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Canopy Epiphyte Studies in the Central Oregon Cascades: Implications for the Management of Douglas-Fir Forests

by

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Abstract

This thesis includes four separate studies. The first two studies assessed edge effects in a 700-year-old forest. After 20 years of exposure, epiphyte assemblages on the clearcut edge were similar to those of the forest interior, but there were some differences in vertical distribution patterns. Several species restricted to the upper canopy of the forest interior occurred farther down in the crowns of trees on the clearcut edge. Many species were associated with thick moss mats. Thalli of two cyanolichen species were reciprocally transplanted among four tree crowns. *Lobaria oregana* grew less on the clearcut edge than in the forest interior. Populations of *Pseudocyphellaria rainierensis* had acclimated to the edge environment. The third study evaluated whether these two species require old growth and/or thick, underlying moss mats to achieve normal rates of growth and mortality. Thalli were transplanted into tree crowns in 13 forest stands representing 4 age classes: old growth, mature, young, and recent clearcut. Wooden racks were used instead of trees in clearcuts. Half of the cyanolichen thalli were transplanted onto thick moss mats, half onto bare bark. Both species grew at least as well in the younger forests as they did in old growth, but growth rates were significantly lower in clearcuts. Mortality rates were very low in young, mature, and old-growth forests but high in clearcuts. *P. rainierensis* grew significantly better on moss than bare bark. The fourth study evaluated the long-term potential of live tree retention for cyanolichen conservation. Lichen litterfall was sampled in a natural, multiple-age stand containing remnant trees and regenerating forest. Two lichen species (*L. oregana* and *Sphaerophorus globosus*) were strongly associated with remnant trees. Biomass of both species was highest near remnant trees and was significantly higher within groves of remnant trees than at the edges of these groves or near isolated trees. Cyanolichen populations appear to have persisted on remnant trees since before the last fire. They are slowly recolonizing the regenerating forest. Retention of live trees, including hardwoods, combined with longer rotation periods, has great potential to maintain cyanolichens in managed forests.

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Canopy Epiphyte Studies in the Central Oregon Cascades: Implications for Management of Douglas-Fir Forests

Chapter 1. Introduction

Canopy epiphyte research in the Pacific Northwest has entered its third decade, and three basic patterns of epiphyte distribution are now known. First, epiphyte biomass and diversity slowly increase during forest succession. This trend is most obvious with cyanolichens, which dominate epiphyte communities in old-growth forests but are scarce in younger forests. Second, epiphyte functional groups seem to migrate upwards in the forest canopy during succession. In the oldest and wettest forests, bryophytes come to dominate epiphyte communities, and several species of terrestrial plants actually grow on branches in the upper canopy. Third, cyanolichens are most abundant in old-growth forests on lower slopes. They are scarce in similar forests located farther upslope away from streams. Causes of these three patterns are not clearly understood, but they have important consequences for epiphyte recovery in managed forests. In this introductory chapter, I review several key studies of epiphytes in the Pacific Northwest in order to establish the context of my thesis research in Douglas-fir forests of the central Oregon Cascades.

Epiphytic lichens and bryophytes are a conspicuous and ecologically significant component of westside forests in the Pacific Northwest, where their biomass can exceed three tons per hectare (McCune 1993, Neitlich 1993). These epiphytes can be divided into four functional groups based on their ecological roles: cyanolichens, 'alectorioid' or forage lichens, 'other' lichens, and bryophytes (McCune 1993). Cyanolichens, or nitrogen-fixing lichens, are the dominant epiphytes in old-growth forests where they constitute over half of the total epiphyte biomass (Pike et al. 1977, Rhoades 1981, McCune 1993, Neitlich 1993).

They fix large quantities of atmospheric nitrogen (Pike 1978, Denison 1979), making it available for plant uptake. Nitrogen-rich leachates from these lichens also serve as a base for complex food webs in the forest canopy (Carroll 1979). Epiphytes have other important functions in forest ecosystems, such as providing critical winter forage for mammals, serving as food and habitat for invertebrates, and providing nesting material for birds (Slack 1988, Rhoades 1994).

Early studies of epiphytes documented the floristic composition of the old-growth forest canopy (Denison 1973, Pike et al. 1975) and quantified epiphyte biomass in selected tree crowns (Pike et al. 1977, Rhoades 1981). Recently, McCune (1993) proposed the similar gradient hypothesis which provides a framework for understanding the distribution of epiphytes in westside forests. According to this hypothesis, "epiphyte species are ordered similarly on three distinct spatial and temporal gradients. These gradients are 1) vertical differences in species composition in 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" (McCune 1993). Although, empirical support for McCune's hypothesis is currently insufficient to fully test it, supporting evidence is increasing, especially for cyanolichens.

SLOW DEVELOPMENT OF EPIPHYTE COMMUNITIES

Studies in Europe (Rose 1992, Esseen and Renhorn 1995), New England (Selva 1994), Montana (Lesica et al. 1991), and Oregon (McCune 1993, Neitlich 1993) have demonstrated that old-growth forests support far more diverse and abundant epiphyte communities than do younger forests. In westside Douglas-fir forests of the Pacific Northwest, the most striking difference between epiphyte communities of old-growth

forests and younger forests occur with cyanolichens, which dominate the old-growth canopy (Pike et al. 1975) but are scarce or absent in younger forests (Figure 1.1). Several epiphytic cyanolichen species are seldom found in forests less than a century old (Table 1.1, U.S.D.A. 1994). The reasons for this slow development of epiphyte communities during forest succession are not entirely clear. Possible explanations include dispersal limitations, unsuitable substrates, and unsuitable canopy microclimates in younger forests.

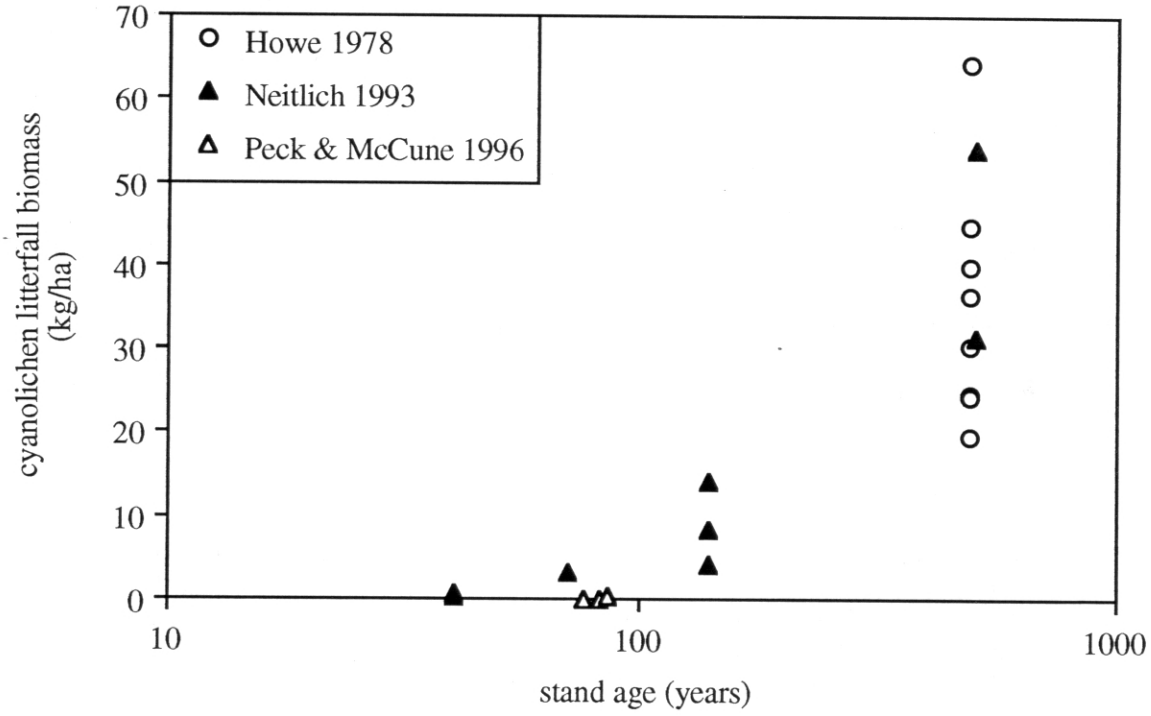

Figure 1.1. The relationship between epiphytic cyanolichen biomass and stand age for 19 forest stands in the central Oregon Cascades. All stands were below 900 m elevation, less than 100 m above a major stream, and dominated by Douglas-fir. The X-axis is on a log scale.

Dispersal limitations appear to be important in certain cases. The effects of dispersal limitations can be most readily observed when barriers to dispersal are removed. For

Table 1.1. Rare epiphytic cyanolichen species associated with late-successional and old-growth coniferous forests in the Pacific Northwest. A dagger (†) signifies species endemic to the Pacific Northwest of North America.

Species	Occurrence	Notes
Dendriscocaulon intricatulum	3, 16, 17	extremely rare
Lobaria linita	1, 3, 4, 7, 11, 16, 17, 18, 19	mostly on rock at high elevations in CA, OR, and WA; also epiphytic at low elevations in AK, rarely south to OR and WA
Nephroma occultum†	3, 4, 16, 17	middle to upper canopy in in OR and WA; occurs lower in canopy in BC and AK
Pannaria rubiginosa	2, 3, 4, 11, 16	lower to middle elevation forests
Pseudocyphellaria sp. (close to *P. aurata*)	4, 14	primarily coastal; known from 4 collections, all in OR
Pseudocyphellaria rainierensis†	1, 3, 4, 7, 16, 17	lower canopy and understory
Sticta weigelii	1, 3, 4, 7, 16	lower to middle canopy and understory
Sticta wrightii	16, 17	extremely rare

Occurrence Codes:
1. Olympic Peninsula
2. Western Washington Lowlands
3. Western Washington Cascades
4. Western Oregon Cascades
5. Eastern Washington
6. Eastern Oregon Cascades
7. Oregon Coast Range
8. Willamette Valley
9. Oregon Klamath
10. California Klamath
11. California Coast Range
12. California Cascades
13. California Coast
14. Oregon Coast
15. Washington Coast
16. British Columbia
17. Southeast Alaska
18. Idaho
19. Montana

example, late successional epiphytes can become abundant in a young forest growing within 10 m of an old-growth forest edge even though they are scarce in the interior of the young forest. Many of these species might be capable of long-distance dispersal via

spores, tiny asexual propagules, or both, and their complete absence from younger forests is not to be expected unless suitable substrates or microclimates are lacking in younger forests. Long-term studies involving inoculations of bark surfaces with epiphyte propagules are needed to determine if dispersal is a major factor limiting epiphyte colonization of tree crowns.

Support for substrate limitation as a factor contributing to epiphytic differences between old and young forests comes from a study in Glacier Bay, Alaska (P. Neitlich, unpublished). There, cyanolichen species richness was considerably higher on *Alnus sinuata* than *Picea sitchensis* in young stands, whereas 200-year-old Picea trees harbored a richness similar to that found in *Alnus* trees one hundred years younger (Figure 1.2). In some conifer forests of western Oregon, a similar phenomenon seems to occur on *Acer*, *Fraxinus*, and *Quercus* instead of *Alnus*. Perhaps the smooth bark of young conifers is less likely to retain epiphyte propagules than the rougher bark of older trees or hardwoods (Armstrong 1990). Alternatively, bark chemistry, crown architecture, and/or light environment may account for differences in epiphyte communities between conifers and hardwoods (Hyvärinen et al. 1992). Controlled studies of epiphyte establishment on a wide range of bark substrates available in westside forests are greatly needed. The potential of hardwood retention as a means of boosting epiphyte species diversity in managed forests is a promising area for future research.

A third impediment to epiphyte community development in young forests may be unsuitable canopy microclimates. Young, even-aged forest canopies are very shaded and sheltered from direct precipitation in contrast to the more open and structurally complex old-growth forest canopy (see Ch. 6, Geiger 1965). Thus, low moisture and light availability in young, managed forests may limit the growth of some canopy epiphytes (Rose 1992). The idea that the suitability of epiphytic habitats in a forest canopy improves during succession is compelling, but so far no studies have demonstrated such an effect.

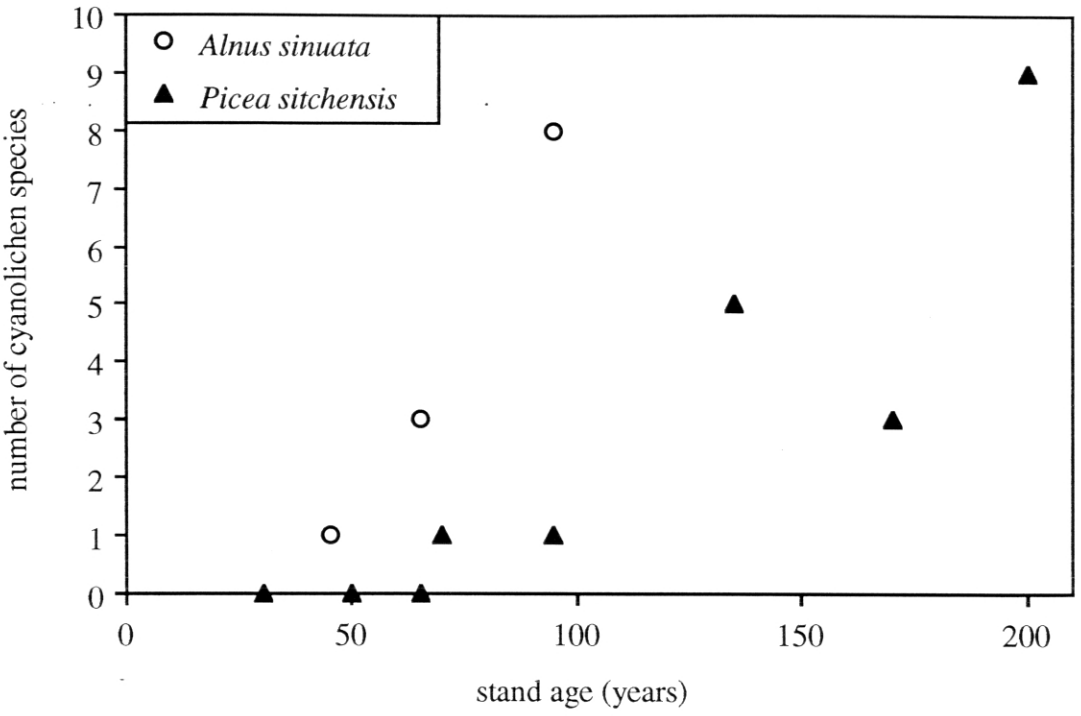

Figure 1.2. The effect of forest age on cyanolichen species richness on two tree species in spruce forests of Glacier Bay, Alaska. Total number of cyanolichen species are presented for each tree species in each site where they were found in the chronosequence. Tree species in each site were surveyed until four trees were climbed with no additional lichen species encountered. Unpublished data provided by P. Neitlich.

Documentation of the micrometeorological basis for this effect (i.e., light and humidity regimes) requires an enormous and costly effort. Experiments involving transplanting epiphytes in tree crowns (Chapters 2 and 4) are a reasonable alternative in which growth rates provide a relative measure of epiphyte habitat suitability in forests of different ages.

UPWARD MIGRATION OF EPIPHYTE FUNCTIONAL GROUPS

McCune (1993) described an apparent upward migration of epiphyte functional groups in forest canopies over time: 'other' and 'alectorioid' lichens are the first epiphytes to colonize young forests, but they are steadily displaced upwards in tree crowns by cyanolichens and bryophytes, which come to dominate the lower forest canopy. The oldest forest included in McCune's study was just over 400 years. Does this upward migration continue? Studies of very old Douglas-fir forests (Chapter 2) are needed to evaluate this hypothesis. In the oldest, wettest forests of the Pacific Northwest, such as those found in the true rainforests of Mount Rainier and Olympic National Parks, Washington, as well as parts of Vancouver Island and southeast Alaska, the upward migration of epiphytes appears to have progressed to its limit—an almost complete domination of the canopy by bryophytes. In fact, many terrestrial species of mosses and vascular plants have been observed growing on branches in the upper canopies of these forests (Table 1.2). Factors controlling the rates of upward migration of epiphytes are not understood, although bryophyte domination of the canopy appears to be most rapid in very wet coastal forests.

THE RIPARIAN EFFECT ON EPIPHYTIC CYANOLICHENS

Cyanolichen biomass in westside forests depends not only on stand age but also on landscape position. For example, old-growth Douglas-fir forests close to major streams support a far greater cyanolichen biomass than comparable upland forests (Howe 1978, Figure 1.3). The cause of this pattern is not entirely understood. Perhaps a zone of elevated atmospheric humidity extends for over 100 m above the stream channel, enabling epiphytic cyanolichens to flourish in the more humid microclimates of the riparian forest

Table 1.2. Examples of terrestrial plants occasionally found as epiphytes in the upper canopy of the oldest and wettest Douglas-fir forests in the Pacific Northwest.

Vascular plants	Mosses
Epilobium angustifolium	*Eurhynchium oreganum*
Gaultheria shallon	*Hylocomium splendens*
Oplopanax horridum	*Isopterygium pulchellum*
Sambucus racemosa	*Mnium spinulosum*
Tsuga heterophylla	*Polytrichum juniperinum*
Vaccinium spp.	*Rhytidiadelphus loreus*
	Rhytidiadelphus triquetrus

canopy compared with drier upland conditions. A similar but less pronounced effect on cyanolichen biomass occurs with elevation: lower elevation forests support a larger cyanolichen biomass than do higher elevation forests even if their proximity to a stream is the same (Howe 1978, Figure 1.3). The effects of streams on canopy microclimate may be less pronounced at higher elevations simply because stream and channel sizes decrease with increasing elevation. Experimental support for both hypotheses, which predict a tight relationship between cyanolichens and moisture availability, is currently lacking.

If epiphytic cyanolichens are restricted to relatively mesic forests, then they should be absent from many inland sites in the Pacific Northwest, including a large portion of westside forests. In fact, epiphytic cyanolichens are scarce in forests east of the Cascades in Oregon and Washington. Only the oldest and wettest sites in the interior forests of Idaho and Montana regularly harbor epiphytic cyanolichens (McCune 1984, Lesica et al. 1991). And given the scarcity of cyanolichens in managed forests, nitrogenous inputs from the canopy may currently be significant in only a tiny portion of the current landscape, that is, old-growth forests on lower slopes west of the Cascades. Efforts to bolster cyanolichen biomass in managed forests would benefit from a clearer understanding of the potential of forests to support epiphytic cyanolichens. Such information can easily be obtained by sampling epiphyte litterfall in a large number of forest stands.

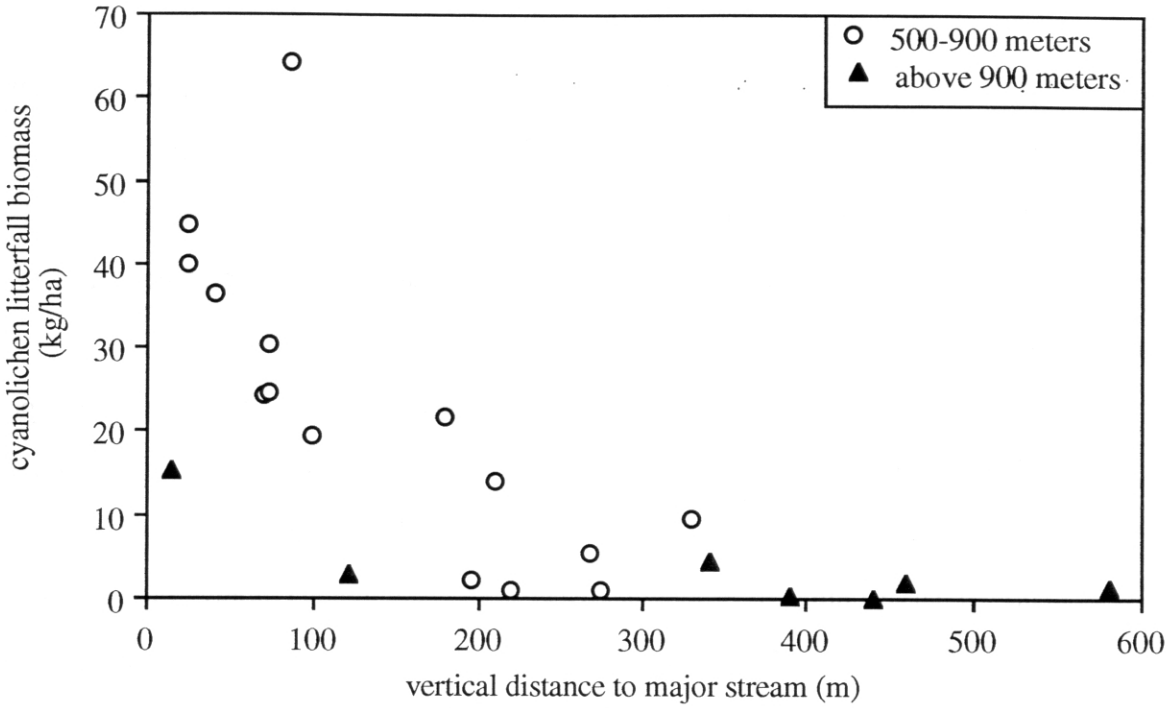

Figure 1.3. The relationship between epiphytic cyanolichen biomass and proximity to major streams for 22 stands of old-growth Douglas-fir forest in the H.J. Andrews Experimental Forest.

EPIPHYTE RESEARCH AND FOREST MANAGEMENT

Knowledge of epiphyte ecology in the Pacific Northwest is growing rapidly as a result of recent improvements in canopy access techniques and epiphyte sampling methods. The crowns of tall trees can now be safely accessed by ropes in a few hours without the use of harmful bolts or climbing spurs (Dial and Tobin 1994). Such rope techniques are now complemented by permanent installations such as platforms and construction cranes, which give researchers prolonged and intimate contact with the forest canopy. Although direct access to the canopy is essential for detailed studies of epiphyte communities and their

arboreal habitat, canopy-based sampling is not always the best approach for larger-scale questions about epiphyte development in forests. These studies require sampling from many stands throughout the landscape. A recently developed litterfall sampling method that permits rapid assessment of epiphyte abundance and diversity at the stand level (McCune 1994b) provides a ground-based alternative to more intensive canopy sampling. These alternative approaches are enabling scientists to initiate studies of epiphytes that will have important implications for forest management.

Maintaining late-successional species in managed forests is one of the most important challenges in forestry. Recent discussions of forest management alternatives in the Pacific Northwest (e.g., Spies et al. 1991) have focused on the retention of living trees and woody debris in harvest units. If propagule dispersal limits epiphyte colonization, epiphyte populations on retained trees could serve as propagule sources for the re-establishment of these species in the regenerating forest canopy. On the other hand, if microclimates or substrates strongly limit rates of propagule establishment, live tree retention would do little to facilitate epiphyte recovery in managed forests. Controlled experiments involving inoculations and transplantations of substrates in tree crowns are needed to resolve this dilemma. Furthermore, the extent to which late-successional epiphyte species can withstand the microclimatic changes following logging is currently unknown.

