULTS

SPATIAL DIFFERENCES WITHIN INDIVIDUAL TREES

There were pronounced vertical differences in species composition on both trunks and branches. In general the sequence of dominance of the four functional groups, from top to bottom was: "other" lichens, alectorioid lichens, cyanolichens, and bryophytes (Fig. 1–2). This pattern was consistent among all three stands, except that the series was truncated in the younger stands where cyanolichens were essentially absent and bryophytes were much less abundant.

Biomass on branches was typically 10–100 times higher than that on the trunks (e.g., Table 1); however this pattern is quite variable, both among and within stands. Apparently the ratio of biomass on branches to biomass on trunks increases with stand age, but more data are needed.

DIFFERENCES AMONG TREES IN THE SAME STAND

The strongest pattern of differences in biomass among trees within stands is that there is more biomass on larger trees. This relationship is typically quite strong, with regressions on log-log (or square-

TABLE 1. Biomass (kg) of epiphytes in four functional groups on five individual trees in the Cascades (trees A, B, C, D, and E correspond to those in Fig. 1).

			Cyano- lichens	Alectorioid lichens	Other lichens	Bryophytes	Total
A	<i>Pseudotsuga</i> , 50 cm dbh, 37 m tall, 95- year stand	trunk	0.0	< 0.1	0.2	< 0.1	0.2
		branches	0.0	0.3	2.3	0.0	2.6
		total	0.0	0.3	2.5	0.0	2.8
B	<i>Pseudotsuga</i> , 96 cm dbh, 55 m tall, 145- year stand	trunk	0.0	< 0.1	0.2	< 0.1	0.2
		branches	0.0	0.9	7.1	0.0	8.0
		total	0.0	0.9	7.3	0.0	8.2
C	<i>Pseudotsuga</i> , 107 cm dbh, 48 m tall (bro- ken top), 400-year stand	trunk	0.0	< 0.1	0.1	< 0.1	0.1
		branches	1.1	0.1	0.4	< 0.1	1.6
		total	1.1	0.1	0.5	< 0.1	1.7
D	<i>Tsuga</i> , 42 cm dbh, 35 m tall, 400-year stand	trunk	0.0	< 0.1	< 0.1	< 0.1	< 0.1
		branches	22.9	0.5	1.7	0.4	25.5
		total	22.9	0.5	1.7	0.4	25.5
E	<i>Thuja</i> , 109 cm dbh, 48 m tall, 400-year stand	trunk	< 0.1	< 0.1	0.1	< 0.1	0.1
		branches	2.2	0.2	1.5	2.9	6.8
		total	2.3	0.2	1.6	2.9	7.0

root-log transformed) plots typically having an r^2 between 0.75 and 0.95 with tree dbh ranging over one order of magnitude and epiphyte biomass ranging over three or more orders of magnitude.

Insufficient data were collected to describe accurately the differences in epiphyte biomass among tree species within a size class. The problem was exacerbated by the difficulty of obtaining accurate estimates for the large *Pseudotsuga* in old growth stands because such trees tended to disintegrate as they hit the ground when felled. Field observations suggest, however, that *Pseudotsuga* supports more epiphyte biomass for a given size than does *Thuja* or *Tsuga*.

STAND-LEVEL BIOMASS

Epiphyte biomass was greatest in the old-growth stand, with about 2.6 t/ha (Table 2). In two younger stands total epiphyte biomass was about 1 t/ha. The old-growth stand differed from the younger stands in having over 1 t/ha of cyanolichens, while this group was essentially absent from the younger stands (Table 2, Fig. 3). [Although cyanolichens did not occur in the quantitative sample from these stands, small amounts of cyanolichens were observed.] "Other" lichens were dominant in the 95-year stand and were less so in the 145- and 400+-year stands. Alectorioid lichens showed the opposite pattern, with increasing abundance in the older stands (Table 2, Fig. 3).

DISCUSSION

The vertical sequence of epiphyte dominance in the old-growth stand appeared to correspond with

the pattern of dominance in the sequence of stand ages. "Other" lichens dominated the upper canopy in the old growth and had highest biomass in the 95-year stand (Fig. 2-3). Alectorioid lichens tended to peak at a height just below "other" lichens, and had only slightly higher biomass in the 400- than the 145-year stand which, in turn, had more alectorioid biomass than the 95-year stand. At over 1 t/ha, cyanolichens peaked at a height below alectorioid lichens in the old growth and were virtually absent from the younger stands. Bryophytes dominated closest to the ground in the old growth and, although present on tree bases in all stands, were much more abundant in the 400-year stand.

The many studies of vertical and radial within-tree gradients in epiphyte distribution and abundance all speculate on environmental and successional controls. In some cases environmental variables and successional age have been measured (e.g., Barkman 1958; Stone 1989; Yarranton 1972). All such studies face a problem that seems to preclude simple, general, mechanistic explanations of epiphyte distribution and abundance. The problem is that environmental and successional gradients are thoroughly confounded. For example, temperature, moisture, frequency of wetting and drying, light, nutrients, substrate age, bark characteristics, and accumulation of humus are all intercorrelated. It may be both futile and unnecessary to attempt a mechanistic separation of these factors when, from a biological standpoint, the most significant observation about these factors is that they change in concert. An alternative approach is to step back from the mechanistic explanation and observe the large scale commonalities in distributional patterns. Then, using these common-

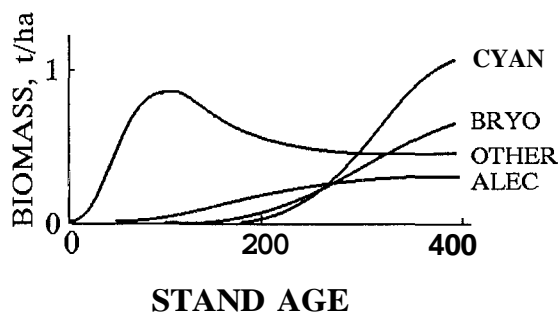


FIGURE 3. Semi-empirical curves for changes in epiphyte biomass through time in *Pseudotsuga-Tsuga* forests of the western Cascades. Each curve passes through the three data points representing the 95-, 145-, and 400+-year old stands sampled in this study. The curves were interpolated between those points to produce smooth curves.

as guidance, we can revisit environmental and successional factors, and perhaps suggest how those combined factors control species distributions through the life histories of those species.

THE SIMILAR GRADIENT HYPOTHESIS

A description of the pattern of epiphyte distribution within any particular forest does not correspond directly with patterns in other forests differing in structure, stand age, and local climate. For example the patterns described by Pike et al. (1975) differ from those observed in other old-growth forests, even a short distance from the trees they studied. Likewise many of the species largely restricted to old-growth forests in western Montana (Lesica et al. 1991) are common in young forests in western Oregon. Many species that are restricted to the tree-tops in temperate rainforests are found in drier climates (western Montana) only on lower trunks on mesic sites. Hale (1965) found that certain species restricted to lower heights in a young forest in Connecticut were found higher in the trees of an old forest in Wisconsin (Hale 1952).

Although these may seem like disparate observations, they can be understood through a common framework. These observations can be considered specific expressions of a more general principle that can be called the "similar gradient hypothesis."

The observation of parallel gradients is not new. Both Pike et al. (1975) and Szczawinski (1953) noted that zones of occurrence of epiphytes on trunks of trees in xeric sites were displaced upward on trunks in more mesic sites. Similar shifts were reported by Barkman (1958, p. 39).

The present study, along with other studies of epiphytes on conifers of western North America, led to the following hypothesis: epiphyte species are ordered similarly on three distinct spatial and tem-

TABLE 2. Biomass of epiphytes (t/ha) for each of four functional groups in three stands of different ages (years) in the Cascade Range, Oregon and Washington. All stands were dominated by *Pseudotsuga menziesii* and *Tsuga heterophylla*.

Functional group	Stand age		
	95	145	400+
Cyanolichens	0.00	0.00	1.14
Alectorioid lichens	0.03	0.12	0.18
Other lichens	0.92	0.75	0.55
Bryophytes	0.18	0.01	0.78
Total	1.13	0.88	2.65

poral gradients. These gradients are 1) vertical differences in species composition within a given stand, 2) species-compositional differences among stands differing in *moisture* regime but of the same age, 3) changes in species composition *through time* in a given stand.

Although the hypothesis suggests that there are commonalities in response of epiphytes to these three gradients, the underlying spatial and temporal gradients are distinct, because one could just as easily imagine different species-compositional changes along each of the gradients. The hypothesis is not tautological because it is falsifiable (Peters 1992). A larger data set would be needed to test the hypothesis convincingly, the data set spanning temporal, vertical, and climatic gradients. An appropriate statistical test would be to compare rank orderings of species maxima along the three gradients. To the extent that the hypothesis survives closer scrutiny, it would carry predictive value. For example, if one knew the vertical profile of species in an area, one could potentially predict future changes in species composition in a stand. Similarly, the hypothesis has potential explanatory value in reconciling seemingly disparate results from different study areas. Tentative explanations for the correspondences among these three gradients are described below.