This thesis makes several contributions to canopy science in the Pacific Northwest, particularly as this science relates to forest management. Chapter 2 describes a community-level study of epiphytes in a 700-year-old forest rich in epiphytic cyanolichens. Epiphyte assemblages in tree crowns from the forest interior and on the clearcut edge of this stand were surveyed by direct canopy sampling and litterfall sampling. Chapter 3 describes a cyanolichen transplant experiment in this 700-year-old forest. Two cyanolichen species were reciprocally transplanted among four tree crowns: two in the forest interior and two on the clearcut edge. Chapter 4 describes another transplant experiment involving two

cyanolichen species as well as moss mats. Epiphytes were transplanted into tree crowns from thirteen forest stands representing four age classes: old growth, mature, young, and clearcut. Rates of cyanolichen growth and mortality are compared among the age classes for thalli transplanted onto bare bark and thick moss mats. Chapter 5 describes a retrospective study on the potential of live tree retention to maintain epiphytic cyanolichens in managed forests. The distribution of epiphytic lichen litterfall is related to the distribution of large remnant trees in a natural, multiple-age forest with a complex fire history.

Chapter 2

Branch Epiphyte Assemblages in the Forest Interior and on the Clearcut Edge of a 700-Year-Old Douglas-Fir Forest in Western Oregon

Stephen C. Sillett

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ABSTRACT

A total of 65 epiphyte species (macrolichens, bryophytes, and a fern) were found on the branches of four 700-year-old Douglas fir trees, two growing in the forest interior and two growing on the edge of a 20-year-old clearcut. The moss *Antitrichia curtipendula* and the cyanolichen *Lobaria oregana* dominated the epiphyte assemblages. Branch epiphyte assemblages were similar to those reported for a 450-year-old Douglas fir forest, but *A. curtipendula* and *Pseudocyphellaria rainierensis* were much more abundant in the older forest. Epiphyte species tended to be positively associated with other members of their functional group. Alectorioid and "other" lichens tended to be negatively associated with bryophytes. Several species were closely associated with moss mats. Ordination revealed one dominant gradient in epiphyte composition which was correlated with height. The gradient could be partitioned into an exposed portion with high lichen cover and low bryophyte cover, an intermediate portion, and a sheltered portion dominated by bryophytes. Biomass and species richness of macrolichen litterfall did not differ between the forest interior and clearcut edge, but there were some differences in the vertical distributions of epiphytes. The exposed and intermediate portions of the compositional gradient extended farther down in the crowns of the edge trees. After two decades of exposure on a clearcut edge, moss mats and associated species were still widely distributed within the edge tree crowns.

INTRODUCTION

A considerable amount of canopy epiphyte research has occurred in old-growth Douglas fir forests since the pioneering work of Denison (1973), including an extensive

floristic survey of canopy epiphytes (Pike et al. 1975), a detailed examination of the components of individual tree crowns (Pike et al. 1977), an analysis of the distribution of epiphytes within a watershed (Howe 1978), experiments on cyanolichen growth rates in the canopy (Chapters 3 and 4), and comparisons between old-growth and younger forests (McCune 1993, Neitlich 1993). These last two studies demonstrated that both biomass and diversity of canopy epiphytes, especially cyanolichens and bryophytes, increase with increasing stand age. McCune (1993) noticed that Douglas fir canopy epiphytes could be classified into functional groups based on both their ecological roles and their patterns of vertical distribution during forest succession. Bryophytes and cyanolichens, or nitrogen-fixing lichens, were only prevalent in old-growth forests, where they occupied the lower and middle portions of tree crowns, respectively. Alectorioid lichens, or forage lichens, and other non-nitrogen-fixing lichens (hereafter "other" lichens) were prevalent in younger forests as well as old-growth forests, where they occupied the upper portion of tree crowns. The old-growth forests studied by Denison, Pike, McCune, and Neitlich were all between 400 and 500 years old and located within the H. J. Andrews Experimental Forest. Aside from Chapter 3, there are few, if any, published studies of canopy epiphytes from old-growth Douglas fir forests located outside of this single watershed in western Oregon.

In the Pacific Northwest, management for timber production has converted large areas of old-growth forest into a mosaic of remnant forest patches surrounded by clearcuts and regenerating vegetation. The area of interior forest has been dramatically reduced while edge habitats have been proliferated (Spies et al. 1994). Edges of old-growth forests bordering clearcuts are characterized by drier microclimates and higher rates of large tree mortality compared to the forest interior (Chen et al. 1992, 1993). Very little is known about the impacts of these changes on epiphytes, although several endemic epiphyte species appear to be closely associated with old-growth Douglas fir forests (U.S.D.A. 1994, Neitlich 1993).

This study is the first to investigate canopy epiphytes in a Douglas fir forest well over 500 years old. Branches were sampled in large trees growing in the forest interior and on the edge of a clearcut. Epiphyte litterfall was also sampled in these two areas of the forest. There were four principle objectives: 1) analysis of within-tree structure of branch epiphyte assemblages, 2) elucidation of major compositional gradients in epiphyte assemblages, 3) floristic comparison of epiphytes between 700-year-old and 450-year-old Douglas fir canopies, and 4) a comparison between epiphytes of a forest interior and a clearcut edge.

METHODS

Study area

The site of this field study is a 30 ha forest stand in the southeastern corner of the Middle Santiam Wilderness Area in the western Cascades of Oregon (44°30'N, 122°12'W). Annual rainfall exceeds 2 m with a pronounced summer drought (Daly et al. 1994). The stand lies between 650 and 700 m elevation on a gently sloping north-facing terrace about 50 m above the Middle Santiam River. The forest canopy is dominated by very large (1.5-3.0 m dbh, 55-75 m tall) Douglas fir trees (*Pseudotsuga menziesii* [Mirb.] Franco) approaching or exceeding 700 years of age. Tree age in the stand was estimated by counting annual rings on stumps of large Douglas fir in an adjacent clearcut. Trees of this age and size are unusual at similar sites in the central western Cascades of Oregon where the fire return interval averages 150 years (Teensma 1987). The large Douglas fir trees are widely scattered in the stand, and most of them have broken tops. A butt rot fungus, *Phaeolus schweinitzii* (Fr.) Pat., appears to be the major cause of Douglas-fir mortality in the stand. Three other tree species are also prevalent in the stand: *Tsuga heterophylla* (Raf.) Sarg. (max. dbh = 1.5 m), *Thuja plicata* Donn *ex* D. Don (max. dbh = 2.5 m), and

Taxus brevifolia Nutt. (max dbh = 1.0 m). The stand is bordered by a steep slope leading to the river on the north, by younger (~250 yr), more recently burned forests on the east and west, and by a 20-year-old clearcut with regenerating Douglas fir on the south. Many of the large Douglas fir trees near the clearcut edge have blown down.

Tree selection and access

Four large Douglas fir trees occurring at least 100 m apart were selected for epiphyte sampling. Two of these trees grew in the forest interior (at least 200 m from the edges of the stand), and two grew within 5 m of the clearcut edge. Crowns of the edge trees were completely exposed to the clearcut on their south sides. All four trees were of similar stature, although one of the edge trees had lost about 10 m of its top within the last 20 years. Additional information about each tree is presented in Table 2.1.

Tree crowns were nondestructively accessed by shooting a monofilament over sturdy lower branches with a compound bow, hauling a parachute cord followed by a climbing rope over the branches, tying one end of the rope at ground level, and ascending the rope

Table 2.1. Descriptions of four approximately 700-year-old Douglas fir trees selected for epiphyte sampling in western Oregon. The dagger (†) indicates that tree 3 had recently lost at least 10 m of its top. Both the average and maximum diameters of the 0.5 m axis segments sampled in each tree are listed. Total sampling length is the estimated length of all living branch axes with diameters greater than 7 cm. All measurements are in m.

Tree	Area of Forest	Total Height	Trunk Diameter at 1.5 m	Number of Living Branches	Average Axis Diameter	Maximum Axis Diameter	Total Sampling Length	Sampling Intensity
1	interior	66	2.1	106	0.12	0.29	103	0.243
2	interior	68	2.8	70	0.20	0.37	120	0.108
3	edge	55†	2.4	69	0.11	0.20	165	0.152
4	edge	66	2.0	106	0.10	0.19	93	0.118

using vertical rope technique (Perry 1978). A pulley secured to the trunk near the top of each tree was used to haul a climbing rope into place (via parachute cord) for subsequent ascents. Rope techniques developed by arborists (Dial and Tobin 1994) were used to safely access branch surfaces throughout the tree crowns. Individual branches consisted of complex systems of ramifying axes. Large branch systems sloped downwards, extended 5 to 10 m from the trunk, and occupied extensive portions of the lower crown. Access to epiphyte habitats far out on these branch systems was achieved by gently walking down the length of the axes with body weight supported from above on an arborist-style rappel (Dial and Tobin 1994).

Canopy epiphyte sampling

Access to branchlets and twigs in the periphery of tree crowns was possible with rope techniques, but some portions of the outer crown were only accessible by traversing ropes suspended from adjacent trees. Therefore, epiphyte sampling was restricted to substrates in the inner crown, operationally defined as axes with diameters greater than 7 cm. Epiphytes occurring on smaller substrates in the outer crown were not sampled. Trunks and dead branches were also not sampled.

Epiphyte sampling occurred in two stages, each requiring at least one ascent. The first stage involved locating sites in the inner crown for epiphyte sampling. All living branches in the inner crown were sketched with length of axes visually estimated to the nearest half meter. In this way, the epiphytic habitat in the inner crown was partitioned into 0.5 m axis segments. Sample locations were then selected randomly from the estimated total length of axes in the inner crown (even if two or more samples occurred on the same branch system or axis) such that an equal number of samples occurred in the upper and lower halves of the live crown. A total of 150 sites, or 75 m of branch length, were selected for epiphyte

sampling in the inner crowns of the four trees. Two trees (trees 1 and 3) received twice the number of samples (i.e., 50 each) of the other two trees.

The second stage involved directly sampling epiphytes from the randomly selected sites in the inner crown. Epiphytes were sampled from the entire cylindrical surface area of branches. A nylon tape with marks at 3 cm intervals was attached to the upper surface of each 0.5 m axis segment and spiralled around the branch five times so that coils were exactly 10 cm apart. Epiphyte cover in a sample was estimated by counting the number of point intercepts (hereafter "hits") for each species along the spiral transect and dividing by the total number of potential hits in the sample (i.e., transect length in cm divided by 3). Estimated cover for each epiphyte species in the inner crown was calculated as the total number of hits for a given species on a tree divided by the total number of potential hits on that tree. Height above ground, distance to trunk, crown radius, and branch circumference were also recorded at the midpoint of each 0.5 m axis segment. Canopy sampling occurred during the summer of 1992 (trees 1 and 3) and the spring of 1994 (trees 2 and 4).

The dominant moss (*Antitrichia curtipendula*), the most conspicuous liverwort (*Porella navicularis*), and all cyanolichens were removed from the bark on roughly two-thirds of the samples, sorted to species in the laboratory, dried at 70°C for 24 hr, and weighed to the nearest 0.01g. These data were used to develop equations relating epiphyte biomass and surface area and to estimate biomass totals for these species in the inner crown of each tree. Surface areas of epiphytes in each sample were estimated by multiplying total surface area of the 0.5 m axis segment (0.1·spiral transect length) by estimated cover of individual species. Biomass of a species in the inner crown of each tree was estimated by summing dry weights of the species for all samples on the tree and dividing the total by the sampling intensity for that tree. Dry weights were either obtained directly from harvested material or estimated by applying the equations to branch samples from which they were

not harvested. Sampling intensity was the length of sampled axes (i.e., either 25 m or 12.5 m) divided by the estimated total length of axes in the inner crown.

Epiphyte litterfall sampling

In designing a canopy sampling scheme, there is always a trade-off between intensive sampling within individual trees and extensive sampling of many trees. The former option was chosen since a main objective of this study was to analyze within-tree structure of epiphyte assemblages. This decision necessarily compromised another objective, that is, comparison of epiphyte assemblages in a forest interior to those on a clearcut edge. Too few trees were sampled to statistically test hypotheses about epiphytic differences between these areas of the forest with the canopy dataset. A recently developed litterfall sampling method which permits rapid assessment of epiphytic macrolichen abundance and diversity at the stand level (McCune 1994b) provided a ground-based alternative to more extensive canopy sampling and enabled hypothesis testing with reasonable statistical power. Unfortunately, this method does not provide good estimates of epiphytic bryophyte abundance (McCune 1994b), so bryophyte litterfall was not collected.

Twenty 2.0 m radius circular plots were located on the forest floor: 10 in the forest interior and 10 within 10 m of the clearcut edge. Plots were positioned within projected crown areas (determined with a clinometer) of 10 randomly selected Douglas fir trees in each region of the stand. All fragments of macrolichens occurring as litterfall were collected from each plot unless they were attached to a fallen branch or tree greater than 10 cm diameter, or unless they were less than 1 cm in size. In the laboratory, litterfall samples were sorted by species, dried at 70°C for 24 hr, and weighed to the nearest 0.01 g. Litterfall sampling occurred in April 1994.

Nomenclature of lichens, mosses, and liverworts generally follows Egan (1987), Anderson et al. (1990), and Stotler and Crandall-Stotler (1977), respectively. Voucher specimens are in the Oregon State University Herbarium.

Statistical analyses

Differences in macrolichen litterfall abundance between the forest interior and clearcut edge were tested with two sample *t*-tests (Sokal and Rohlf 1995). Variables for litterfall biomass of individual species were square root transformed prior to analysis to alleviate positive skews. One test was performed for each species collected. The statistical power of these comparisons was calculated using equation 13.33 of Zar (1984: 227, 260).

Ordination analysis (samples in species space) was performed on the canopy data using nonmetric multidimensional scaling (NMS) from the statistical package PC-ORD (McCune and Mefford 1995). NMS is an iterative search for a ranking and placement of n samples on k dimensions that minimizes the stress of the k-dimensional configuration. "Stress" is a measure of departure from monotonicity in the relationship between distance in the original s-dimensional space and distance in the reduced k-dimensional ordination space. Calculations are based on an n x n distance matrix calculated from a data matrix consisting of n rows and s columns, where n is the number of samples and s is the number of species. NMS was run with the quantitative version of the Sørenson coefficient (Greig-Smith 1983) as the distance measure, 150 iterations, and random starting coordinates. Epiphyte species occurring in 10% or fewer of the samples or on only a single tree were excluded, leaving 25 species in the data matrix.

Presence/absence data for epiphytes in the 150 samples were transformed with the Beals smoothing function prior to ordination analysis. This transformation smooths the pattern of joint occurrences of species and facilitates the extraction of the major patterns in community data (McCune 1994a). Presence/absence data are replaced with quantitative values (range 0-

1 inclusive) that represent the probability of a species occurring in a particular sample based on the other species that were also present in that sample. A two dimensional ordination of the transformed data matrix was produced after determining that higher dimensional solutions failed to substantially improve fit (i.e., reduce stress). The amount of variation in the transformed data extracted by each ordination axis was calculated as a percentage based on the coefficients of determination between distances in the original s-dimensional ($s = 25$ species) space (using the Sørenson coefficient) and Euclidean distances in the two-dimensional ordination spaces (McCune and Mefford 1995).

Association analysis was performed using the procedure CROSSTABS in SPSS/PC+ (SPSS 1988). This analysis tested whether individual epiphyte species pairs occurred together more or less often than expected by chance. A 2 x 2 contingency table was generated for each pair of species. The likelihood ratio (G, Sokal and Rohlf 1995) was used as the test statistic.

RESULTS

The epiphyte flora of a 700-year-old Douglas fir canopy

Sixty-four nonvascular epiphyte species (excluding crustose lichens) were encountered on sampled Douglas fir branches in the inner crown: 18 cyanolichens, 7 alectorioid lichens, 20 "other" lichens, 13 mosses, and 6 liverworts (Table 2.2). Thirty-one species were found on all four trees. Thirteen species were found on only a single tree. Only 12 species covered more than one percent of sampled branch surface area: in decreasing order of abundance, *Antitrichia curtipendula, Lobaria oregana, Douinia ovata, Sphaerophorus globosus, Dicranum fuscescens, Hypnum circinale, Peltigera britannica, Isothecium myosuroides, Porella navicularis, Pseudocyphellaria rainierensis, Platismatia glauca,* and

Table 2.2. Alphabetical list of branch epiphytes by functional group for a 700-year-old Douglas fir forest in western Oregon. *Bryoria* spp. include *B. capillaris*, *B. friabilis*, *B. fuscescens*, *B. oregana*, and *B. pikeii*. *Cladonia* spp. include *C. coniocraea* and *C. squamosa*. *Hypnum* spp. include *H. circinale* and *H. subimponens*. *Parmelia* spp. include *P. hygrophila*, *P. pseudosulcata*, and *P. sulcata*. A dagger (†) signifies species endemic to the Pacific Northwest. Correlations of species with the first NMS ordination axis are presented for each epiphytes used in the ordination analysis. The mean and standard error (n = 4 trees) of cover are presented along with a list of trees on which each species occurred (in decreasing order of estimated cover from left to right). Frequencies of each species were calculated separately for the exposed, intermediate, and sheltered portions of the epiphyte compositional gradient (see text).

	Correlation (R) with Ordination Axis	Cover (%) Mean (S.E.)	Trees	Frequency (%) Exposed	Intermediate	Sheltered
Cyanolichens						
Lobaria oregana†	0.84	20.62 (3.45)	4 3 2 1	98	98	88
Lobaria pulmonaria		0.31 (0.12)	2 1 3	0	0	6
Lobaria scrobiculata	–0.36	0.17 (0.06)	3 2 1 4	6	10	14
Massalongia carnosa		0.04 (0.03)	2 3	0	4	2
Nephroma bellum	0.38	0.36 (0.19)	4 3 1 2	15	24	6
Nephroma occultum†	0.71	0.53 (0.22)	4 2 3 1	23	20	4
Nephroma parile	–0.45	0.19 (0.05)	3 1 4 2	8	16	22
Nephroma silvae-veteris†		0.05 (0.03)	4 2 3	2	6	2
Pannaria saubinetii		0.08 (0.07)	2 3	4	0	6
Peltigera britannica	–0.97	2.92 (0.94)	2 3 1 4	29	80	78
Pseudocyphellaria anomala†	–0.26	0.57 (0.19)	3 4 2 1	21	47	27
Pseudocyphellaria crocata	–0.50	0.12 (0.04)	3 4 2 1	4	8	20
Pseudocyphellaria rainierensis†	–0.85	1.37 (0.45)	3 2 1 4	2	24	45
Sticta fuliginosa	–0.39	0.40 (0.13)	2 3 4 1	15	35	29
Sticta weigelii	–0.67	0.80 (0.25)	2 3 4 1	10	45	47
Alectorioid Lichens						
Alectoria sarmentosa	0.93	1.12 (0.52)	4 2 1 3	58	31	4
Bryoria spp.	0.95	1.47 (0.82)	4 2 3 1	75	27	6
Usnea spp.	0.73	0.30 (0.22)	4 2 3	17	8	0

Table 2.2 (continued)

	Correlation (R) with Ordination Axis	Cover (%) Mean (S.E.)	Trees	Frequency (%) Exposed	Intermediate	Sheltered
"Other" Lichens						
Cetraria chlorophylla		0.04 (0.01)	3 1 4	10	4	0
Cetraria orbata		0.02 (0.01)	1 3	2	4	0
Cladonia spp.	–0.07	1.16 (0.36)	2 1 3 4	44	53	47
Hypogymnia enteromorpha	0.90	0.47 (0.13)	3 4 1 2	44	10	0
Hypogymnia inactiva		0.05 (0.03)	4 3 1	2	4	0
Hypogymnia occidentalis		0.11 (0.06)	3 2	4	6	2
Hypogymnia physodes		0.04 (0.04)	4	6	0	0
Parmelia spp.	0.92	0.61 (0.26)	4 1 3 2	54	22	0
Parmeliopsis hyperopta		0.02 (0.01)	4 1	4	0	0
Platismatia glauca	0.95	1.35 (0.42)	4 2 1 3	62	16	0
Platismatia herrei†		0.05 (0.02)	4 1 2	8	2	2
Platismatia stenophylla†		0.02 (0.02)	3	6	0	0
Sphaerophorus globosus	0.67	4.80 (1.15)	4 2 1 3	88	86	76
Mosses						
Antitrichia curtipendula	–0.84	25.71 (5.89)	1 2 3 4	94	100	96
Bryum gemmascens		0.41 (0.33)	2 1 3	0	4	20
Dicranum fuscescens	–0.95	3.54 (1.37)	2 1 3 4	27	71	84
Dicranum tauricum		0.02 (0.01)	1 3	4	2	2
Hypnum spp.	–0.89	3.13 (0.70)	2 4 1 3	23	59	61
Isothecium cristatum		0.10 (0.08)	3 1	0	4	2
Isothecium myosuroides	–0.96	2.66 (1.13)	1 3 4 2	2	37	82
Orthotrichum consimile		0.02 (0.02)	1	2	6	0
Ulota crispa		0.14 (0.14)	3	15	4	6
Liverworts						
Cephaloziella rubella		0.15 (0.06)	2 3 4 1	8	16	4
Douinia ovata	–0.99	7.40 (1.44)	3 2 1 4	37	86	100
Porella navicularis	–0.94	2.07 (0.77)	3 1 2 4	35	76	80
Radula bolanderi	–0.95	0.41 (0.01)	3 1 2 4	8	33	47

The following additional species were found in only one or two canopy samples: *Eurhynchium oreganum*, *Frullania tamarisci* var. *nisquallensis*, *Hypogymnia apinnata*, *H. imshaugii*, *H. tubulosa*, *Leptogium lichenoides*, *Letharia vulpina*, *Neckera douglasii*, *Nephroma helveticum*, *Pseudocyphellaria anthraspis*, *Ptilidium californicum*, and *Zygodon viridissimus* var. *rupestris*.

Table 2.3. Equations relating epiphyte surface area (X, m^2) to biomass (Y, g dry weight) for some epiphyte species encountered in the canopy of a 700-year-old Douglas fir forest in western Oregon. Coefficients of determination (R^2), and sample size (N), and estimated biomass of each species in the four inner crowns are indicated for each equation.

Species	Equation	R^2	N	Estimated Biomass (g/inner crown) Tree1	Tree2	Tree3	Tree4
Antitrichia curtipendula	logY = 1.48logX + 2.84	0.85	95	6900	7000	4400	1000
Lobaria oregana	logY = 1.32logX + 2.91	0.87	95	2100	4700	5500	4200
L. scrobiculata	logY = 2.56logX + 5.41	0.65	15	1.1	2.3	26	2.6
Nephroma bellum	logY = 2.12logX + 4.28	0.62	22	0.5	1.0	33	14
N. occultum	logY = 1.81logX + 3.50	0.77	23	2.6	17	17	28
Peltigera britannica	logY = 1.92logX + 3.78	0.73	61	210	2200	260	30
Porella navicularis	logY = 1.40logX + 2.40	0.54	69	230	33	190	6.2
Pseudocyphellaria anomala	logY = 1.42logX + 2.65	0.44	39	2.1	8.0	72	17
P. rainierensis	logY = 1.62logX + 3.42	0.79	34	130	200	740	52
Sticta fuliginosa	logY = 1.45logX + 2.45	0.43	28	1.5	10	9.5	8.0
S. weigelii	logY = 1.41logX + 2.68	0.59	42	8.3	70	65	13

Alectoria sarmentosa (Table 2.2). *Antitrichia curtipendula* and *Lobaria oregana* dominated the inner crowns in terms of total cover (Table 2.2) and biomass (Table 2.3).