The vertical gradient in epiphyte composition is related to gradients in macroclimatic (stand-level) moisture regime because the vertical gradient in a canopy is, in part, a moisture gradient. Upper canopy epiphytes are exposed to an overall drier environment than are lower canopy epiphytes. There is also a vertical difference in frequency of wetting and drying, lower canopy positions having more evenly humid conditions while upper canopy positions are wetted most frequently (by light rains and dew), but dry rapidly (Geiger 1965).

The stand-age gradient is related to a moisture gradient among stands because as young even-aged stands begin to break up through time into vertically complex irregular structures, light and moisture

penetration into the lower canopy increase, improving the moisture availability to lower- and mid-canopy epiphytes (see Ch. 6, Geiger 1965). Furthermore the ability of epiphytes to colonize upper and outer branches necessarily coincides with tolerance of relatively dry microsites. This means that species that appear early in branch succession will, in general, be able to occupy relatively dry stands.

The stand-age gradient is related to the vertical gradient because 1) species with relatively good colonizing ability will be found on younger substrates, whether the comparison is made among stands or within a stand, and 2) the stand age and vertical gradients are linked by the gradients in moisture regime as described above.

Some preliminary empirical evidence supporting this hypothesis is available from conifer forests of the Pacific Northwest of North America, as described below. A comprehensive test of the hypothesis has yet to be done.

Correspondence between the vertical gradient and the stand-age gradient was seen in the present study. The four functional groups colonize the forest in the same sequence through time as the order of vertical dominance in old growth, from top to bottom: "other" lichens (mainly *Hypogymnia* and *Platismatia*), alectorioid lichens (mainly *Alectoria sarmentosa*), cyanolichens (mainly *Lobaria oregana*), and bryophytes. It follows from these observations that zones of epiphytes migrate upwards in forests through time. For example, the *Hypogymnia* and *Platismatia* that dominate throughout young forests are found primarily in the upper canopies of old forests. Similarly, bryophytes enter a stand near the forest floor and gradually expand their dominance upwards.

The link between the stand age and among-stand moisture gradients was seen in conifer forests in western Montana. Epiphytes responded to stand moisture and stand-age gradients—defined by vascular plants—as though to a single gradient (McCune & Antos 1982). This was shown by superimposing an ordination of epiphyte communities onto an ordination of vascular plant communities, using the same reference stands for both ordinations. Epiphyte communities in young stands were similar to those in dry stands; similarly epiphyte communities in old stands were similar to those in wet stands.

Like most generalizations in ecology, the similar gradient hypothesis will have limited predictive capabilities, and will suffer numerous exceptions. The hypothesis does, however, draw attention to the similarities in epiphyte response to the three gradients and may be useful in integrating epiphyte studies across regional climatic gradients and in different continents.

ACKNOWLEDGMENTS

This paper is dedicated to Mason Hale, who taught me during the summer of 1977 at the University of Montana Biological Station, and who helped me get a firm footing in lichen taxonomy during my Master's field work. I am greatly indebted to my field and lab helpers: Bill Daly, John Davis, Ann DeBolt, Jeff Green, Roger Rosentreter, and Laura Wilson. Tree felling, stand and tree data, and other assistance were provided by Mark Easter, Tom Spies, and other cooperators in a study of processes in forest gaps funded by the National Science Foundation (BSR 8909038) to T. Spies, J. Franklin, and C. Vogt. Logistic support was provided by the H. J. Andrews and Wind River Experimental Forests. I appreciate the comments and advice of Bill Denison, Per-Anders Esseen, Patricia Muir, William Reese, Fred Rhoades, Lorene Sigal, Steve Sillett, Susan Stevenson, and an anonymous reviewer. The Oregon State University Research Council provided partial support of this research.