Thirty-nine macrolichen species were recovered in litterfall, but almost 90% of the macrolichen litterfall biomass in this 700-year-old forest was contributed by cyanolichens, primarily *Lobaria oregana* (Table 2.4). Several lichen species were much more prevalent in litterfall than on branches. Canopy sampling was restricted to the inner crown, while litterfall sampling yielded abundance estimates of species in proportion to their total canopy biomass (McCune 1994b). Therefore, canopy sampling underestimated the abundance of species occurring primarily in the outer crown (e.g., *Hypogymnia inactiva* and *Usnea*

Table 2.4. Macrolichen litterfall summary for the interior (n = 10 plots) and edge (n = 10 plots) of a 700-year-old Douglas fir forest in western Oregon based on an early spring collection. Litterfall biomass of each species is expressed as kg dry weight per ha. Epiphyte species are listed in decreasing order of abundance (n = 20 plots). Results of *t*-tests performed on square root transformed data are also presented. Asterisks indicate species that were significantly more abundant in either the forest interior or the clearcut edge (** =P<0.01, *** =P<0.001).

Species	Percent Total Litterfall Biomass	Forest Interior Mean(S.E.)	%Freq.	Clearcut Edge Mean(S.E.)	%Freq.
Lobaria oregana	80.01	87.85 (12.87)	100	83.68 (13.58)	100
Lobaria pulmonaria	4.89	4.39 (1.96)	100	6.10 (3.47)	100
Sphaerophorus globosus	3.17	3.92 (0.72)	100	2.88 (0.79)	100
Platismatia glauca	2.57	3.19 (0.31)	100	2.32 (0.74)	100
Hypogymnia enteromorpha	1.57	1.63 (0.41)	100	1.73 (0.46)	100
Pseudocyphellaria rainierensis	1.30	1.43 (0.59)	70	1.36 (0.45)	100
Hypogymnia inactiva	1.19	1.38 (0.35)	90	1.18 (0.36)	100
Pseudocyphellaria anthraspis	1.13	1.40 (0.59)	80	1.02 (0.60)	40
Usnea spp.	0.47	0.64 (0.25)	80	0.38 (0.15)	80
Hypogymnia imshaugii	0.46	0.56 (0.21)	60	0.43 (0.18)	50
Pseudocyphellaria anomala	0.45	0.57 (0.15)	80	0.40 (0.15)	90
Alectoria sarmentosa	0.44	***0.78 (0.20)	100	0.17 (0.09)	80
Hypogymnia apinnata	0.34	0.52 (0.27)	30	0.21 (0.12)	30
Peltigera britannica	0.27	0.45 (0.28)	70	0.13 (0.05)	70
Hypogymnia physodes	0.25	0.25 (0.10)	50	0.29 (0.10)	60
Platismatia herrei	0.24	0.42 (0.12)	60	0.10 (0.08)	20
Nephroma bellum	0.23	0.28 (0.11)	100	0.22 (0.07)	90
Sticta weigelii	0.14	**0.28 (0.10)	70	0.02 (0.02)	20
Nephroma helveticum	0.10	0.18 (0.08)	70	0.03 (0.02)	20
Parmelia sulcata	0.06	0.01 (0.01)	10	0.11 (0.08)	30
Lobaria scrobiculata	0.05	0.07 (0.05)	30	0.03 (0.02)	40
Parmelia hygrophila	0.05	0	0	**0.10 (0.04)	40
Bryoria spp.	0.04	0.02 (0.01)	50	0.06 (0.04)	60
Pseudocyphellaria crocata	0.03	0.06 (0.03)	60	0.01 (0.01)	20
Nephroma occultum	0.03	0.03 (0.02)	50	0.02 (0.02)	30
Sticta fuliginosa	0.01	0.01 (0.01)	20	0.01 (0.01)	30
Macrolichen Species Richness	—	18.40 (0.91)	—	16.70 (1.06)	—

The following additional species were found in only one or two litterfall plots: *Cavernularia hultenii, Cetraria chlorophylla, C. idahoensis, C. orbata, Cladonia spp., Hypogymnia metaphysodes, H. occidentalis, H. tubulosa, Nephroma parile, Parmelia pseudosulcata, Platismatia norvegica,* and *Ramalina farinacea.*

spp.) and in the understory (e.g., *Lobaria pulmonaria* and *Pseudocyphellaria anthraspis*). Five species were found in litterfall but not on branches in the canopy: *Cavernularia hultenii*, *Cetraria idahoensis*, *Hypogymnia metaphysodes*, *Platismatia norvegica*, and *Ramalina farinacea*. Each of these five species occurred in 10% or fewer of the plots.

There were few significant differences in epiphyte litterfall between the forest interior and clearcut edge. *Alectoria sarmentosa* and *Sticta weigelii* were significantly more abundant in the forest interior, while *Parmelia hygrophila* was more abundant on the edge (Table 2.4). Overall, macrolichen biomass and species richness in litterfall were remarkably similar between these two areas of the forest, and the null hypothesis (i.e., no difference between the forest interior and clearcut edge) was accepted in most cases (power = 0.75-0.95).

Associations between epiphyte species

There were many strong positive and negative associations among epiphytes on branches in this 700-year-old forest (Figure 2.1). Classification of epiphyte species into functional groups (McCune 1993) explained some of the variation in these patterns. For example, species tended to be positively associated with other members of their group (except *Ulota crispa*), and alectorioid and "other" lichens tended to be negatively associated with bryophytes (except *Cladonia* spp.). Several species obviously differed in their patterns of association from other members of their group. The cyanolichen *Nephroma occultum* was positively associated with several alectorioid (especially *Bryoria* spp.) and "other" lichens but negatively associated with the dominant moss (*A. curtipendula*) and the dominant liverwort (*Douinia ovata*). *Peltigera britannica* and *Pseudocyphellaria rainierensis*, on the other hand, exhibited the opposite pattern (i.e., positive associations with bryophytes and negative associations with alectorioid and "other" lichens).

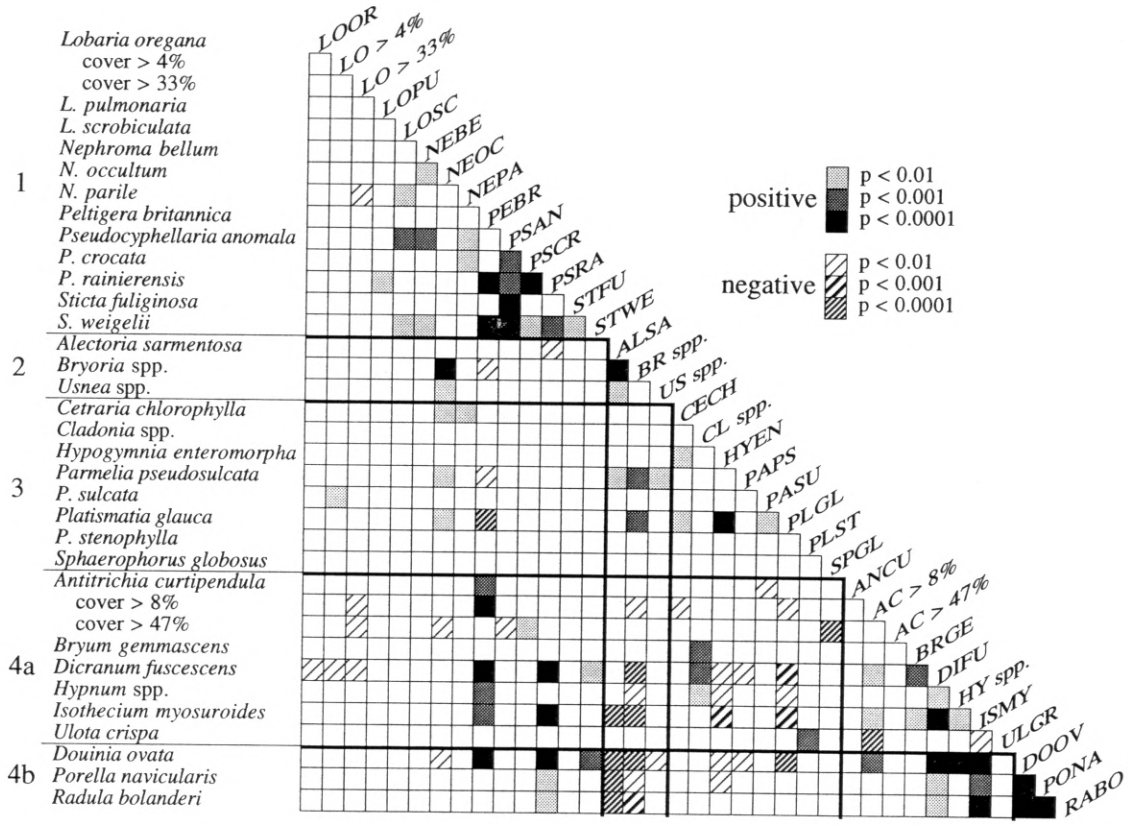

Figure 2.1. Association analyses for epiphyte species in a 700-year-old Douglas fir forest in western Oregon. Each square represents the result of a 2 by 2 contingency table for one species pair. Only species showing statistically significant ($p < 0.01$) positive or negative associations are included. Species are listed alphabetically by group (1 = cyanolichens, 2 = alectorioid lichens, 3 = "other" lichens, 4a = mosses, 4b = liverworts). Codes along the diagonal represent taxa by the first two letters of their genus and species names. *Lobaria oregana* and *Antitrichia curtipendula,* two species which occurred in nearly every sample, were analyzed as three categories: total presence, presence excluding the lower quartile of the species' distributions, and presence including only the upper quartile of the species' distributions. Cover values for the quartile cut-offs are indicated. *Bryoria* spp. include *B. capillaris, B. friabilis, B. fuscescens, B. oregana,* and *B. pikeii. Cladonia* spp. include *C. coniocraea* and *C. squamosa. Hypnum* spp. include *H. circinale* and *H. subimponens.*

A major component of epiphyte assemblages was thick (up to 10 cm) moss mats covering the upper surfaces of branches. These mats were mostly composed of *Antitrichia curtipendula* and (to a lesser extent) *Dicranum fuscescens.* Many epiphytes were positively or negatively associated with moss mats (Figure 2.1). The cyanolichen *Peltigera britannica* always grew intermingled with bryophytes. Decaying remnants of living *P. britannica* thalli were frequently found buried beneath *A. curtipendula* in these mats. Both morphotypes of *P. britannica* were found. The cyanobacterial morphotype, "*P. avenosa,*" sometimes occurred independently, but lobes of the typical morphotype were usually present. The liverwort *Douinia ovata,* which dominated lower surfaces of branches, occurred more frequently on branches with substantial moss mats. Extensivemats of *A. curtipendula* were particularly unsuitable to the fruticose lichen *Sphaerophorus globosus.* Large quantities of *Lobaria oregana* seldom occurred on branches substantially covered by moss mats. Finally, one vascular epiphyte, the fern *Polypodium glycyrrhiza* D. C. Eaton, was occasionally encountered on branches, but only in moss mats with thick layers of underlying humus.

Vertical distribution of epiphytes

Ordination analysis revealed one major gradient in epiphyte composition within the Douglas fir canopy; over 94 percent of the variation in the transformed species data was extracted by the first NMS axis. Branch sample scores on this axis were positively correlated with height above ground ($R = 0.68$, $P < 0.0001$). Epiphyte groups were differentially distributed along this vertical gradient (Table 2.2): bryophytes had strong negative correlations (i.e, the favorability of samples for bryophytes steadily decreased), alectorioid and "other" lichens had strong positive correlations, and cyanolichens had positive and negative correlations. The second ordination axis was uninterpretable.

A more detailed portrayal of the epiphyte compositional gradient was achieved by ranking samples according to their ordination scores. The ranked list was then divided into thirds (50 samples each) representing exposed, intermediate, and sheltered portions of the gradient (see Discussion). Branches in the exposed portion had relatively high cover of alectorioid lichens, "other" lichens, and cyanolichens and relatively low cover of bryophytes. Branches in the sheltered portion had very high cover of bryophytes, lower cyanolichen cover, and virtually no alectorioid or "other" lichens (Figure 2.2).

Samples from the three portions of the epiphyte compositional gradient were plotted by height above ground and distance from the trunk in each tree (Figure 2.2). There was quite a bit of overlap within each tree crown, but the exposed and intermediate portions extended farther down in the crowns of the edge trees. The vertical component of the epiphyte compositional gradient within the interior trees was more pronounced than in the edge trees (correlations of ordination scores with height: $R^2 = 0.57$ for interior trees, $R^2 = 0.42$ for edge trees). The profile diagram presented in Figure 2.2 also revealed differences in crown shape between the trees. The two edge trees had narrower crowns than the two interior trees, especially below 40 m in height.

Recall that ordination analysis was performed on data that had been transformed with the Beals smoothing functions. A consequence of this smoothing is that correlations of individual species with the ordination axis (Table 2.2) were not entirely reflective of their actual distributions within the canopy. Superimposing unsmoothed species distributions on plots of sample locations clearly illustrated the portion of inner crowns occupied by individual species as well as the individuality of epiphyte assemblages on each tree. These profiles are presented for representatives of each epiphyte functional group in Figure 2.3. *Lobaria oregana* occurred in nearly every sample but was more abundant in the lower crowns of the edge trees than in the lower crowns of the interior trees (Figure 2.3A). *Nephroma occultum* was widely scattered within the inner crowns but occurred in almost

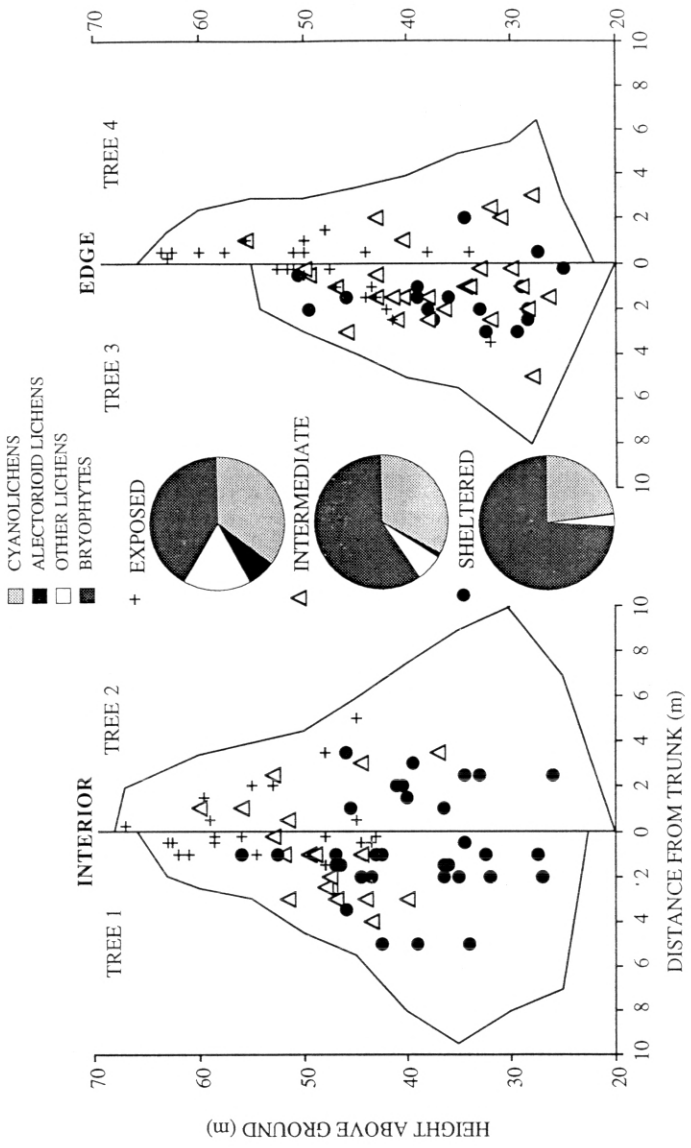

Figure 2.2. Profile diagrams for branch samples in the inner crowns of four Douglas fir trees in a 700-year-old forest in western Oregon. For comparative purposes, groups of two tree crowns are shown as if they represented a single crown. The solid lines represent approximate boundaries of the live crowns based on estimates of crown radii at different heights within each tree. Locations of sample sites within the inner crowns are indicated according to each sample's height above ground and distance from trunk. Trees 1 and 3 have twice the number of samples as trees 2 and 4. Exposed, intermediate, and sheltered represent upper, middle, and lower thirds of a ranked list of sample scores from the first ordination axis, respectively (see text). Relative proportions of epiphyte functional groups are indicated for each portion of the gradient based on whole tree estimates of cover for each group.

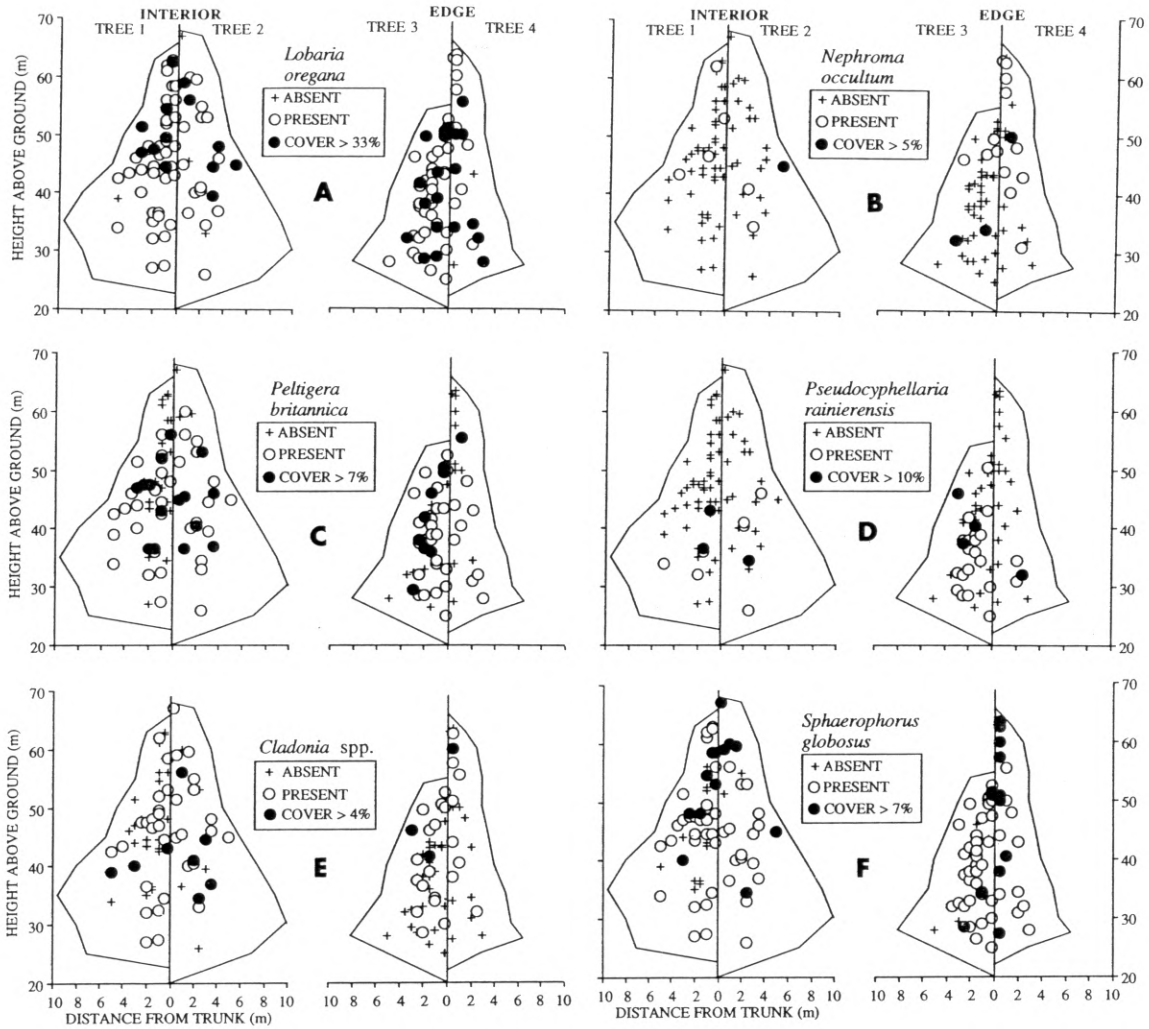

Figure 2.3. Profile diagrams of epiphyte distributions in the inner crowns of four Douglas fir trees in a 700-year-old forest in western Oregon. For comparative purposes, groups of two tree crowns are shown as if they represented a single crown. The solid lines represent approximate boundaries of the live crowns based on estimates of crown radii at different heights within each tree. Locations of sample sites within the inner crowns are indicated according to each sample's height above ground and distance from trunk. Trees 1 and 3 have twice the number of samples as trees 2 and 4. Actual distributions of 12 epiphytes representing each functional group are presented (cyanolichens = A, B, C, and D, "other" lichens = E, F, and G, alectorioid lichens = H, bryophytes = I, J, K, and L). *Cladonia* spp. (E) include *C. coniocraea* and *C. squamosa.* "Other" lichens (G) include *Cetraria* spp., *Hypogymnia* spp., *Letharia vulpina, Parmelia* spp., *Parmeliopsis hyperopta,* and *Platismatia* spp. Alectorioid lichens (H) include *Alectoria sarmentosa, Bryoria* spp., and *Usnea* spp. Plus signs (+) indicate sample sites where the epiphyte did not occur. Unfilled circles indicate sample sites where the epiphyte was present. Solid circles indicate sample sites where the epiphyte was present with a cover greater than the upper quartile cut-off (equivalent cover value indicated) for that epiphyte.

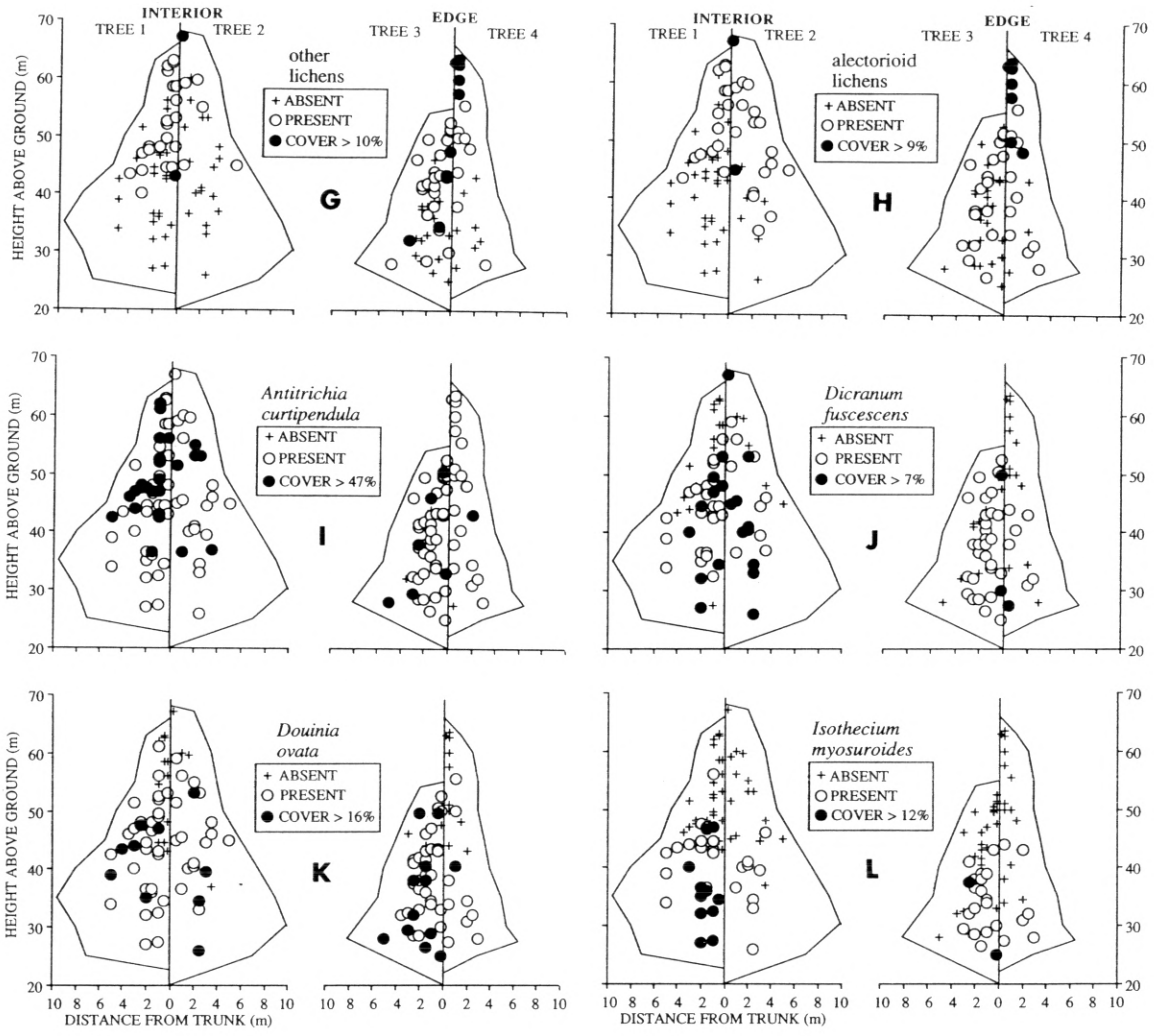

Figure 2.3 (continued)

half the samples on tree 4 (Figure 2.3B). *Cladonia* spp., *Douinia ovata, Peltigera britannica,* and *Sphaerophorus globosus* occurred throughout in the inner crowns of all four trees (Figures 2.3E, 2.3K, 2.3C, and2.3F). *Pseudocyphellaria rainierensis* occurred only below 50 m in all four trees and was especially abundant on tree 3 (Figure 2.3D). Alectorioid and "other" lichens (excluding *Cladonia* spp. and *S. globosus*) were restricted to the upper crowns of the interior trees but were distributed throughout the inner crowns of the edge trees (Figs. 2.3G and 2.3H). *Antitrichia curtipendula* and *Dicranum*

fuscescens were widespread in all four trees but were more abundant on the interior trees (Figures 2.3I and 2.3J). Finally, *Isothecium myosuroides* was nearly restricted to the lower half of all four tree crowns (Figure 2.3L).

DISCUSSION

Epiphytic comparisons with younger old-growth Douglas fir forests

Most (75%) of the species reported in the inner crowns of 700-year-old Douglas fir trees were also reported on branches in a 450-year-old Douglas fir forest in western Oregon (Pike et al. 1975), but there were some notable exceptions. *Douinia ovata, Nephroma occultum,* and *Nephroma silvae-veteris* were not reported by Pike et al., yet they consistently occurred as inner crown epiphytes in this study. The two species of *Nephroma* were first described after the publication of Pike's study (Goward and Goffinet 1993, Wetmore 1980). Both have since been found in the forest canopy very near Pike's study site (Chapter 1). In terms of cover, *Douinia ovata* was the third most abundant epiphyte in this study, occurring in over half of the samples. It was misidentified as *Diplophyllum taxifolium* in Pike's study. *Massalongia carnosa* is a terrestrial cyanolichen reported here for the first time as an epiphyte in a Douglas fir forest.

Pseudocyphellaria rainierensis was the third most abundant cyanolichen on branches in this study, yet Pike et al. found this species to be restricted to the understory (i.e., below 20 m). I found it in the lower crowns of less than twenty percent of the tall trees I climbed in the central Oregon Cascades (Sillett 1996). I found this species epiphytic on Douglas fir in forests as young as 140 years, but it was only abundant as a canopy epiphyte in this 700-year-old forest (Sillett 1996). Therefore, this cyanolichen appears to be one of the last to reach the upper canopy during forest canopy development (McCune 1993, Chapter 1).

Another major difference between epiphyte assemblages in these two forest canopies was the difference in abundance of *Antitrichia curtipendula.* This moss was the most abundant epiphyte on branches in this study, but Pike et al. found it only occasionally. The 250 year age difference could account for this discrepancy if *A. curtipendula* biomass in Douglas fir forests continues to increase beyond the fifth century of succession. Alternatively, moisture regimes in the two forests may differ enough to affect development of *A. curtipendula* biomass. Pike's study site was approximately 100 m lower in elevation than the forest on the Middle Santiam River. Old-growth Douglas fir forests occurring in wetter sites at higher elevations very near Pike's study site do indeed have substantial cover of *A. curtipendula* in the canopy (pers. obs.).

Comparing results from this study with those of Pike et al. (1975, 1977) is complicated by the fact that Pike et al. surveyed epiphytes on whole trees, while sampling in this study was restricted to the inner crown. Therefore, aside from the striking differences noted above, canopy epiphyte floras are not directly comparable between the two forests. Comparisons of epiphyte biomass between the two forests are also complicated by differences in methodology. Pike et al. (1977) estimated epiphyte biomass on different substrate types, including axes, within a single tree crown. In this tree, the estimated biomass of *Lobaria oregana* on axes was just over 3 kg, a figure comparable to the estimates for this species in the inner crowns of the four 700-year-old trees (Table 2.3). Bryophyte biomass on axes in the 450-year-old tree was estimated at only 2 kg, whereas 7 kg of a single moss species, *Antitrichia curtipendula,* was estimated to occur in the inner crowns of the interior trees in this study (Table 2.3). In Pike's study, however, axes included all horizontal stems greater than 4 cm in diameter, while I sampled only axes with diameters greater than 7 cm. Biomass estimates for species in the inner crowns of the 700-year-old trees would have been higher had smaller diameter axes been included.

The vertical distribution of epiphytes in a 400-year-old Douglas fir forest near Pike's study site (McCune 1993) was somewhat different than the vertical distribution observed in this study. In both old-growth forests, alectorioid and "other" lichens were most abundant in the upper canopy. Bryophytes and cyanolichens, however, occurred throughout the inner crowns of the 700-year-old trees, whereas they were restricted to the lower and middle portions of tree crowns in the 400-year-old forest. McCune (1993) hypothesized that epiphyte functional groups migrate upwards in the forest canopy over time. Results from this 700-year-old forest suggest that this upward migration may continue beyond the fifth century of forest succession. Epiphyte studies in other very old Douglas fir forests are needed in order to evaluate this hypothesis. Unfortunately, very little Douglas fir forests of this age remain in western Oregon. The few stands that I have found occur at substantially higher elevations and are therefore not directly comparable in terms of canopy epiphytes (Chapter 1).

Interpreting the epiphyte compositional gradient

The dominant gradient in epiphyte composition revealed by ordination analysis may correspond to a microclimatic gradient ranging from exposed microsites preferred by alectorioid and "other" lichens to the more sheltered microsites preferred by bryophytes and many of the cyanolichens. A mechanistic separation of the various environmental factors influencing epiphytes in a forest canopy is not possible without detailed measurements. However, factors such as light and humidity covary within tree crowns (Geiger 1965), and the vertical gradient within a forest canopy represents a complex suite of confounded microclimatic factors affecting moisture availability (McCune 1993). Within a tall forest, exposure to desiccating wind and sunlight tends to increase from the lower canopy to the upper canopy (Geiger 1965), but these factors are likely to vary within individual tree

crowns depending on their local neighborhood. The forest canopy surrounding the four Douglas fir trees was not uniform. For example, some portions of the tree crowns faced gaps in the canopy, while others were sheltered by crowns of adjacent trees. Thus, some branch surfaces were more exposed than others regardless of their height in the canopy. Within branches, water-storing moss mats may greatly modify the moisture regimes of epiphytes in their immediate vicinity by virtue of high water storage capacities (Veneklaas et al. 1990), effectively lowering vapor pressure deficits in these microhabitats (Lawrey 1991). Three epiphyte species (i.e., *Dicranum fuscescens, Douinia ovata,* and *Peltigera britannica*) were strongly negatively correlated ($R^2 > 0.9$) with the compositional gradient, yet they were widespread in the inner crowns of the four trees. Each of these species was associated with thick moss mats on branches. Therefore, a branch surface located high in the canopy and covered with a thick moss mat may be "lower" on the gradient than a branch surface located farther down in the tree on a side of the crown facing a gap.

Edge effects in a 700-year-old forest canopy

Comparison of litterfall between the forest interior and clearcut edge demonstrated that these areas of the forest were very similar in terms of canopy macrolichen biomass and species richness. The high statistical power of these comparisons indicated that litterfall sampling could have detected differences if they existed. Canopy sampling, however, indicated some differences in the vertical distributions of epiphytes between the two groups of trees. Edge trees were exposed to the clearcut on the south sides of their crowns. Epiphytic habitats on branches facing such large gaps may experience higher light levels and vapor pressure deficits than microsites at similar heights within the crowns of the interior forest trees. While exposed sites may become wetted more rapidly than sheltered sites, desiccation rates are likely to be higher following a precipitation event (Geiger 1965).

Narrower crowns of the edge trees could also have contributed to observed differences in vertical distributions of epiphytes, but the extent to which individual tree crowns buffer microclimates of epiphytic habitats remains unclear. Casual observations suggested that branches within edge trees facing away from the clearcut had higher bryophyte cover than those facing toward the clearcut.

Epiphyte assemblages in this 700-year-old forest inhabit branches that must be centuries old themselves. None of the large Douglas fir trees in this stand appeared to be growing appreciably in height; their tops were either flattened or snapped. Even branches near the top of their inner crowns are likely to be very old. A consequence of the great age of branch surfaces is that epiphyte succession is well advanced in the inner crown. Clearcutting of the adjacent stand subjected epiphyte assemblages on edge trees to sudden microclimatic change (Chen et al. 1993) very late in their development. After twenty years of exposure on the clearcut edge, these assemblages were not dramatically different from those of the forest interior. Moss mats and associated species were still widely distributed within the edge tree crowns, and some cyanolichen species (e.g., *Pseudocyphellaria rainierensis*) had become acclimated to the altered microclimates of the edge tree crowns (Chapter 3). Differences in vertical distribution patterns of epiphytes on the edge may reflect downward expansion of species limited by microclimatic factors (e.g., light availability) in the lower canopy of the forest interior. Clearly, more sampling in a larger number of trees and stands is required to rigorously evaluate this hypothesis.

CONCLUSION

The inner canopy of this 700-year-old Douglas fir forest harbored an impressive assortment of epiphytes, including a number of endemic species thought to be closely associated with old-growth Douglas fir forests (U.S.D.A. 1994). The vulnerability of

such epiphytes to forest management activities depends on their abilities to withstand microclimatic changes accompanying these disturbances. Well-developed epiphyte assemblages in very old forests may be somewhat resistant to moderate levels of disturbance. After two decades of exposure on a clearcut edge, no epiphyte species in this forest appeared to be lost or seriously declining. An important component of these assemblages may be thick moss mats that can regulate moisture regimes of epiphytic microsites, thus benefitting desiccation-sensitive species. Quantifying the extent of microclimatic and epiphytic changes in forest canopies subjected to a range of disturbances is a promising area for future research.

Chapter 3

Growth Rates of Two Epiphytic Cyanolichen Speciesat the Edge and in the Interior of a 700-Year-Old Douglas-Fir Forest in the Western Cascades of Oregon

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ABSTRACT

Thalli of two epiphytic lichens, *Lobaria oregana* (Tuck.) Müll. Arg. and *Pseudocyphellaria rainierensis* Imsh., were collected from the canopy of an old-growth forest. Thalli were individually attached to nylon monofilament and transplanted into the crowns of four trees, two growing in the forest interior and two growing on the edge of a clearcut, at heights between 35 and 45 m above the ground. Half of the transplants in each tree were derived from thalli collected in the interior and half were derived from thalli collected on the edge. After one year, *L. oregana* transplants grew significantly less on the edge than they grew in the interior. The source of *P. rainierensis* thalli significantly affected transplant growth rate. Thalli that came from the interior and were transplanted to the edge did not grow, on average, while thalli that came from the edge and were transplanted back to the edge grew well.

INTRODUCTION

Cyanolichens are a major component of epiphyte communities in the Pacific Northwest, where their biomass can exceed 3 t/ha (McCune 1993). Over twenty cyanolichen species are thought to be closely associated with late successional or old-growth forests in western Oregon and Washington (F.E.M.A.T. 1993). The most prevalent of these cyanolichens, *Lobaria oregana* (Tuck.) Müll. Arg., accounts for over half of the total epiphyte biomass in old-growth Douglas-fir forests (Pike et al. 1977), but it is much less abundant in younger forests (Neitlich 1993, Spies 1991). A rare but similar-looking species, *Pseudocyphellaria rainierensis* Imsh., appears to be restricted to old-growth forests (Neitlich 1993) where it grows epiphytically on understory trees and shrubs (Pike et al.

1975). This species is occasionally found in the crowns of large Douglas-fir trees (Sillett 1996). Both *L. oregana* and *P. rainierensis* are endemic to the Pacific Northwest.

Old-growth Douglas-fir forests in the Pacific Northwest have been severely fragmented by timber harvesting, resulting in a mosaic of remnant forest patches surrounded by clearcuts and regenerating vegetation (Morrison et al. 1991). In the Willamette National Forest of Oregon, for instance, less than one fourth of the land area is covered by old-growth forest, and less than one third of this area persists as interior forest given an edge width of two tree heights (Harris 1984, Norse 1990). Edges of old-growth forests bordering clearcuts are microclimatically and structurally different from undisturbed forests. Forest edges are warmer, brighter, windier, and less humid than the forest interior (Chen et al. 1993). Rates of large tree mortality are also much higher on forest edges compared to the forest interior (Chen et al. 1992). The implications of these changes for canopy epiphytes are poorly understood.

The purpose of this experiment was to compare the growth rates of epiphytic cyanolichens at the edge and in the interior of an old-growth forest. Thalli of *L. oregana* and *P. rainierensis* from an interior forest and a clearcut edge were reciprocally transplanted among four tree crowns using a modified method for culturing cyanolichens on nylon monofilament (cf. Denison 1988).

METHODS

Study area

The site of this experiment is a 30 ha forest stand in the southeastern corner of the Middle Santiam Wilderness in the western Cascades of Oregon (44°30'N, 122°12'W). Annual rainfall exceeds 2 m with a pronounced summer drought (Daly et al. 1994). The

stand lies between 650 and 700 m elevation on a gently sloping, north-facing terrace about 50 m above the Middle Santiam River. The forest canopy is dominated by very large (1.5-3.0 m dbh, 55-75 m tall) Douglas-fir (*Pseudotsuga menziesii*) trees approaching 700 years of age. Tree age in the stand was estimated by counting rings on stumps of large Douglas-fir in an adjacent clearcut. Trees of this age and size are unusual at similar sites in the central western Cascades of Oregon where the fire return interval averages 150 years (Teensma 1987). These trees are widely scattered in the stand, and most of them have broken tops. A butt rot fungus, *Phaeolus schweinitzii,* appears to be the major cause of Douglas-fir mortality in the stand. Three other tree species are also prevalent in the stand: *Tsuga heterophylla, Thuja plicata,* and *Taxus brevifolia.* The stand is bordered by a steep slope leading to the river on the north, by younger, more recently burned forests on the east and west, and by a twenty year old clearcut with regenerating Douglas-fir on the south. Many of the large Douglas-fir trees near the clearcut edge have blown down.

Transplant procedures

Live, healthy thalli of *L. oregana* and *P. rainierensis* were collected from branches within the middle portion of the crowns of two large Douglas-fir trees (i.e., between 35 and 45 m above the ground). One of these trees grew in the forest interior and the other grew on the edge of the clearcut. Thalli were taken to the laboratory, cleaned of debris, and cut into pieces (cuttings) averaging 5-10 cm in length and 2-5 cm in width. Each cutting included at least two young lobes, or growing tips.

Cuttings were air-dried (i.e., allowed to equilibrate under ambient conditions) in the laboratory overnight and weighed to the nearest 0.001 g. Five cuttings (hereafter 'sacrificed cuttings') of each species were also dried in an oven at 70°C for 24 hours, reweighed, and stored at ambient conditions in the laboratory. Oven-dried weights of the

live cuttings were estimated by multiplying their air-dried weights by the ratio of oven-dried to air-dried weights for the sacrificed cuttings. Knotted loops of 12-pound test nylon monofilament (2-3 cm in length) enclosing a small, plastic label were attached to the undersides of the live cuttings away from the growing tips with a small amount of silicone sealant. Labelled cuttings were air-dried in the laboratory overnight and then reweighed to the nearest 0.001 g. The sacrificed cuttings were weighed again at this time. Weights of the label materials, including nylon monofilament, plastic label, and silicone sealant, were calculated by the following formula: $L_1 - L_0(R_1/R_0)$, where L_1 is the air-dried weight of a labelled cutting, L_0 is the air-dried weight of an unlabeled cutting, R_1 is the mean air-dried weight of the sacrificed cuttings at the first weighing, and R_0 is the mean air-dried weight of the sacrificed cuttings at the second weighing. Thus, R_1/R_0 is a correction factor for any difference in lichen water content between L_1 and L_0. A total of 400 labelled cuttings were prepared, 200 of each lichen species, half from thalli collected in the interior tree and half from thalli collected in the edge tree.

Labelled cuttings (hereafter 'lichen transplants') of both lichen species were transplanted into the crowns of four large Douglas-fir trees. Two of these trees grew in the forest interior and two grew on the edge of the 20 year old clearcut. All four trees were of similar stature (2.0-2.5 m dbh, 60-70 m tall). Lichen transplants were attached to tree branches with 0.5 m lengths of 3 mm nylon cord. Six lichen transplants, three of each species, were tied onto each cord such that the transplants were evenly spaced and alternating by species. The cords were wrapped around tree branches and tied so that the lichen transplants were positioned close to undisturbed branch surfaces in a natural orientation. All cords were tied to separate branches within the middle portion of the tree crowns. Each of the four trees received about 16 cords, or 50 lichen transplants of each species. Half of the lichen transplants in each tree were derived from thalli collected in one of the interior trees and half were derived from thalli collected in one of the edge trees.

Lichen transplants were left in the forest canopy from October 1992 to October 1993. They were then brought back to the laboratory, oven-dried at 70°C for 24 hours, and weighed to the nearest 0.001 g. Annual percentage growth rate was calculated for each lichen transplant by the following formula: 100(final weight - label weight - initial weight)/initial weight.

Statistical analyses

Not all of the lichen transplants yielded data suitable for analysis. Many lichen transplants were lost during 12 months in the canopy. Some of the surviving lichen transplants had been torn, that is, only a portion of the original thallus remained attached to the monofilament. However, many of the lichen transplants lost weight without tearing, so removing torn transplants from the data set was not so straightforward. Also, a few lichen transplants gained weight by accumulating tree resin, which resulted in abnormally high apparent growth rates. Therefore, transplants with growth rates less than or greater than two standard deviations from the mean were removed from the data set as outliers. The removal of outliers from the data set had no major effects on results of statistical analyses.

Data were analyzed by two-factor ANOVA, the factors being source of the lichen thalli (forest interior vs. clearcut edge) and transplant site (forest interior vs. clearcut edge). Trees were the units of replication. The dependent variable was the average annual growth rate of lichen transplants per tree in each of the four treatment combinations (i.e., transplants from interior to interior, edge to interior, interior to edge, and edge to edge). Data for *L. oregana* and *P. rainierensis* were analyzed separately.

RESULTS

The biomass of both cyanolichen species increased during a year in the canopy, but a substantial portion of the transplants actually lost weight (Table 3.1). The average growth rate of *L. oregana* transplants was significantly higher than that of *P. rainierensis* (n = 4, paired *t*-test, $P < 0.05$). There was no significant relationship between the initial weight of transplants of either species and their annual growth rates ($R^2 = 0.026$ and 0.002, for *L. oregana* and *P. rainierensis,* respectively).

L. oregana transplants grew less on the clearcut edge than they grew in the forest interior ($P < 0.02$, Table 3.2). The source of *P. rainierensis* thalli significantly affected

Table 3.1. Summary of cyanolichen transplants before and after one year in a forest canopy in western Oregon.

	L. oregana	*P. rainierensis*
Initial number of transplants	200	200
Average initial dry weight (g)	0.669	0.295
Maximum/minimum initial dry weights (g)	1.480/0.225	0.777/0.103
Missing after 1 year (%)	12.5	31.0
Considered outliers (%)	4.5	5.5
Losing weight (%, not including outliers)	11.5	18.0
Maximum observed annual % growth	35.5	33.8
Average annual % growth	10.0 ± 0.73 (S.E.)	5.7 ± 0.92 (S.E.)

Table 3.2. ANOVA tables for transplant experiments involving two species of cyanolichen in western Oregon.

	L. oregana				*P. rainierensis*			
Source of variation	df	MS	*F*	*P*	df	MS	*F*	*P*
Source of lichen thalli	1	7.47	2.70	0.18	1	74.91	15.74	0.02
Transplant site	1	56.02	20.24	0.01	1	19.16	4.03	0.12
Source X site interaction	1	0.08	0.03	0.88	1	36.12	7.59	0.05
Residual	4	2.77			4	4.76		

transplant growth rate ($P < 0.02$, Table 3.2). Specifically, thalli that came from the forest interior and were transplanted to the clearcut edge lost weight, on average, while thalli that came from the clearcut edge and were transplanted back to the clearcut edge grew an average of 9.5 percent (Figure 3.1). A similar but less pronounced effect was apparent for *Lobaria oregana* transplants: the average growth rate of thalli that came from the forest interior and were transplanted to the clearcut edge was the lowest of all four treatment combinations (Figure 3.1).