LITERATURE CITED

- BARKMAN, J. J. 1958. Phytosociology and Ecology of Cryptogamic Epiphytes. Assen.
- BASKERVILLE, G. L. 1972. Use of logarithmic regression in the estimation of plant biomass. Canadian Journal of Forest Research 2: 49–53.
- DURING, H. J. 1992. Ecological classification of bryophytes and lichens, pp. 1–31. In J. W. Bates & A. M. Farmer (eds.), Bryophytes and Lichens in a Changing Environment. Oxford.
- EASTER, M. J. & T. A. SPIES. 1993. Description of an experimental study of canopy gaps in old-growth and mature forests in the Pacific Northwest, USA. USDA Forest Service, Forestry Services Laboratory, Corvallis.
- EDWARDS, R. Y., J. SOOS & R. W. RITCEY. 1960. Quantitative observations on epidendric lichens used as food by caribou. Ecology 41: 425–431.
- GEIGER, R. 1965. The Climate Near the Ground. Cambridge, MA.
- GRIME, J. P., E. R. RINCON & B. E. WICKERSON. 1990. Bryophytes and plant strategy theory. Botanical Journal of the Linnean Society 104: 175–186.
- HALE, M. E., JR. 1952. Vertical distribution of cryptogams in a virgin forest in Wisconsin. Ecology 33: 398–406.
- . 1965. Vertical distribution of cryptogams in a red maple swamp in Connecticut. THE BRYOLOGIST 68: 193–197.
- LESICA, P., B. McCUNE, S. COOPER & W. S. HONG. 1991. Differences in lichen and bryophyte communities between old-growth and managed second-growth forests. Canadian Journal of Botany 69: 1745–1755.
- MASER, C., Z. MASER, J. W. WITT & G. HUNT. 1986. The northern flying squirrel: a mycophagist in southwestern Oregon. Canadian Journal of Zoology 64: 2086–2089.
- MASER, Z., C. MASER & J. M. TRAPPE. 1985. Food habits of the northern flying squirrel (*Glaucomys sabrinus*) in Oregon. Canadian Journal of Zoology 63: 1084–1088.
- MCCUNE, B. & J. A. ANTOS. 1982. Epiphyte communities of the Swan Valley, Montana. THE BRYOLOGIST 85: 1–12.
- PETERS, R. H. 1992. A Critique for Ecology. Princeton.
- PIKE, L. H., W. C. DENISON, D. TRACY, M. SHERWOOD & F. RHOADES. 1975. Floristic survey of epiphytic lichens and bryophytes growing on living, old-growth

- conifers in western Oregon. *THE BRYOLOGIST* 78: 39 1-404.
- , R. A. RYDELL & W. C. DENISON. 1977. A 400-year-old Douglas fir tree and its epiphytes: biomass, surface area, and their distributions. *Canadian Journal of Forest Research* 7: 680-699.
- , D. M. TRACY, M. A. SHERWOOD & D. NIELSEN. 1972. Estimates of biomass and fixed nitrogen of epiphytes from old-growth Douglas-fir, pp. 177-187. *In* J. F. Franklin et al. (eds.), *Proceedings—Research on Coniferous Forest Ecosystems—A Symposium*. Bellingham, WA. March 23-24, 1972. USDA Forest Service, Pacific Northwest Forest and Range Experiment Station. Portland, OR.
- RHOADES, F. M. 1981. Biomass of epiphytic lichens and bryophytes on *Abies lasiocarpa* on a Mt. Baker lava flow, Washington. *THE BRYOLOGIST* 84: 39-47.
- RICHARDSON, D. H. S. 1988. Understanding the pollution sensitivity of lichens. *Botanical Journal of the Linnean Society* 96: 31-43.
- ROMINGER, E. M. & J. L. OLDEMEYER. 1989. Early-winter habitat of woodland caribou, Selkirk Mountains, British Columbia. *Journal of Wildlife Management* 53: 238-243.
- SERVHEEN, G. & L. J. LYON. 1989. Habitat use by woodland caribou in the Selkirk Mountains. *Journal of Wildlife Management* 53: 230-237.
- STEVENSON, S. K. 1978. Distribution and Abundance of Arboreal Lichens and their Use as Forage by Black-tailed Deer. M.S. thesis, University of British Columbia, Vancouver.
- STONE, D. 1989. Epiphyte succession on *Quercus garryana* branches in the Willamette Valley of western Oregon. *THE BRYOLOGIST* 92: 8 1-94.
- SZCZAWINSKI, A. 1953. Corticolous and lignicolous communities in the forest associations of the Douglas-fir forest on Vancouver Island. Ph.D. dissertation, University of British Columbia, Vancouver.
- WARING, R. H., H. R. HOLBO, R. P. BUEB & R. L. FREDRIKSEN. 1978. Documentation of meteorological data from the coniferous forest biome primary station in Oregon. USDA Forest Service, General Technical Report PNW-73. Portland, OR.
- YARRANTON, G. A. 1972. Distribution and succession of epiphytic lichens on black spruce near Cochrane, Ontario. *THE BRYOLOGIST* 75: 462-480.