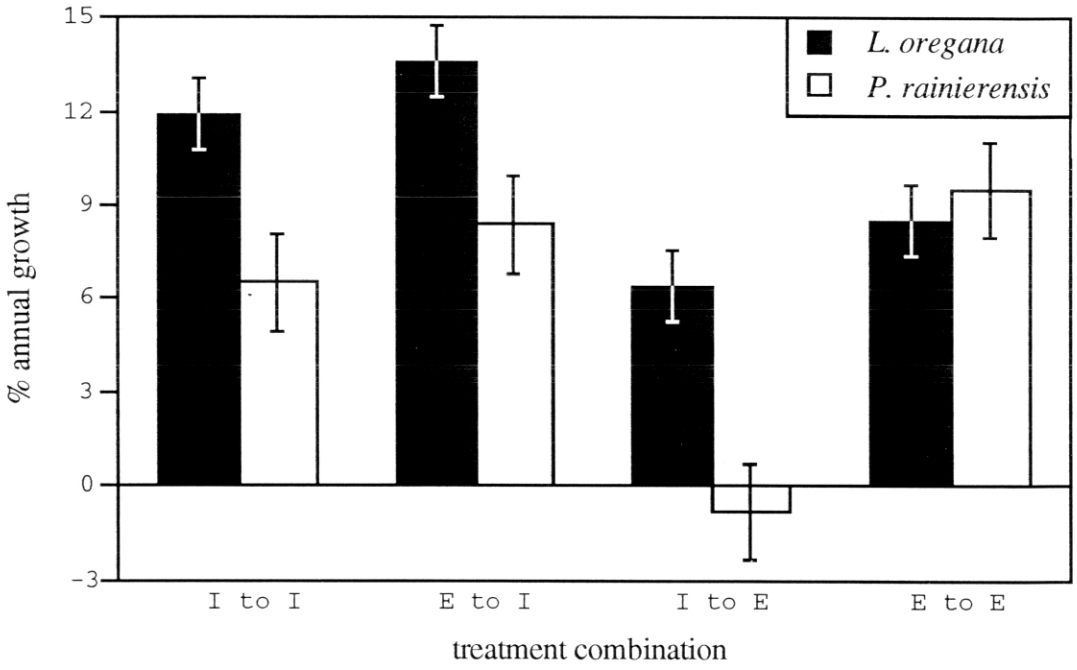

Figure 3.1. Average growth rates of transplants of two species of cyanolichen after one year in a forest canopy in western Oregon. Treatment combinations are indicated as transplants from source to site, that is, interior to interior (I to I), edge to interior (E to I), interior to edge (I to E), and edge to edge (E to E). Error bars represent one standard error of the mean (n = 2).

DISCUSSION

The transplant experiment presented in this paper tested two questions. First, do growth rates of cyanolichen transplants differ between the edge and interior of an old-growth forest? Second, does the source of lichen thalli influence growth rates of cyanolichen transplants? The answer to both questions is "yes," but the two cyanolichen species responded differently to experimental treatments.

The higher growth rate of *L. oregana* in the interior forest compared to the clearcut edge is explicable in terms of differences in canopy microclimate. Growth rates of foliose lichens are positively correlated with moisture availability (Armstrong 1993). Lichens become dormant when the water content of the thallus falls below a certain threshold (Kershaw 1985). Tree crowns at forest edges are more exposed to sunlight and wind than those of the forest interior, and epiphytes in these trees may dry more rapidly as a consequence of higher vapor pressure deficits (Geiger 1965). Thus, lichens at the forest edge may spend less time in a photosynthetically active state, and therefore grow less, than those of the forest interior even if both sites receive the same amount of precipitation.

The fact that growth rates of *P. rainierensis* transplants on the clearcut edge were influenced by the source of the thalli suggests that these cyanolichens had become acclimated to canopy microclimatic conditions prior to being transplanted. If indeed epiphytic habitats in tree crowns near the clearcut edge are subjected to more frequent and severe periods of desiccation than those of the forest interior, cyanolichens from the clearcut edge may be more tolerant of desiccation than those from the forest interior. Possible mechanisms for a higher desiccation tolerance of lichens at the clearcut edge include drought-hardening (Dilks & Proctor 1976) and morphological changes, such as a thicker thallus, which increase water storage capacity and decrease drying rates (Snelgar & Green 1981).

The lichen transplant method used in this study has potential applications for future studies of epiphytic habitat suitability. In this case it appears that the ability of some cyanolichen species to acclimate to more desiccating microclimates may be an important factor in their persistence within managed forests. For example, the retention of large, living trees in harvest units may be one way to facilitate the carryover of late successional epiphyte species into younger forests if the species can acclimate to the new microclimate within the isolated tree crowns.

Chapter 4

Growth and Mortality of Cyanolichen Transplants in Douglas-Fir Forest Canopies

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ABSTRACT

In the Oregon Cascades, nitrogen-fixing lichens are abundant in old growth, but this cyanolichen biomass develops very slowly in young forests. Our purpose in this study was to evaluate whether epiphytic cyanolichens require old growth and/or thick, underlying moss mats to achieve normal rates of growth and mortality. We transplanted over one thousand mature thalli of two cyanolichen species (*Lobaria oregana* and *Pseudocyphellaria rainierensis*) into the crowns of Douglas-fir trees in thirteen forest stands representing four age classes: old growth (430-700 yr), mature (140-150 yr), young (35-40 yr), and recent clearcut. Wooden racks were used instead of trees in the clearcuts. Half of the cyanolichen thalli were transplanted onto thick moss mats and half were transplanted onto bare bark. Rates of growth and mortality were measured after one year. Both species grew at least as well in the younger forests as they did in old growth (20 to 30% increase in mass), but growth rates were significantly lower in clearcuts. Mortality rates were very low (<10%) in young, mature, and old-growth forests, but high (50 to 90%) in clearcuts. *P. rainierensis* grew significantly better on moss than bare bark (30 vs. 23% increase in mass). Since our results show that cyanolichens can find suitable habitat in young forest canopies, silvicultural treatments such as live tree retention have great potential to maintain cyanolichens in managed forests.

INTRODUCTION

Epiphyte biomass increases slowly during succession in many temperate forests (Lesica et al. 1991, Rose 1992, McCune 1993, Neitlich 1993, Selva 1994, Esseen and Renhorn 1995). Old growth supports much higher epiphyte loads than younger, managed forests.

In the Douglas-fir forests of Oregon's western Cascades, the most striking epiphytic difference between old growth and managed forests involves cyanolichens. These nitrogen-fixing lichens dominate the old-growth canopy (Pike et al. 1975, Chapter 2) but are scarce or absent in younger conifer forests (McCune 1993, Neitlich 1993). Many epiphyte species, including several endemic cyanolichens, are seldom found in Douglas-fir forests less than a century old (U.S.D.A. 1994).

Reasons for the slow accumulation of epiphyte biomass are poorly understood. Unsuitable microclimate in younger forests is one of several possible explanations (Chapter 1). Microclimatic differences between old-growth and younger forests presumably arise from structural differences such as the frequency and size of gaps, abundance of standing dead material, and complexity of canopy architecture. Dense, young, even-aged Douglas-fir canopies shade and shelter the undergrowth from direct sunlight and precipitation in contrast to more open and structurally complex old-growth canopies (Kuiper 1988, Spies and Franklin 1991). Furthermore, bryophytes develop in thick mats on branches in old Douglas-fir forests, and many epiphyte species are closely associated with these mats (Chapter 2). Perhaps these water-storing mats ameliorate temperature and moisture fluctuations of epiphytes in their immediate vicinity, making these microhabitats more suitable to desiccation-sensitive species (Lawrey 1991).

Conservation of old growth-associated epiphytes, particularly cyanolichens, is an important consideration in the ongoing reassessment of forest management in the Pacific Northwest (Franklin 1992, Swanson and Franklin 1992). Epiphytes constitute a significant part of biodiversity in Pacific Northwest forests, where the number of macrolichen and bryophyte species often equals or exceeds the number of vascular plant species (e.g., Lesica et al. 1991). Nitrogen fixed by cyanolichens in Douglas-fir forests represents a major input (3-4 kg $N \cdot ha^{-1} \cdot yr^{-1}$, Pike 1978, Denison 1979) in this nitrogen-limited ecosystem. Nitrogen-rich leachates from cyanolichens also contribute to complex

food webs in the forest canopy (Carroll 1979). Many invertebrates, particularly oribatid mites, spend their entire lives among epiphytic lichens and bryophytes in old-growth forests (Voegtlin 1982, Winchester and Ring 1995), and different species of cyanolichens appear to support discrete groups of arthropods (Neitlich 1993). Cyanolichens are also home to a plethora of microfungi, including parasymbiotic and parasitic species (Stone et al. 1995).

This study evaluates one explanation for the slow development of this critical component of Douglas-fir forests: that epiphytic cyanolichens demand the environment created by the structure of old-growth forest canopies. We also consider the possible effects of moss mats on cyanolichen growth and mortality in the forest canopy. Two cyanolichen species (*Lobaria oregana* and *Pseudocyphellaria rainierensis*) were collected from old growth and transplanted into mature, young, and recently clearcut forests. Their annual rates of growth and mortality in these forests are compared to observed rates in old growth. Our purpose is to determine if younger forest canopies provide suitable habitats for these old growth-associated species.

METHODS

Study sites

Thirteen forest stands comprising four age classes (old growth, mature, young, and recent clearcut) were selected from the Willamette National Forest in the central Oregon Cascades (Table 4.1). They represent the relatively mesic *Tsuga/Polystichum-Oxalis* and *Tsuga/Polystichum* plant associations of the *Tsuga heterophylla* Zone (Franklin and Dyrness 1973). Stands were chosen arbitrarily, but without preconceived bias, such that age classes were interspersed within the study area (Figure 4.1). All of the stands occur

Table 4.1. Characteristics of study sites in the Willamette National Forest in western Oregon. Trunk diameter (dbh) and height are listed for the two Douglas-fir trees climbed in each stand.

Stand Number	Age Class	Elevation (m)	Estimated Age	Tree DBH (m)	Tree Height (m)
1	old growth	610	700	2.77, 2.08	68.0, 66.0
2	old growth	830	560	1.84, 1.65	82.5, 78.0
3	old growth	490	450	1.56, 1.41	74.0, 66.5
4	old growth	590	430	1.62, 1.31	71.0, 67.5
5	mature	890	150	0.87, 0.76	48.5, 49.5
6	mature	560	140	1.30, 1.26	59.5, 62.5
7	mature	650	140	1.02, 0.93	54.5, 48.0
8	young	780	40	0.40, 0.38	25.0, 23.5
9	young	760	37	0.46, 0.38	25.5, 20.0
10	young	500	36	0.33, 0.30	25.0, 26.0
11	clearcut	670	—	—	—
12	clearcut	460	—	—	—
13	clearcut	790	—	—	—

between 450 and 900 m elevation and are located on lower slopes within 100 vertical meters of the nearest major stream. Average annual rainfall in the stands ranges from 1.5 to 2.2 m (Figure 4.1). Most of the precipitation occurs from November through March. The average annual temperature is approximately 9.5°C, with January and July means of 2 and 22°C respectively (Waring et al. 1978). During the study period (May 1994 to May 1995), temperatures were relatively close to average, the winter was slightly wetter than average, but summer (July and August) was exceptionally dry (precipitation < 20% of average, George Taylor, pers. com.).

The old growth and mature stands originated from stand-replacing fires and are dominated by large Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) with varying amounts of codominant and understory western hemlock (*Tsuga heterophylla* (Raf.)

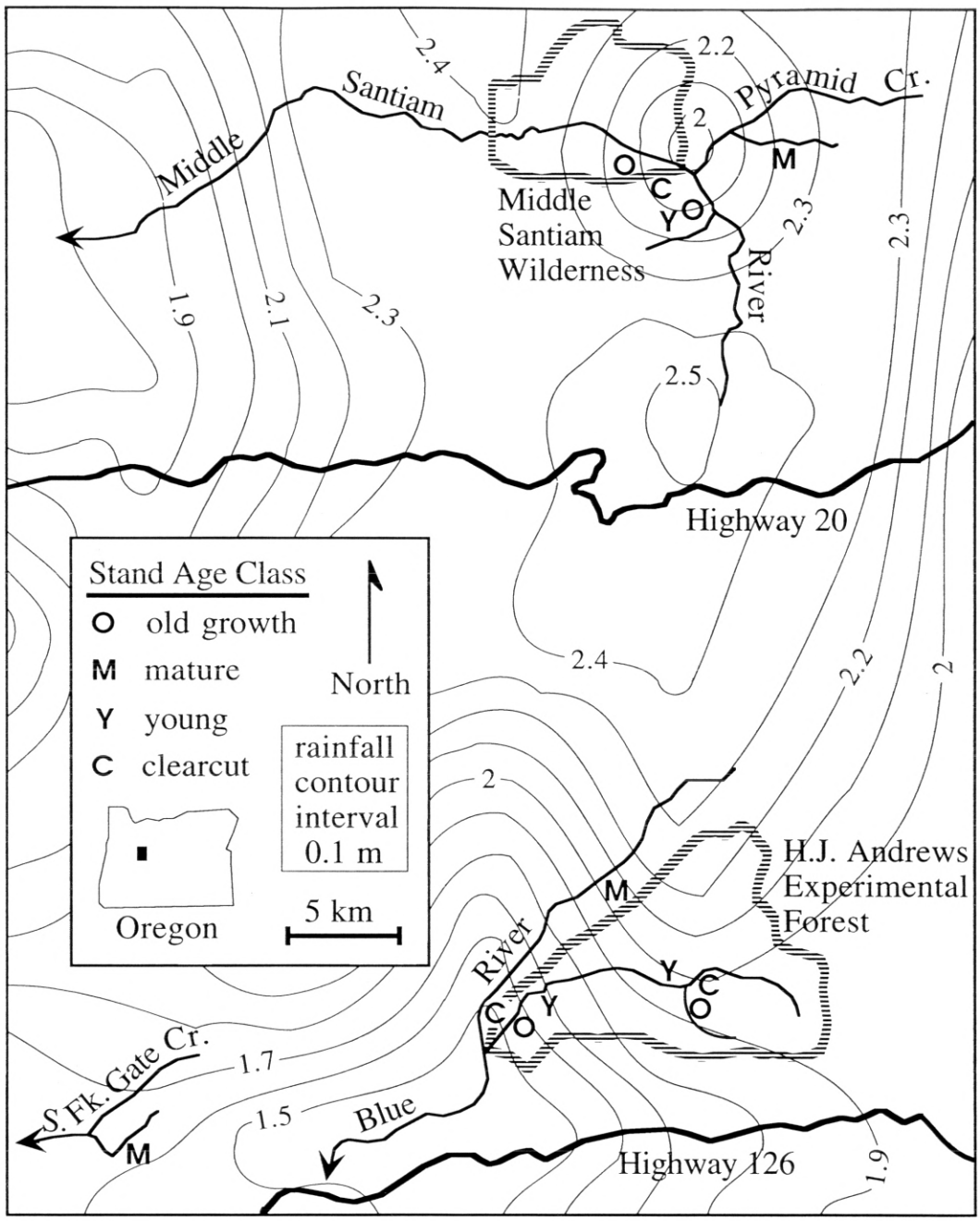


Figure 4.1. Map of the study area in the central Oregon Cascades showing locations of 13 forest stands used in cyanolichen transplant experiments. Average annual rainfall contours are based on Daly et al. (1994). Study sites near the Middle Santiam Wilderness Area are (from west to east) stands 1, 11, 9, 4, and 5. Study sites near the H. J. Andrews Experimental Forest are stands 6, 12, 3, 10, 7, 8, 2, 13 (see Table 4.1).

Sarg.) and western redcedar (*Thuja plicata* Donn.). Understory reinitiation (Oliver and Larson 1990) is well advanced in the mature stands. The young stands originated from clearcuts (10-30 ha) that were replanted exclusively with Douglas-fir and contain very little naturally regenerated western hemlock. None of the young stands have been thinned since replanting, and stem exclusion (Oliver and Larson 1990) is well underway. The clearcut stands (5-20 ha) contain scattered Douglas-fir, western hemlock, and shrubs not exceeding 1.5 m in height.

Tree selection and access.

Two emergent Douglas-fir trees occurring within 100 m of each other in the interior (i.e., over 200 m from the nearest clearcut edge) of each forest stand were selected for detailed study (Table 4.1). Excessively leaning trees and trees with dead tops were avoided. Tall tree crowns were nondestructively accessed by shooting a nylon monofilament over sturdy lower branches with a compound bow, hauling a nylon cord followed by a climbing rope over the branches, tying one end of the rope at ground level, and ascending the rope using vertical rope technique (Perry 1978). Rope techniques developed by arborists (Dial and Tobin 1994) were used to access higher branches. A pulley secured to the trunk near the top of each tree was used to haul a climbing rope into place (via nylon cord) for subsequent ascents. In the clearcuts, wooden racks with horizontal Douglas-fir beams (5 cm thick, 2.5 m long) elevated 2 m above the ground were used instead of trees. Two racks, each with 2 horizontal beams, were installed in each clearcut at least 50 m from the nearest forest edge.

Study organisms.

Lobaria oregana (Tuck.) Müll. Arg. (hereafter *L. oregana*) is well documented as an old growth-associated epiphyte (McCune 1993, Neitlich 1993). It is a large, yellow-green, foliose lichen that grows loosely appressed to bark or draped over branches. It reproduces primarily by tiny, vegetative lobules which are borne on the margins and ridges of the thallus and are easily detached (Rhoades 1983). The primary photobiont is a green alga, but the thallus contains internal cephalodia with nitrogen-fixing, photosynthetic cyanobacteria. *L. oregana* is endemic to coniferous forests of the Pacific Northwest, ranging from southeast Alaska to California, mostly west of the Cascade crest. It dominates epiphyte communities of old-growth Douglas-fir forests (Neitlich 1993, Pike et al. 1975, Chapter 2).

Pseudocyphellaria rainierensis Imsh. (hereafter *P. rainierensis*) is a rare species more restricted to old growth than *L. oregana* (Neitlich 1993, Sillett 1996). Like *L. oregana*, *P. rainierensis* is a large, foliose lichen that reproduces primarily by tiny asexual propagules (in this case, isidia), and its cyanobacteria are confined to internal cephalodia. Unlike *L. oregana*, *P. rainierensis* is pale blue-green in color with tiny pores, known as pseudocyphellae, scattered over its lower surface. *P. rainierensis* is also endemic to coniferous forests of the Pacific Northwest, ranging from southeast Alaska to central Oregon, exclusively west of the Cascade crest. This species occurs primarily in the understory of old growth (Pike et al. 1975) but can be abundant in the upper canopy of very old (> 600 yr) and wet forests (Chapter 2, Sillett 1996).

Antitrichia curtipendula (Hedw.) Brid. is a mat-forming moss capable of dominating epiphyte assemblages in moist Douglas-fir forests (Chapter 2). It often covers the largest branches in mats several meters in length and 5-10 cm thick. Individual tree crowns can support more than 7 kg dry weight of this species. Several epiphyte species, including

mosses, liverworts, cyanolichens, and a fern, are closely associated with *A.curtipendula* in the canopy. When intact moss mats fall to the ground, *A. curtipendula* frequently survives and comes to dominate areas of the forest floor and fallen logs (pers. obs.).

Epiphyte transplanting

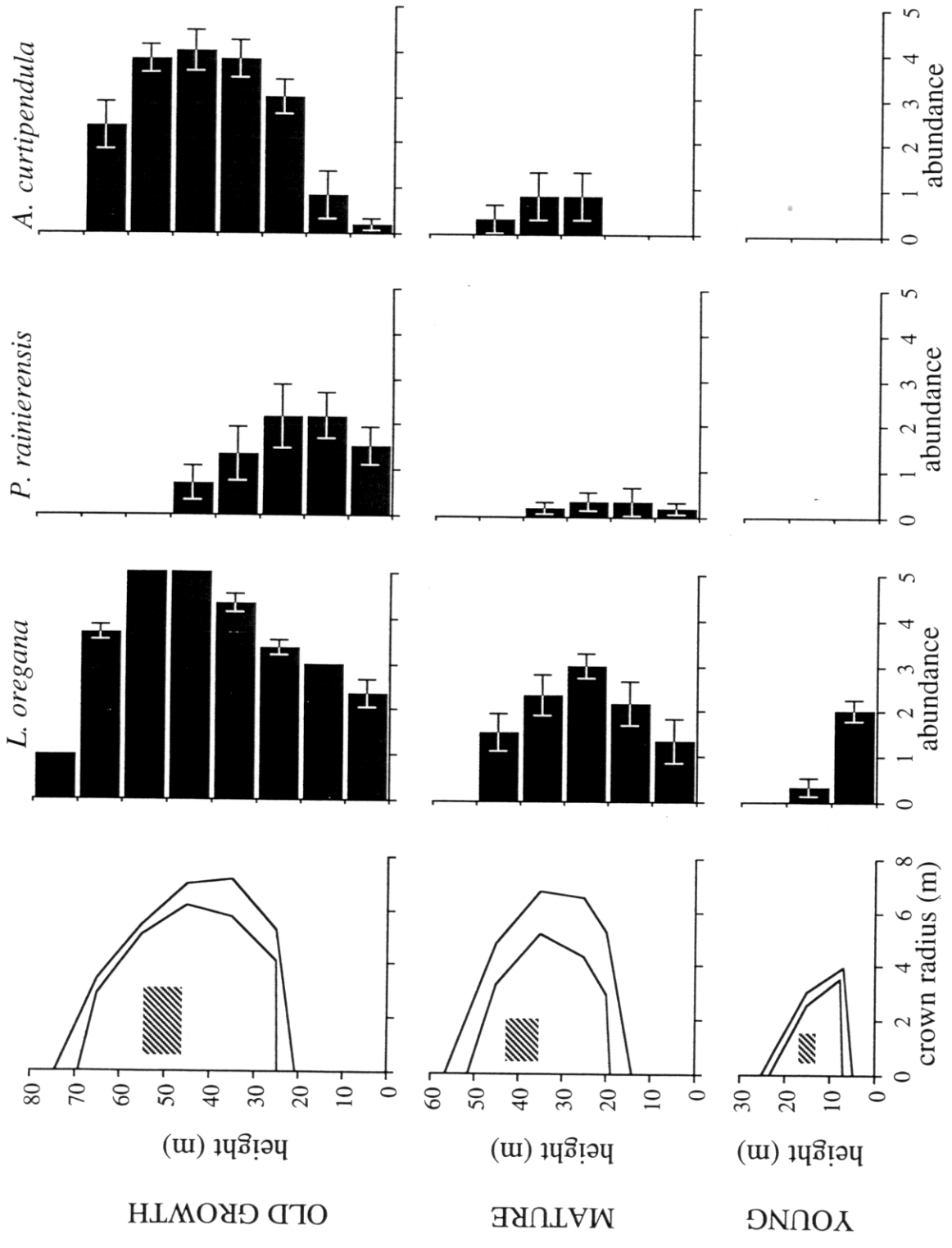
We collected fresh thalli of the two cyanolichen species from living tree crowns in the H. J. Andrews Experimental Forest. Since preliminary work indicated that the source of thalli significantly affects transplant growth rates (Chapter 3), all fresh material of a given species was gathered from a single tree. Thalli of *Lobaria oregana* were collected from the mid-crown (40-50 m) of a single Douglas-fir tree (dbh 1.5 m, height 70 m) in a 450-year-old forest (elevation 500 m). Thalli of *Pseudocyphellaria rainierensis* were collected from the crown (10-20 m) of a single western hemlock tree (dbh 0.5 m, height 25 m) growing on the 40-year-old edge of a 560-year-old forest (elevation 750 m). Preliminary work (Chapter 3) demonstrated that *P. rainierensis* thalli from forest edges are more robust and amenable to transplanting than thalli from the forest interior.

Healthy thalli of both cyanolichen species were taken to the laboratory, cleaned of debris, and cut into pieces averaging 5-10 cm in length and 2-5 cm in width. Each piece included at least two young lobes, or growing tips. These thalli were individually weighed, attached to labelled loops of nylon monofilament with silicone, and prepared for transplanting according to methods outlined in McCune et al. (1995). Prior to transplanting, the sizes and shapes of the thalli were recorded in sketches.

Transplanting began with the random selection of ten 0.5 m long sections of live branch from between one-half and two-thirds of the live crown height and up to half of the crown width in each tree (Figure 4.2). Heavily shaded branch sections were avoided. Substrate types were manipulated in two ways. Five of the branch sections in each tree were manually stripped of epiphytes for the bare bark treatment. The other five branch sections

Figure 4.2. Profiles of Douglas-fir tree crowns and vertical distributions of resident epiphyte populations in three forest age classes. In the profile diagrams, inner and outer boundaries represent 1 S.E. below and above the mean radii of the live crowns. The shaded areas represent the portion of the crowns into which cyanolichens were transplanted. Epiphyte abundance is expressed on a 0-5 scale (see text). Values are means ± 1 S.E..

Figure 4.2


OLD GROWTH
MATURE
YOUNG
height (m)
crown radius (m)
abundance
L. oregana
P. rainierensis
A. curtipendula

were covered with thick (5 to 10 cm) *A. curtipendula* mats for the moss treatment. Resident moss mats were utilized in the old-growth forest trees, but moss mats from the old-growth forest canopy were transplanted onto the branch sections in the younger age classes since these forest canopies lacked thick moss mats. These mats were cut into 0.5 m lengths and tied onto the branch sections with twine. In the clearcuts, moss mats were transplanted at 1 m intervals on the beams of each rack.

Two thalli of *L. oregana* and *P. rainierensis* were transplanted onto the upper surface of each branch or beam section by tying them (through the monofilament loop) down with 3 mm nylon cord. Each tree or rack received a total of 40 cyanolichen transplants (20 of each species). Half of the thalli were transplanted onto moss mats, half onto bare bark or wood. A total of 1040 cyanolichen thalli were used in this transplant experiment (13 stands, 2 trees or racks per stand, 10 branch sections per tree or rack, 2 species per branch or beam section, and 2 thalli per species).

Data collection

Trunk diameter (dbh), total height, height to first branch, and average crown width at 10 m height intervals was recorded for each tree used in this study. The abundance of resident populations of the three epiphyte species used in the transplant experiment (*L. oregana*, *P. rainierensis*, and *A. curtipendula*) was also recorded in each tree on a 0-5 scale: 0) absent, 1) 1-3 individuals, 2) 4-12 individuals, 3) up to 25 % cover, 4) 25 to 50% cover, and 5) greater than 50 % cover. Epiphyte cover was visually estimated on the upper surfaces of branches within each 10 m height stratum. Below the live crown, epiphyte cover was estimated on understory vegetation (primarily western hemlock and western redcedar) occurring within the projected crown area of each Douglas-fir tree.

The age of forest stands was estimated by three methods. In two of the old-growth stands (1 and 4), tree age was estimated by counting annual rings on several stumps of large Douglas-fir in adjacent clearcuts. A published fire history (Teensma 1987) was used to estimate the ages of stand 2 and 3. Tree age in the mature and young stands was determined with an increment bore. Ages of the mature and young stands were estimated by counting annual rings on two cores per stand.

Cyanolichen transplants were left in the forest canopy for one year (May 1994 to May 1995). After careful removal from trees and racks, they were taken to the laboratory. Each thallus was inspected for physical changes and separated into three categories: healthy (no necrosis), partially alive (some necrosis), and dead (complete necrosis). The number of missing thalli was also recorded. Dead, torn, and broken thalli were then discarded. Unfragmented, living thalli were reweighed. Growth rates were calculated based on air dried weights before and after transplanting, and after subtracting the weight of the label (see McCune et al. 1995). Corrections to a standard moisture content were made by weighing thalli after they had equilibrated for 24 hours in the laboratory. Several thalli were then oven-dried. The ratio of oven-dried to air-dried weights of the sacrificed thalli was used as the correction factor. Two estimates of annual growth rate were made: one based only on healthy thalli (hereafter 'potential growth') and one based on all unfragmented thalli, including those with some necrosis (hereafter 'average growth'). Each tree yielded two independent estimates of five dependent variables (potential growth, average growth, % healthy, % dead, and % lost): one for each substrate type (bare bark vs. moss).

Statistical analyses

Results were analyzed using a three-way, mixed model analysis of variance with one level of nesting (Abacus Concepts 1990). This analysis tested for two fixed effects (age

Table 4.2. Format of analyses of variance presented in this chapter. Degrees of freedom are those for the balanced design with no missing data (i.e., 4 age classes, 3 stands per age class, 2 trees per stand, 2 substrate types per tree).

Source of variation [df]	Error term [df]
Age [3]	Stand(age) [8]
Substrate [1]	residual [24]
Stand(age) [8]	residual [24]
Age X substrate [3]	Substrate X stand(age) [8]
Substrate X stand(age) [8]	residual [24]

class and substrate), one random effect (stand nested within age class), and two interactions (Table 4.2). Old growth was considered the control in a series of a prioricomparisons among age classes designed to test whether the younger age classes differed from old growth in any of the dependent variables. Experimentwise error rates were controlled in these comparisons by employing Dunnett's test (Zar 1984) in a stepwise manner. Homogeneity of variance among age classes was tested with the F_{max}-test (Sokal and Rohlf 1995). When present (e.g., % dead *L. oregana*), heterogeneous variance among age classes was accommodated by applying the Game and Howell method to Dunnett's test (Day and Quinn 1989). A few trees and racks failed to yield data suitable for analysis of some variables because of excessive loss and/or fragmentation of transplanted thalli. For instance, all of the *P. rainierensis* thalli in stand 2 were lost or fragmented. This stand was omitted from all analyses of variance for *P. rainierensis*. Unequal sample sizes resulting from missing data were accommodated by applying Kramer's modification prior to performing Dunnett's test (Day and Quinn 1989). Results for *L. oregana* and *P. rainierensis* were analyzed separately.

RESULTS

Resident epiphyte populations

The old-growth, mature, and young Douglas-fir forest canopies differed markedly in both the abundance and vertical distributions of resident populations of *L. oregana*, *P. rainierensis*, and *A. curtipendula* (Figure 4.2). All three species were most abundant in old growth. *Lobaria oregana* dominated epiphyte assemblages in the old-growth canopy. It was present throughout the vertical profile, reaching greatest abundance (cover > 50 %) between 40 and 60 m. In contrast, *L. oregana* was absent from the tops of the Douglas-fir trees in the mature and young forests. In the mature forests, *L. oregana* was most abundant (cover up to 25 %) between 20 and 30 m. In the young forests, *L. oregana* was most abundant (3-12 thalli per tree) below 10 m. *Pseudocyphellaria rainierensis* was absent from the upper canopy of the old growth, reaching its greatest abundance (cover < 25 %) between 10 and 30 m. *P. rainierensis* was seldom found in the mature forests and then only below 40 m. In the young forests, *P. rainierensis* was absent. *Antitrichia curtipendula* was widespread in the old-growth canopy, forming thick mats at heights between 30 and 60 m, but it was scarce in the understory. Mature forests harbored a few scattered individuals of *A. curtipendula* between 20 and 50 m. The young forests also lacked *A. curtipendula.*

Differences among age classes

Potential growth rate of *L. oregana* was almost 50 percent higher in old growth than in clearcuts ($P < 0.01$; Table 4.3, Figure 4.3). Average growth rate of *L. oregana* was four times higher in old growth than in clearcuts ($P < 0.01$). Five times as many *L. oregana* thalli remained healthy in old growth as in clearcuts ($P < 0.05$), but 50 percent more thalli

remained healthy in the young forests than in old growth ($P < 0.05$). Mortality rates of *L. oregana* thalli were almost ten times higher in clearcuts than in old growth ($P < 0.01$). Half as many *L. oregana* thalli were lost in young forests as in old growth ($P < 0.05$). Responses of *P. rainierensis* to forest age were rather similar to those of *L. oregana*, but *P. rainierensis* was even more intolerant of clearcuts (Figure 4.3). No *P. rainierensis* thalli remained healthy after a year in the clearcuts. Average growth of *P. rainierensis* was much higher in old growth than in clearcuts ($P < 0.05$); surviving thalli actually lost weight in clearcuts. Finally, mortality rates of *P. rainierensis* were over ten times higher in clearcuts than in old growth ($P < 0.01$).

Overall, observed differences in growth rates for both cyanolichen species were relatively small (≤ 5 %) between the old-growth, mature, and young forests. Mortality rates were also very low (< 10 %) in all three forest age classes. There was no mortality of *L. oregana* thalli in the young forests. Most of the significant age class effects were attributable to the distinctiveness of the clearcuts (Figure 4.3). The statistical power (calculated from equation 13.33 in Zar 1984) of these analyses to detect 5-10 % differences in growth rates among the age classes was relatively high (0.5 to 0.9). However, high stand to stand variation within an age class precluded the detection of rather large differences among age classes for some variables (e.g., % healthy and % lost *L. oregana*, Table 4.3).

Effects of moss mats

Transplanted moss mats survived in all age classes. New shoots were observed growing from all of the mats after one year. Moss mats affected growth and survivorship of cyanolichen thalli, but the two species responded somewhat differently to substrate type (Table 4.3, Figure 4.4). Potential growth of *P. rainierensis* was 30 percent higher on

Table 4.3. ANOVA tables for transplant experiments involving two cyanolichen species (*Lobaria oregana* and *Pseudocyphellaria rainierensis*) in Douglas-fir forests of western Oregon.

Dependent Variable	Source of variation	*L. oregana* df	MS	*F*	*P*	*P. rainierensis* df	MS	*F*	*P*
Potential	Age	3	89.8	3.9	0.05	2	7.2	0.1	0.89
Annual	Substrate	1	37.9	1.7	0.21	1	459.5	6.2	0.02
Growth	Stand(age)	9	23.3	1.0	0.45	6	62.6	0.8	0.55
	AgeXsubstrate	3	14.5	0.3	0.85	2	92.1	1.3	0.35
	SubstrateXstand(age)	8	54.6	2.4	0.05	6	72.4	1.0	0.47
	Residual	20	22.6			16	73.7		
Average	Age	3	408.8	10.8	<0.01	3	693.2	5.2	0.03
Annual	Substrate	1	75.9	2.9	0.11	1	151.4	2.1	0.16
Growth	Stand(age)	9	37.9	1.4	0.24	8	134.6	1.9	0.13
	AgeXsubstrate	3	36.0	0.6	0.65	3	82.3	2.4	0.15
	SubstrateXstand(age)	9	63.5	2.4	0.05	7	34.0	0.5	0.84
	Residual	21	26.6			16	71.3		
% healthy	Age	3	6980.5	9.4	<0.01	2	711.4	0.4	0.69
	Substrate	1	135.7	0.5	0.48	1	1613.4	3.9	0.06
	Stand(age)	9	743.3	2.8	0.02	6	1796.2	4.3	0.01
	AgeXsubstrate	3	224.1	1.3	0.34	2	110.1	0.4	0.70
	SubstrateXstand(age)	9	173.9	0.7	0.74	6	290.4	0.7	0.65
	Residual	22	263.8			18	413.2		
% dead	Age	2	9338.0	14.9	<0.01	3	20770.4	103.0	<0.01
	Substrate	1	86.2	0.3	0.57	1	72.5	0.5	0.48
	Stand(age)	7	627.9	2.4	0.06	8	201.6	1.4	0.24
	AgeXsubstrate	2	161.5	0.3	0.73	3	70.8	0.9	0.49
	SubstrateXstand(age)	7	491.7	1.9	0.13	8	79.5	0.6	0.80
	Residual	18	261.5			24	142.1		
% lost	Age	3	1689.6	3.1	0.08	3	573.8	1.0	0.44
	Substrate	1	1112.4	6.2	0.02	1	3657.5	10.7	<0.01
	Stand(age)	9	546.0	3.0	0.01	8	577.1	1.7	0.15
	AgeXsubstrate	3	406.6	2.7	0.11	3	135.4	0.3	0.81
	SubstrateXstand(age)	9	153.0	0.9	0.58	8	424.8	1.2	0.32
	Residual	26	179.2			24	342.7		

Figure 4.3. Effects of forest age on five dependent variables for two cyanolichen species. Values are means ± 1 S.E. Stand age classes are indicated by the following letters: OG = old growth, M = mature, Y = young, and CC = clearcut.

Figure 4.3

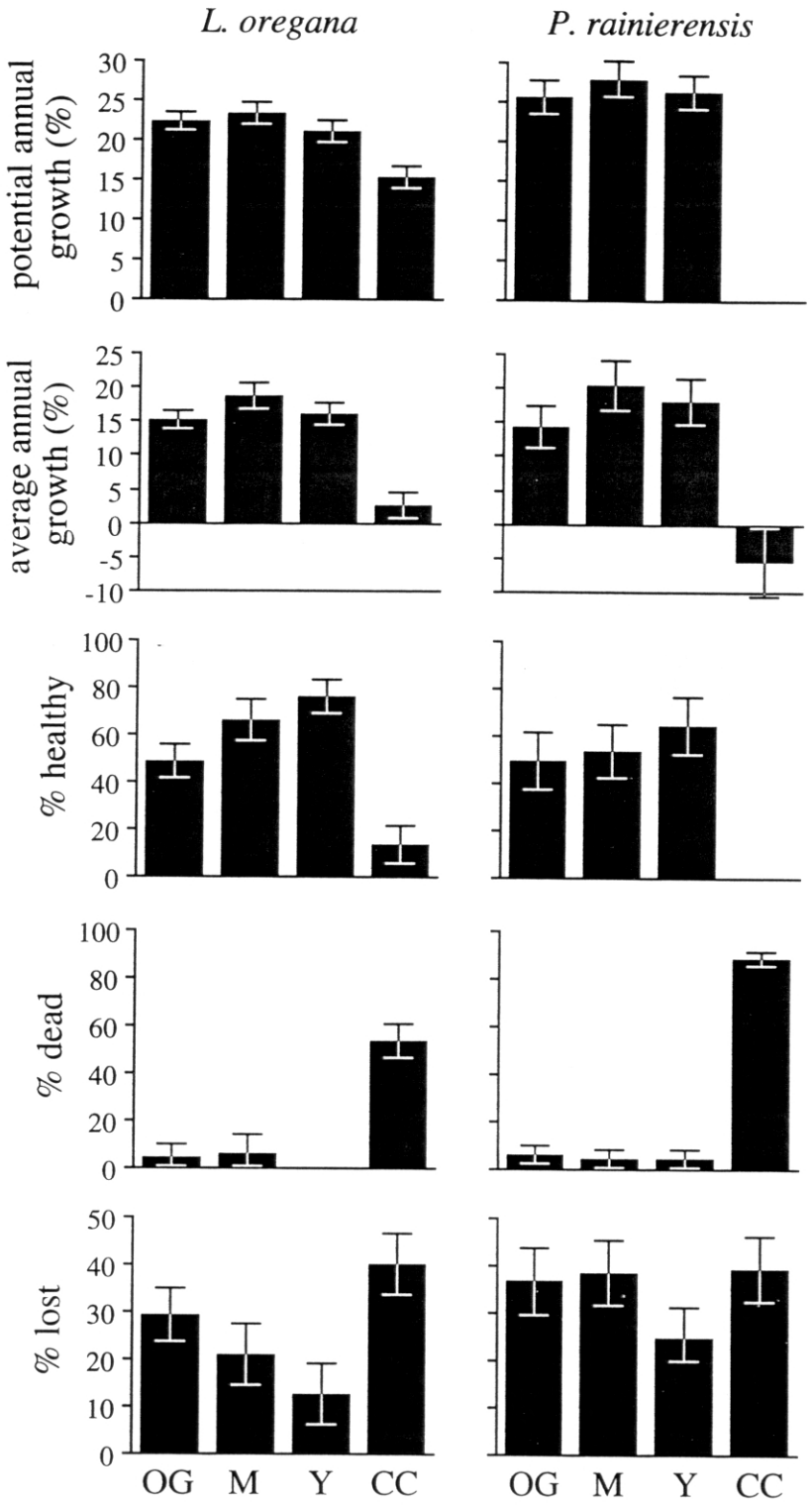
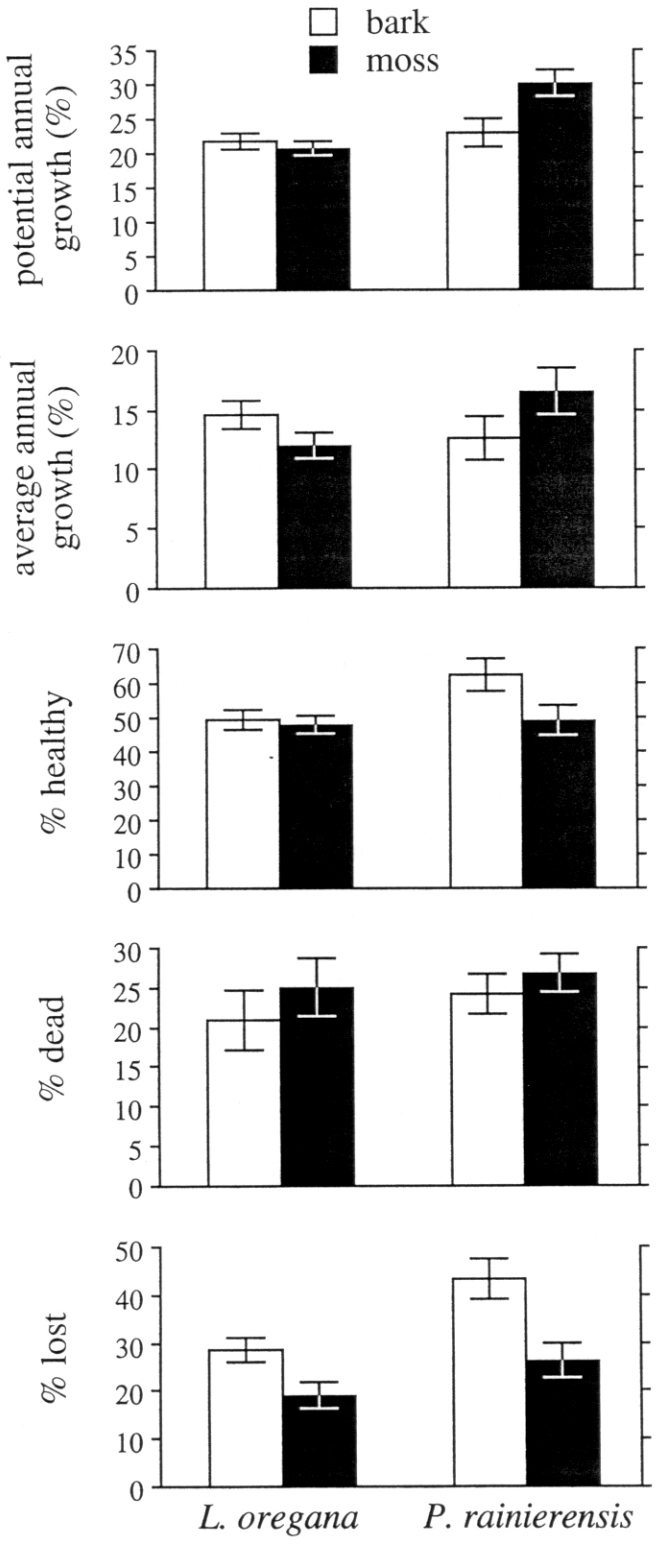

L. oregana
P. rainierensis
potential annual growth (%)
average annual growth (%)
% healthy
% dead
% lost
OG
M
Y
CC

Figure 4.4. Effects of substrate type on five dependent variables for two cyanolichen species. Values are means ± 1 S.E.

Figure 4.4


bark
moss
potential annual growth (%)
35
30
25
20
15
10
5
0
average annual growth (%)
20
15
10
5
0
% healthy
70
60
50
40
30
20
10
0
% dead
30
25
20
15
10
5
0
% lost
50
40
30
20
10
0
L. oregana
P. rainierensis

moss than on bark. Despite higher growth rates on moss, 25 percent more *P. rainierensis* thalli remained healthy on bark than on moss after one year. Moss had little effect on the growth or health of *L. oregana*. Finally, about 50 to 60 percent more thalli of both cyanolichen species were lost on bark than on moss.

DISCUSSION

Estimates of growth and mortality rates

The annual growth rates we report for *L. oregana* and *P. rainierensis* are comparable to those obtained from previous studies. Rhoades (1977) estimated annual growth rates of 40 to 70 percent for mature thalli of *L. oregana* based on sequential photographs of individual thalli in a large tree. These values are considerably higher than the potential annual growth of *L. oregana* observed here. However, only four mature thalli were studied by Rhoades, and several transplanted *L. oregana* thalli in our study had annual growth rates between 40 and 60 percent. Denison (1988) reported an average annual growth rate of about 16 percent for *L. oregana* thalli stacked vertically on nylon cord and hung from racks in a small forest clearing. This estimate of *L. oregana* growth is almost identical to our estimate of potential annual growth in the clearcuts (~15 %). Sillett (1994) observed average annual growth rates of 10 to 15 percent for *L. oregana* and 5 to 10 percent for *P. rainierensis* transplanted into the mid-canopy of an old-growth forest. These values are considerably lower than the ones reported here, but estimates from this earlier study were based on some measurements of unhealthy and/or partially fragmented thalli. The earlier estimates correspond more closely with average annual growth rates reported here.

Overall, our transplant technique was effective for generating estimates of annual growth and mortality of cyanolichens in a range of habitats. A few additional comments are warranted. The average growth estimates are conservative because they are based on both healthy and unhealthy thalli. However, they may be more meaningful biologically than the potential growth estimates because considerable dieback and decomposition of cyanolichen thalli occurs in the canopy (Rhoades 1983, Sillett 1996). The higher incidence of necrosis among living thalli in old growth compared to younger forests may reflect a greater diversity and abundance of microfungi and bacteria in the old-growth canopy (Caldwell et al. 1979, Stone et al. 1996). Our mortality estimates are also conservative; some thalli may have died prior to detaching from the monofilament. This was especially apparent in the clearcuts where we often found remnants of dead thalli on the ground beneath the racks. Finally, many transplanted thalli were lost after one year. High winds during winter storms may have accounted for much of this attrition. Transplanting thalli onto existing epiphyte mats appears to substantially reduce loss rates relative to bare bark, probably because underlying epiphytes provide a thicker boundary layer, thereby protecting thalli from wind damage.

Effects of moss mats

The close association of several cyanolichen species with moss mats in the old-growth canopy (Chapter 2) suggests a possible role of these mats in affecting cyanolichen growth and mortality. Cyanolichen thalli become dormant when their water content drops below a certain threshold (typically about 70 % of their dry weight, Kershaw 1985). By absorbing and retaining large quantities of water (Veneklaas et al. 1990), thick moss mats may enable cyanolichens to remain metabolically active for longer periods following precipitation events than if they grew on bare bark. On the other hand, prolonged contact with wet moss

mats may be detrimental to some lichens by facilitating decomposition and/or prolonging respiratory energy losses. An interplay between these factors is suggested by our results for *P. rainierensis*.

P. rainierensis nearly always grows intermingled with bryophytes, including thick moss mats (Chapter 2). While not dependent on them for survival, the higher potential growth of *P. rainierensis* on moss mats compared to bare bark indicates that this species benefits from the association. However, the basal portions of many of the transplanted thalli became necrotic after a year of being imbedded in moss, resulting in a lower proportion of healthy thalli compared to bare bark. This may merely reflect a problem with the transplant technique; other portions of the thalli were usually quite vigorous. Alternatively, cyanolichens growing on moss mats may have to compete with bryophytes for space on branches. Limited support for this hypothesis comes from the observation that epiphytic cyanolichens are relatively scarce in the wettest old-growth Douglas-fir forests (pers. obs.). The canopies of these temperate rainforests are dominated by bryophytes, including several moss species typically found growing on the forest floor (Chapter 1).

Interpretation of the age effect

The apparent restriction of many epiphytic cyanolichens to older forests has been used as evidence that these species require a particular set of environmental conditions found only in old growth (e.g., Franklin et al. 1981, Lesica et al. 1991). However, our results indicate that cyanolichen growth rates are at least as high in younger forests as they are in old growth. Thalli actually remained healthier and fewer thalli were lost in young forests than in old growth. Therefore, younger forest canopies do provide suitable habitat for epiphytic cyanolichens. These species do not necessarily require an old growth canopy

environment. However, results from this experiment must be interpreted with caution because of the limited spatial and temporal scales of the observations.

Temporal scale of observations

Annual rates of growth and mortality may not be reflective of long-term rates. Year to year variability in rainfall and the severity of winter storms may have dramatic effects on epiphytes. Cyanolichen growth rates could be lower in younger forests than old growth during relatively dry years. The higher water-holding and fog-gathering capacity of old-growth canopies may provide adequate thermal buffering for considerable cyanolichen growth during such periods (Franklin et al. 1981). However, violent winter storms may lead to high rates of thallus loss and mortality (Rhoades 1983). These effects would probably be more severe in the upper canopy of old growth than they would in younger forests because tree crowns in dense, young forests are more sheltered from wind than emergent crowns in old growth, perhaps explaining why young forests had the lowest observed rates of thallus loss in this study.

Even if mature thalli can attain normal annual rates of growth and mortality in young canopies, epiphytic cyanolichens may be unable to persist in these forests. Canopy height in these stands increases rapidly (Hermann and Lavender 1990), resulting in major changes in the light and humidity regimes of the lower canopy (Geiger 1965). Declining moisture and light availability in these habitats probably limits the growth of some epiphyte species in young, managed forests (Rose 1992). Therefore, unless cyanolichens are capable of relatively rapid dispersal within the stand, they may be unable to re-establish in suitable habitats located higher up in the trees. Old growth-associated epiphytes may indeed require the relatively stable environment of older forest canopies (Goward 1994), but empirical support for this hypothesis is currently lacking.

Spatial scale of observations

Cyanolichens were transplanted into the upper, inner portion of a tree crown regardless of the distribution and abundance of resident populations of these species in each tree. Some of the transplant sites may have represented suboptimal habitat for a given species, and actual growth rates may have been higher elsewhere in the tree crown. If one assumes that optimal habitat for an epiphyte species is the habitat where it is most abundant, *L. oregana* would grow better in the understory of the young forests than in the upper canopy, and *P. rainierensis* would grow better in the lower canopy of both old growth and mature forest than in the upper canopy (see Figure 4.2). Higher growth rates in younger forests, however, would still support our conclusion that both species grew at least as well in these forests as they did in old growth. Therefore, factors other than habitat quality appear to limit the distribution of epiphytic cyanolichens in forest canopies.

Many of the epiphyte species thought to be associated with old growth possess limited dispersal capabilities. *P. rainierensis* in particular appears to have lost its ability to reproduce sexually and relies instead on the production of vegetative propagules known as isidia. Perhaps these species are limited by their abilities to disperse into and within younger forests. Alternatively, their propagules may be unable to establish on the smooth bark of young conifers. A biochemical inhibitor in young conifer bark seems unlikely since many of the transplanted thalli had firmly attached themselves to bark in the young forests after only one year. Studies addressing the issues of bark texture, dispersal, and their potential effects on cyanolichen establishment in Douglas-fir forests are currently underway.

Finally, results from this experiment may not apply to a large proportion of the Douglas-fir forests in the central Oregon Cascades. All of the study sites were situated in a particular landscape context: valley bottom locations near major streams. Controlling for

distance to streams was desired because mid-elevation forests on lower slopes support the maximum development of old growth-associated epiphyte species. Epiphytic cyanolichens are relatively scarce in Douglas-fir forests located farther upslope away from streams (Chapter 1). While drier old-growth Douglas-fir forests can support many cyanolichen species, total cyanolichen biomass in these forests is much lower than in comparable forests on wetter sites (Chapter 5). The canopies of younger Douglas-fir forests on dry sites may not provide suitable habitat for some cyanolichens.

Cyanolichen conservation in managed forests

Valley bottom sites at mid-elevations in the Oregon Cascades harbor some of the most productive Douglas-fir forests in the *Tsuga heterophylla* Zone (Franklin and Dyrness 1973). The great abundance of epiphytic cyanolichens in older forests represents a major contribution to the productivity and biodiversity of these ecosystems. Techniques for maintaining cyanolichen populations in managed forests of this region should be seriously considered by forest managers. Our results suggest one possibility.

The practice of retaining large, live trees in harvest units for the duration of stand rotation has received considerable attention in recent discussions of "ecological forestry" (Gillis 1990, Franklin 1992, Swanson and Franklin 1992) and is being slowly implemented in the Pacific Northwest. There is hope that retained trees will help maintain old growth-associated epiphytes in managed forests. Epiphyte populations in retained trees could serve as sources of propagules for recolonization of the regenerating forest canopy. The efficacy of live tree retention for maintaining cyanolichens in managed forests depends on both the ability of these species to tolerate canopy habitats in younger forests and on the persistence of epiphyte populations in the retained tree crowns. Our results show that young forest canopies do provide suitable habitats for mature cyanolichen thalli. Furthermore, large remnant trees in Douglas-fir forests do appear to continue harboring

some epiphytic cyanolichens following major wildfires (Chapter 5). Some cyanolichen species are even capable of acclimating to the altered microclimates of partially exposed trees (Chapter 3). Therefore, live tree retention appears to be a viable method for maintaining cyanolichens in managed forests. Reducing the size of cutting units would also facilitate cyanolichen dispersal from the edges of adjacent, older forests. Additional studies are needed to determine optimal densities and configurations of retained trees and harvest units for the promotion of cyanolichen growth and dispersal in regenerating forests.

Chapter 5

Distribution of Epiphytic Lichens in Relation to Remnant Trees in a Multiple-Age Douglas-Fir Forest

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ABSTRACT

Alternatives to clearcutting, such as the retention of live trees in harvest units, are being implemented to increase biodiversity of managed forests in the Pacific Northwest. Nitrogen-fixing lichens are an integral component of old growth, but this cyanolichen biomass develops slowly in younger forests. We used a retrospective approach to evaluate the long-term potential of live tree retention for cyanolichen conservation in Douglas-fir forests. We sampled litterfall from plots located on a 10 m by 10 m square grid in a 2 hectare stand that had been completely stem-mapped. The stand contained 200 to 600-year-old remnant trees scattered across a regenerating forest composed mostly of 100-year-old trees. We used association analysis, principal components analysis, regression analysis, and GIS to relate lichen litterfall biomass to the proximity of remnant trees. Two epiphytic lichens were strongly associated with remnant trees: the cyanolichen *Lobaria oregana* and the fruticose lichen *Sphaerophorus globosus*. Biomass of both species was highest near remnant trees, and biomass was slightly higher within groves of remnant trees than it was at the edges of these groves or near isolated trees. Cyanolichen populations appear to have persisted on remnant trees since before the last fire, and they are slowly recolonizing the regenerating forest. Retention of live trees, maintenance of regenerating hardwoods, and longer rotation periods have great potential to maintain cyanolichens in managed forests.

INTRODUCTION

Epiphytic lichens are an integral component of many temperate forest ecosystems, where they contribute to nutrient cycles (Pike 1978, Knops et al. 1991), provide food and

habitat for animals (Carroll 1979, Maser et al. 1985, Hayward and Rosentreter 1994), and constitute a significant part of species diversity (Lesica et al. 1991). In general, old forests support much higher lichen biomass than young forests, and many epiphytic species are closely associated with old growth (McCune 1993, Selva 1994, U.S.D.A. 1994, Esseen and Renhorn 1995). Human activities can have severe and lasting effects on epiphytic lichens in temperate forests. For example, air pollution and forest management have greatly reduced the abundance and distribution of many lichen species in Europe (Rose 1988, 1992). Fortunately, efforts to maintain epiphytic lichens in managed forests have begun in some areas.

The ongoing reassessment of forest management practices in the Pacific Northwest has included discussions of lichen conservation (F.E.M.A.T. 1993). Alternatives to clearcutting, such as the retention of some live trees in harvest units for the duration of stand rotation, are being implemented to increase structural complexity of managed forest canopies (Franklin 1992, Franklin and Swanson 1992). In contrast to even-aged plantations, old-growth Douglas-fir forests in this region support a very high biomass and diversity of epiphytic lichens, including many nitrogen-fixing species (Pike et al. 1975, Chapter 2). Nitrogen fixed by these cyanolichens represents a major input to this nitrogen-limited ecosystem (Sollins et al. 1981). There is hope that live tree retention may enable old growth-associated lichens to persist in managed forests, thereby enhancing productivity and biodiversity of these ecosystems. Lichen populations on retained trees could serve as a source of propagules for inoculation of the regenerating forest if the young canopy provides suitable lichen habitat and if lichens can persist on the retained trees.

We used a retrospective approach to evaluate the long-term potential of live tree retention for lichen conservation in Douglas fir forests. Lichen litterfall biomass was related to the distribution of remnant trees (i.e., large trees over 200 years old surviving previous fires) in a natural, multiple-age forest containing predominantly 100-year-old

trees. We had two major objectives: 1) to determine if remnant trees influence the composition of lichen litterfall in this stand and 2) to assess the spatial scale(s), if any, of remnant tree effects on the biomass of old growth-associated lichen species.

METHODS

Study site

The site of this investigation is a 2 ha reference stand near Eagle Rock in the Detroit Ranger District of the Willamette National Forest, western Oregon (40°47'N, 122°3'W). This stand (hereafter Eagle Rock RS) represents the *Tsuga heterophylla / Berberis nervosa* plant association (Hemstrom et al. 1987) of the *Tsuga heterophylla* Zone (Franklin and Dyrness 1973). Average annual rainfall is 1.9 m with over 90 % of the precipitation occurring from October through June (Daly et al. 1994). The average annual temperature is 9°C, with January and July means of 0.5°C and 16.5°C, respectively (National Weather Service).

Topography is relatively uniform (average slope 40 to 60 %) in all but two regions of the Eagle Rock RS (Figure 5.1). The eastern edge of the stand grades into a southeast-facing riparian slope. A small ridge adjoining a seep traverses the western edge of the stand. Vegetation in the lower portion of the ridge is particularly distinctive. It grades into the drier *Pseudotsuga menziesii –Tsuga heterophylla / Berberis nervosa* plant association (Hemstrom et al. 1987). The canopy is sparse here, and cyanolichens cover lower trunks and branches of conifers in the well-illuminated understory. Throughout the rest of the stand, however, cyanolichens are relatively scarce in this habitat, attaining much greater abundance higher up in the conifers and on hardwoods (see Discussion).

Figure 5.1. Stem map of the Eagle Rock RS in western Oregon. Locations of remnant trees and hardwoods are indicated for the 2 hectare stand and a 25 m wide buffer around the perimeter of the stand. Crown projected areas and crown centers are shown for remnant Douglas-fir trees. Elevation contours are drawn at 5 m intervals, beginning with the 700 m contour in the southeastern corner and extending to the 800 m contour in the northwestern corner of the stand. The position of a year-round stream just beyond the eastern boundary is also indicated.

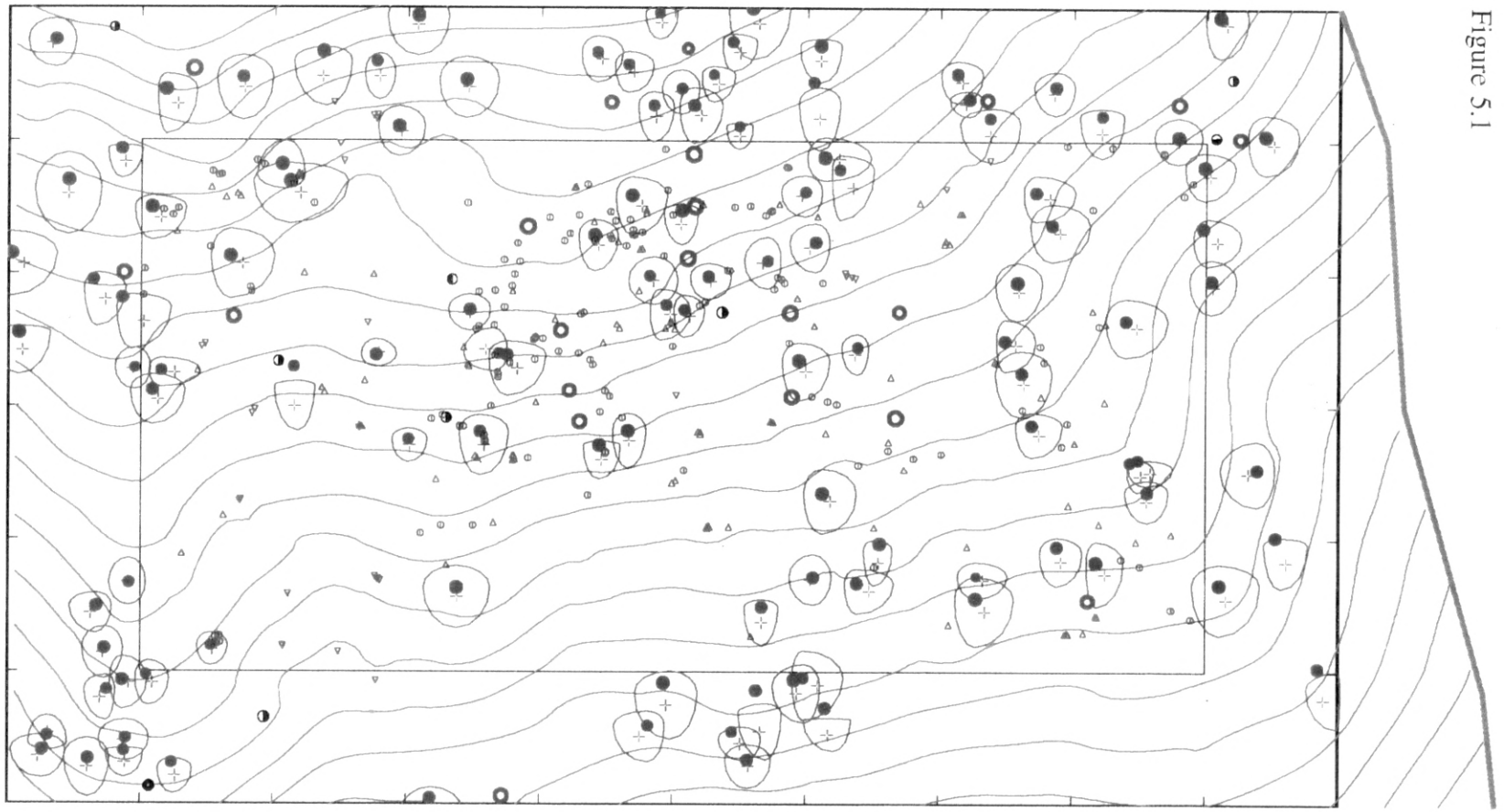


Figure 5.1

Eagle Rock Reference Stand: established 1993 by M. Goslin, T. Spies

Canopy vegetation in the Eagle Rock RS is heterogeneous because of a complex fire history (Goslin 1996). A series of three moderate intensity fires occurred in 1848, 1871, and 1892. Fire intensity was higher in some portions of the stand than others, and crown fires killed large trees in several areas. A few western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), western redcedar (*Thuja plicata* Donn.), and incense cedar (*Libocedrus decurrens* Torr.) survived the fires, but 93 % of the remnant trees are Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco, Figure 5.1). These large trees are up to 63 m tall, 1.7 m dbh, and 600 years old. Most of the remnant tree crowns are asymmetrical with greater crown radii on the south (mean = 6.5 m) versus the north (mean = 2.6 m) side of the trees (Figure 5.1). The regenerating forest is composed primarily of Douglas-fir with significant amounts of western hemlock and western redcedar. Three hardwood tree species are also present (in decreasing order of abundance): giant chinkapin (*Castanopsis chrysophylla* (Dougl.) A. DC.), Pacific dogwood (*Cornus nuttallii* Aud.), and bigleaf maple (*Acer macrophyllum* Pursh). Vine maple (*Acer circinatum* Pursh) is prevalent in the understory throughout the stand. Trees in the regenerating forest are all less than 150 years old; most are less than 100 years old, having established after the 1892 fire.

Litterfall sampling

We collected epiphyte litterfall from 231 circular plots (radius 2 m) distributed on a 10 m square grid overlaid onto the 2 hectare stand. These plots encompassed over 2900 square meters: one eighth of the total surface area of the stand plus about 400 square metres located just outside the reference stand boundaries. All fragments of macrolichens occurring as litterfall were collected from each plot unless they were attached to a fallen branch or tree greater than 10 cm diameter, or unless they were less than 1 cm in size (see McCune 1994b). In the laboratory, litterfall samples were sorted by species, dried at 70°C

for 24 hours, and weighed to the nearest 0.01 g. Nomenclature of lichens generally follows Egan (1987). Litterfall sampling occurred in August 1993.

Stem mapping

Locations and trunk diameters of all trees (dbh > 5 cm) in the Eagle Rock RS were recorded using triangulation survey techniques (Pabst et al. 1993, Goslin 1996). We also recorded locations of remnant trees in a 25 m wide buffer around the perimeter of the 2 hectare stand (Figure 5.1). Cartesian coordinates of trees were calculated using a SAS code written by R. Pabst and modified by M. Goslin. For each remnant Douglas-fir tree, we measured maximum crown radius in each cardinal direction with a clinometer as well as total height and height to first branch with the pole-tangent method (Curtis and Bruce 1968). We incorporated all tree coordinate and attribute data into a geographic information system (GIS) database, creating GIS point coverages joining tree attributes and locations. GIS facilitated analysis of additional coverages, such as polygon coverages representing tree crowns, in conjunction with the stem-mapped data (see below).

Generation of proximity variables

We used ARC/INFO (E.S.R.I. 1995) and SAS (SAS Institute 1988) to generate 16 variables describing the proximity of litterfall plots to remnant Douglas-fir trees. These proximity variables refer to a common coordinate plane and fall into 2 categories: 1) single tree variables and 2) multiple tree variables. Single tree variables include 3 measures of distance between litterfall plot centers and the nearest remnant tree: one based on the location of its trunk (DTRUNK), one on its crown center (DCENTER), and one on its crown edge (DEDGE). We define a crown center as the center of an ellipse connecting the 4 measured radii of a tree crown. We define a crown edge as the vertical projection of a

tree crown in the form of a polygon connecting 16 crown radii (4 measured and 12 interpolated). Projected areas of individual tree crowns (AREA) were estimated as the surface areas of these 16-sided polygons. Volumes of individual tree crowns (VOLUME) were estimated from equations relating crown width, depth, and volume for Douglas-fir (R. Van Pelt pers. com.). In addition to AREA and VOLUME, we used 2 other variables to describe size of the nearest tree: diameter at breast height (DBH) and total height (HEIGHT). Multiple tree variables refer to all remnant trees or portions of remnant trees within a given search radius of a litterfall plot center. We used GIS to calculate basal areas of trees at 5 to 25 m intervals (BA5, BA10, BA15, BA20, and BA25). Variables for total crown area (O5AREA and O10AREA) and volume (O5VOLUME and O10VOLUME) include only those portions of tree crowns occurring within 5 and 10 m of a plot. The last two variables assume a cylindrical crown shape.

Statistical analyses

We used the procedure CROSSTABS in SPSS/PC+ (SPSS 1988) to perform association analyses. These analyses tested whether individual lichen species occurred close to a particular kind of tree more or less often than expected by chance. For each kind of tree (i.e., remnant Douglas-fir, young conifers, and hardwoods by species), we divided litterfall plots into two categories: those with plot centers within 5 m of a tree and those with plot centers over 5 m away from the nearest tree. DCENTER was used for remnant trees and distance to nearest trunk was used for hardwood trees. A 2 x 2 contingency table was generated for each tree/lichen species pair. The likelihood ratio (G, Sokal and Rohlf 1995) was used as the test statistic.

We explored potential effects of remnant trees on epiphytic lichen distribution in the Eagle Rock RS by relating proximity variables to lichen litterfall biomass via regression analysis. Average biomass values (g/m^2) of individual lichen species in each litterfall plot

were used as the dependent variables. When necessary, dependent variables were square-root transformed prior to analysis to alleviate positive skews and normalize residuals. Since there was strong multicollinearity among the proximity variables, we used principal component analysis (PCA) to derive orthogonal linear combinations, or components, of these variables (McCune and Mefford 1995). The amount of variation extracted by a component was calculated as its eigenvalue divided by 16, the number of proximity variables used in the PCA. Significant components (eigenvalues > 1) were then used as independent variables in regression analysis. Interpretation of independent variables was based on correlations (R) between individual proximity variables and components. We applied multiple regression analysis (SPSS 1988) to independent variables and a categorical variable representing the 14 litterfall plots located on the anomalous lower ridge (see above). Use of this categorical variable in multiple regression allowed us to assess the amount of variation in lichen litterfall biomass attributable to the distinctive environment of the lower ridge without reducing either sample size or total variation explained by the analysis.

Contour plots of lichen biomass and independent variables across the Eagle Rock RS were generated with SPW (1994). In these plots, a 5 m square grid was interpolated from the original 10 m square grid by an inverse distance weighting method such that one quarter of the grid points coincided with litterfall plot centers. We used interpolation to smooth contour lines by placing less emphasis on distant points.

RESULTS

A total of 50 macrolichen species was encountered in the 231 litterfall plots (Table 5.1). Two species dominated epiphyte assemblages, contributing over 4 kg/ha to litterfall:

Table 5.1. Summary of macrolichen litterfall composition in the Eagle Rock RS, western Oregon. Proportions of total litterfall biomass are indicated in parentheses for three groups of lichens. Significant positive and negative spatial associations between lichens and tree species (rPM = remnant *Pseudotsuga menziesii*, AC = *Acer circinatum*, AM = *Acer macrophyllum*, CC = *Castanopsis chrysophylla*, CN = *Cornus nuttallii*) are indicated by the following symbols: +++ ($P < 0.001$), + or – ($P < 0.05$).

	Biomass (g/ha)		%	Spatial
Cyanolichens (33.8%)	mean	SE	Frequency	Associations
Lobaria oregana	4026.28	454.26	90.0	rPM+++, CC+, CN+
Lobaria pulmonaria	715.99	268.91	24.7	AC+, CN+
Lobaria scrobiculata	19.47	15.97	2.2	rPM+
Nephroma helveticum	0.14	0.16	0.4	
Nephroma laevigatum	0.10	0.10	0.4	
Nephroma occultum	0.48	0.37	0.9	
Pannaria saubinetii	0.45	0.37	0.9	
Peltigera collina	3.82	3.19	0.9	AM+
Peltigera neopolydactyla	0.86	0.84	0.4	AM+
Pseudocyphellaria anomala	15.23	5.97	9.5	
Pseudocyphellaria anthraspis	37.72	17.54	4.3	CC+, CN+
Pseudocyphellaria crocata	0.10	0.10	0.4	AM+
Pseudocyphellaria rainierensis	6.03	5.24	1.3	
Sticta weigelii	1.83	1.62	0.9	rPM+
Forage lichens (37.0%)				
Alectoria sarmentosa	4734.76	322.63	99.6	
Alectoria vancouverensis	26.28	9.63	6.1	
Bryoria capillaris	24.39	5.50	16.5	
Bryoria friabilis	76.58	11.68	43.7	rPM+
Bryoria fuscescens	9.34	3.82	5.6	rPM+
Bryoria oregana	57.84	12.41	33.3	
Bryoria pseudofuscescens	6.89	2.83	4.8	
Bryoria sp. A	13.57	5.13	10.4	
Usnea spp.	341.36	47.17	59.7	
Other chlorolichens (29.1%)				
Cetraria chlorophylla	17.29	3.35	17.3	
Cetraria idahoensis	14.54	5.13	6.5	
Cetraria orbata	31.07	5.03	26.8	
Cetraria pallidula	0.34	0.26	0.9	

Table 5.1 continued

Other chlorolichens (continued)	Biomass (g/ha) mean	SE	% Frequency	Spatial Associations
Cladonia spp.	4.65	2.20	2.6	
Evernia prunastri	0.31	0.26	0.9	
Hypogymnia apinnata	19.26	6.13	4.8	rPM+
Hypogymnia enteromorpha	887.62	40.58	99.6	
Hypogymnia imshaugii	509.61	27.91	97.0	
Hypogymnia inactiva	980.15	49.06	97.8	
Hypogymnia metaphysodes	4.06	1.57	3.9	
Hypogymnia occidentalis	11.71	5.03	3.0	
Hypogymnia physodes	14.02	3.30	9.5	
Hypogymnia rugosa	0.07	0.05	0.4	
Hypogymnia tubulosa	7.48	2.25	6.5	
Letharia vulpina	1.48	1.05	0.9	rPM+
Parmelia pseudosulcata	1.52	0.63	3.0	
Parmelia saxatilis	2.34	1.26	2.6	
Parmelia sulcata	17.19	9.84	5.2	
Parmeliopsis hyperopta	0.03	0.05	0.4	
Platismatia glauca	967.16	53.88	100.0	
Platismatia herrei	193.74	18.48	52.8	CN–
Platismatia stenophylla	80.47	9.27	43.3	rPM–
Ramalina farinacea	0.24	0.26	0.4	
Sphaerophorus globosus	395.27	62.04	61.5	rPM+++

Alectoria sarmentosa and *Lobaria oregana.* Six other species also occurred in most of the plots (*Hypogymnia enteromorpha*, *H. imshaugii*, *H. inactiva*, *Platismatia glauca*, *P. herrei*, and *Sphaerophorus globosus*), but these species each contributed less than 1 kg/ha to litterfall. Only one species, *Platismatia glauca*, was found in every plot. Fourteen species were found in only one or two plots. About one third of total lichen litterfall biomass was contributed by cyanolichens. Finally, moss biomass was very low in the forest canopy. We found no thick moss mats in the crowns of several remnant trees that we surveyed.

Association analyses revealed several significant associations between lichen species and particular kinds of trees (Table 5.1). Eight species (*Bryoria friabilis*, *B. fuscescens*, *Hypogymnia apinnata*, *Letharia vulpina*, *Lobaria oregana*, *L. scrobiculata*, *Sphaerophorus globosus*, and *Sticta weigelii*) were positively associated with remnant Douglas-fir trees, occurring more frequently in litterfall plots near (< 5 m) remnant trees than in plots farther away from remnant trees. One species (*Platismatia stenophylla*) was negatively associated with remnant Douglas-fir trees. Eight species (*Lobaria oregana*, *L. pulmonaria*, *L. scrobiculata*, *Peltigera collina*, *P. neopolydactyla*, *Pseudocyphellaria anthraspis*, *P. crocata*, and *Sticta weigelii*) were positively associated with hardwood species. One species (*Platismatia herrei*) was negatively associated with Pacific dogwood. No lichens were associated with young conifers. Only two spatial associations were highly significant ($P < 0.001$): those among remnant Douglas-fir trees and the lichens *Lobaria oregana* and *Sphaerophorus globosus* (Table 5.1). Additional analyses focused on these two associations.

Many of the variables describing the proximity of remnant trees to litterfall plots were significantly correlated with biomass of *Lobaria oregana* and *Sphaerophorus globosus* (Table 5.2). Biomass of both species increased with diminishing distance to the nearest remnant tree. A scatterplot of *L. oregana* biomass versus DEDGE clearly illustrates this trend (Figure 5.2). Multiple tree variables were also significantly correlated with lichen biomass, but correlations were highest for variables within 5 or 10 m of litterfall plot centers. The significant correlation of *L.oregana* biomass with the categorical variable "lower ridge" indicates that biomass of this lichen was generally higher here than elsewhere in the reference stand. The first and third principal components were also significantly correlated with biomass of both species (see below).

Severe multicollinearity among the proximity variables was eliminated by PCA, which extracted three significant components accounting for 80 % of the total variation in these 16

Table 5.2. Correlation coefficients (R) between biomass of two lichen species and 16 variables describing the proximity of remnant Douglas-fir trees to litterfall plots in the Eagle Rock RS, western Oregon (n = 231 plots). Principal components were derived from a PCA of 16 proximity variables. 'Lower ridge' is a categorical variable representing 14 plots from the anomalous southwest corner of the stand. Asterisks indicate significance levels (* $P < 0.01$, ** $P < 0.001$).

	Lobaria oregana	*Sphaerophorus globosus*
Single, nearest tree variables:		
DTRUNK	–0.420 **	–0.251 **
DCENTER	–0.490 **	–0.300 **
DEDGE	–0.486 **	–0.304 **
DBH	0.006	0.102
HEIGHT	–0.032	0.066
AREA	0.005	0.143
VOLUME	0.021	0.126
Multiple tree variables:		
O5AREA	0.508 **	0.472 **
O10AREA	0.474 **	0.304 **
O5VOLUME	0.464 **	0.486 **
O10VOLUME	0.432 **	0.305 **
BA5	0.394 **	0.521 **
BA10	0.414 **	0.265 **
BA15	0.266 **	0.126
BA20	0.172 *	0.050
BA25	0.116	0.058
Principal components:		
PCA1	0.482 **	0.360 **
PCA2	0.094	0.102
PCA3	0.236 **	0.342 **
'Lower Ridge'	0.345 **	0.036

Table 5.3. First five principal components from analysis of 16 proximity variables (n = 231 plots).

Component	Eigenvalue	% of Variation
PCA1	8.03	50.19
PCA2	3.07	19.16
PCA3	1.71	10.67
PCA4	0.75	4.67
PCA5	0.55	3.45

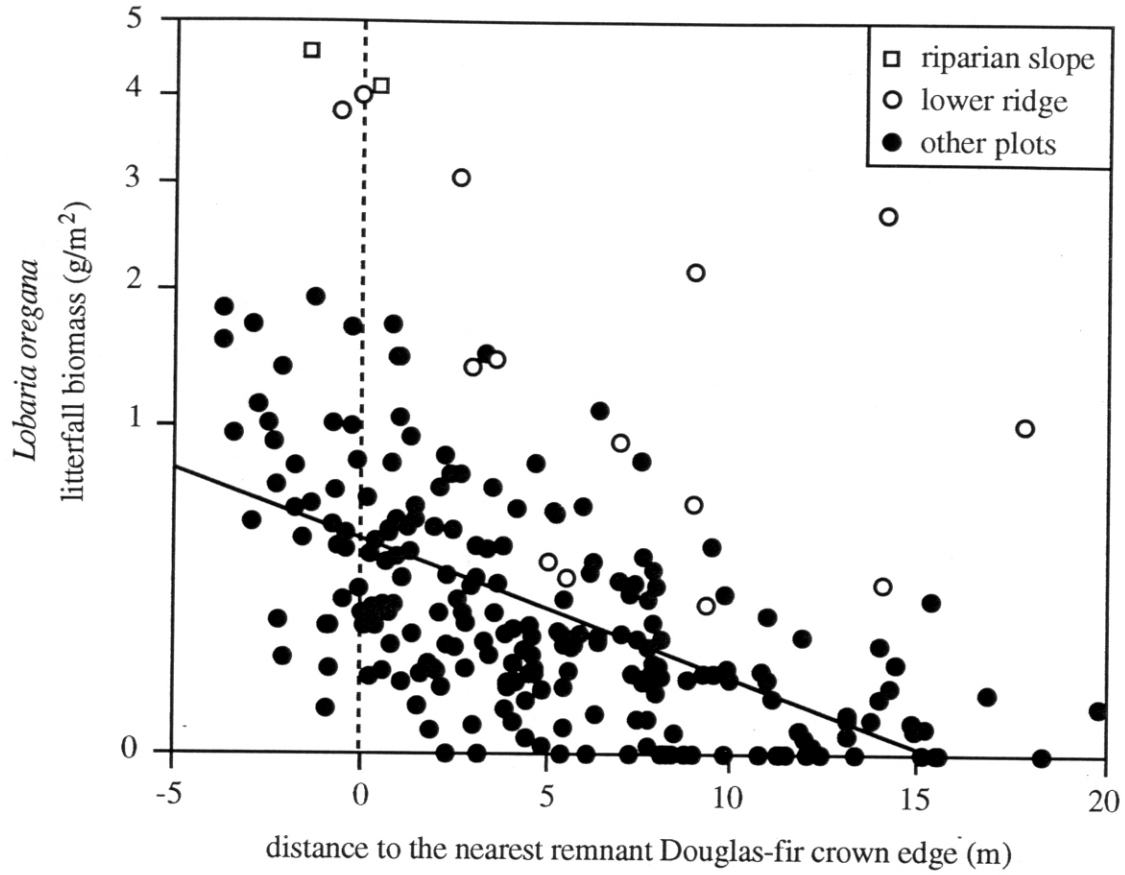


Figure 5.2. Scatterplot of *Lobaria oregana* litterfall biomass versus the proximity variable DEDGE. The solid line is the least squares regression line ($R^2 = 0.41$) for 215 litterfall plots, excluding 14 plots from the lower ridge and 2 plots from the riparian slope (see Discussion). The dashed line represents the edge of remnant Douglas-fir tree crown projected areas. Plots to the left of the dashed line occurred within projected crown areas of remnant trees. The Y-axis is on a squareroot scale.

variables (Table 5.3). Eleven proximity variables were strongly correlated ($R > 0.5$) with the first component (PCA1), four with the second component (PCA2), and two with the third component (PCA3, Table 5.4). PCA1 represented the proximity of litterfall plots to the nearest remnant tree or trees. The highest values of PCA1 occurred close to remnant trees, while the lowest values occurred far from remnant trees (Figure 5.3). PCA2

Table 5.4. Correlation coefficients (R) between 16 proximity variables and the first three principal components (n = 231 plots).

	PCA1	PCA2	PCA3
Single, nearest tree variables:			
DTRUNK	0.854	0.284	–0.052
DCENTER	0.902	0.241	0.041
DEDGE	0.914	0.090	0.042
DBH	–0.078	0.804	0.127
HEIGHT	–0.155	0.777	0.181
AREA	–0.044	0.848	–0.118
VOLUME	–0.124	0.940	–0.024
Multiple tree variables:			
O5AREA	–0.848	–0.008	–0.454
O10AREA	–0.941	0.016	–0.054
O5VOLUME	–0.823	0.144	–0.422
O10VOLUME	–0.904	0.197	–0.026
BA5	–0.649	–0.009	–0.494
BA10	–0.858	–0.035	0.002
BA15	–0.745	–0.007	0.446
BA20	–0.684	–0.055	0.628
BA25	–0.571	–0.036	0.642

represented the size of the nearest remnant tree. PCA3 represented an interior to edge gradient: highest values occurred in the centers of groves of remnant trees (i.e., areas with several remnant trees within 20 to 25 m), and lowest values occurred near the edges of these groves or near isolated trees (Figure 5.4). PCA3 contained only that portion of the variation in BA20 and BA25 that was uncorrelated with PCA1 (Table 5.4).

Multiple regression analysis showed that PCA1 (hereafter 'the nearest remnants effect') and PCA3 (hereafter 'the grove effect') accounted for about one quarter of the variation in litterfall biomass of both *L. oregana* and *S. globosus* (Table 5.5). Biomass of both species was highest near remnant trees, and biomass was slightly higher within groves of remnant trees than it was at the edges of these groves or near isolated trees. Lichen biomass was not correlated with variation in the size of remnant trees. The distinctive environment of the lower ridge accounted for almost 17 % of the variation in *L. oregana*

Figure 5.3. Contour plot of the 5th, 50th, 65th, 80th, and 95th percentiles of the independent variable PCA1 (the nearest remnants effect) in the Eagle Rock RS, western Oregon. Locations of remnant Douglas-fir crown centers are indicated by solid circles. X and Y axes represent distance (m) in the east-west and north-south directions, respectively.

Figure 5.3

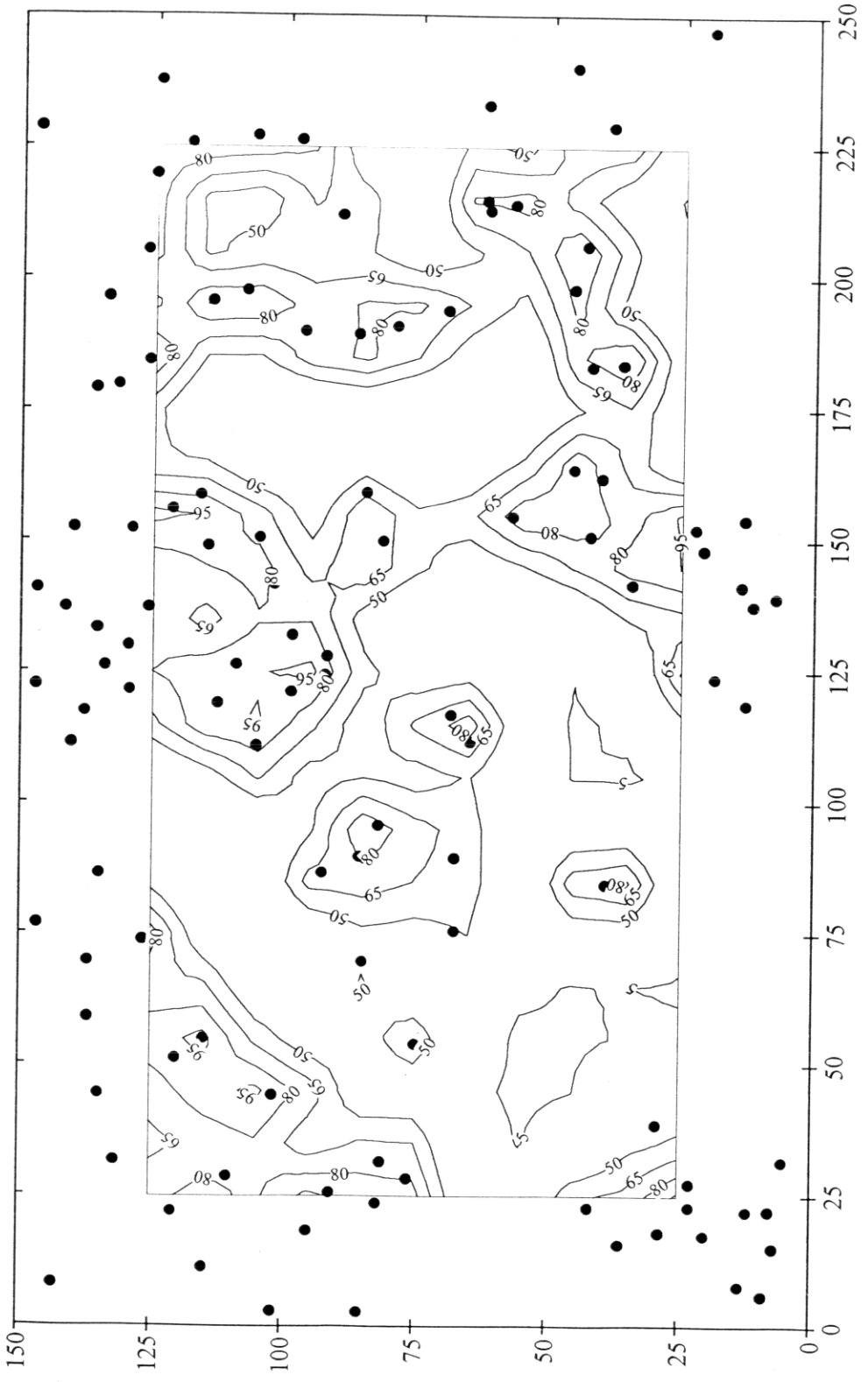


Figure 5.4. Contour plot of the 5th, 50th, 65th, 80th, and 95th percentiles of the independent variable PCA3 (the grove effect) in the Eagle Rock RS, western Oregon. Locations of remnant Douglas-fir crown centers are indicated by solid circles. X and Y axes represent distance (m) in east-west and north-south directions, respectively.

Figure 5.4

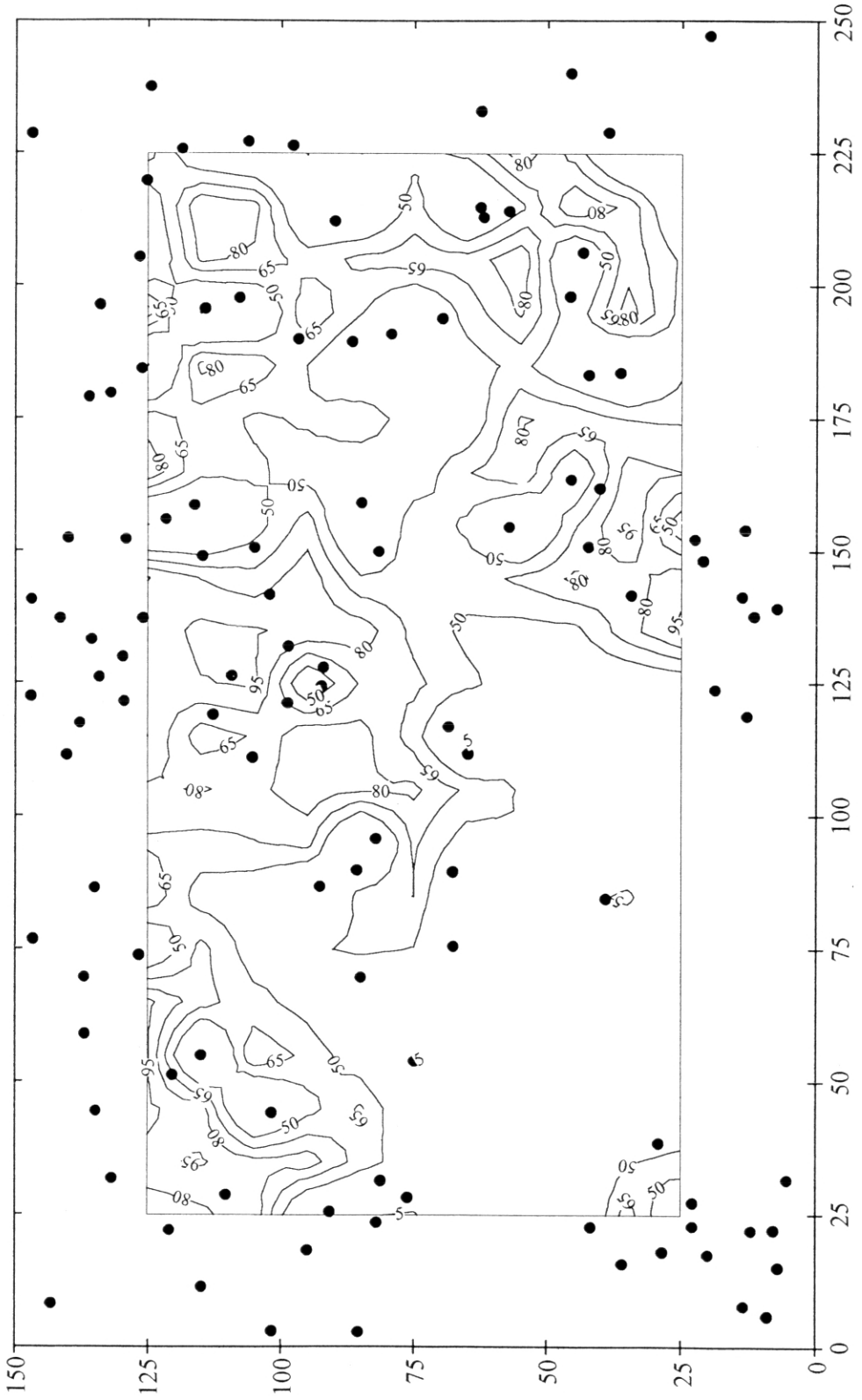


Table 5.5. Proportion of variation (adjusted R^2) explained by variables in multiple regression analysis of lichen litterfall plots (n = 231) in the Eagle Rock RS, western Oregon. 'Lower ridge' is a categorical variable representing 14 plots in the anomalous southwestern corner of the stand. PCA1 (the nearest remnants effect), PCA2, and PCA3 (the grove effect) represent independent variables derived from principal components analysis of the 16 proximity variables.

	Variables				Total	
Lichen species	PCA1	PCA2	PCA3	'lower ridge'	Variation	*P*
Lobaria oregana	0.229	—	0.030	0.168	0.434	<0.0001
Sphaerophorus globosus	0.126	—	0.114	—	0.240	<0.0001

biomass, but it was unrelated to the biomass of *S. globosus*. A contour plot clearly shows the close association of *L. oregana* with remnant trees (Figure 5.5). Biomass of this species was very low (< 0.1 g/m^2) in areas lacking remnant trees, except for the lower ridge, where it was high (> 1 g/m^2) even where no remnant trees occurred within 20 m. Nevertheless, *L. oregana* biomass in the lower ridge was still higher close to remnant trees (Figure 5.2).

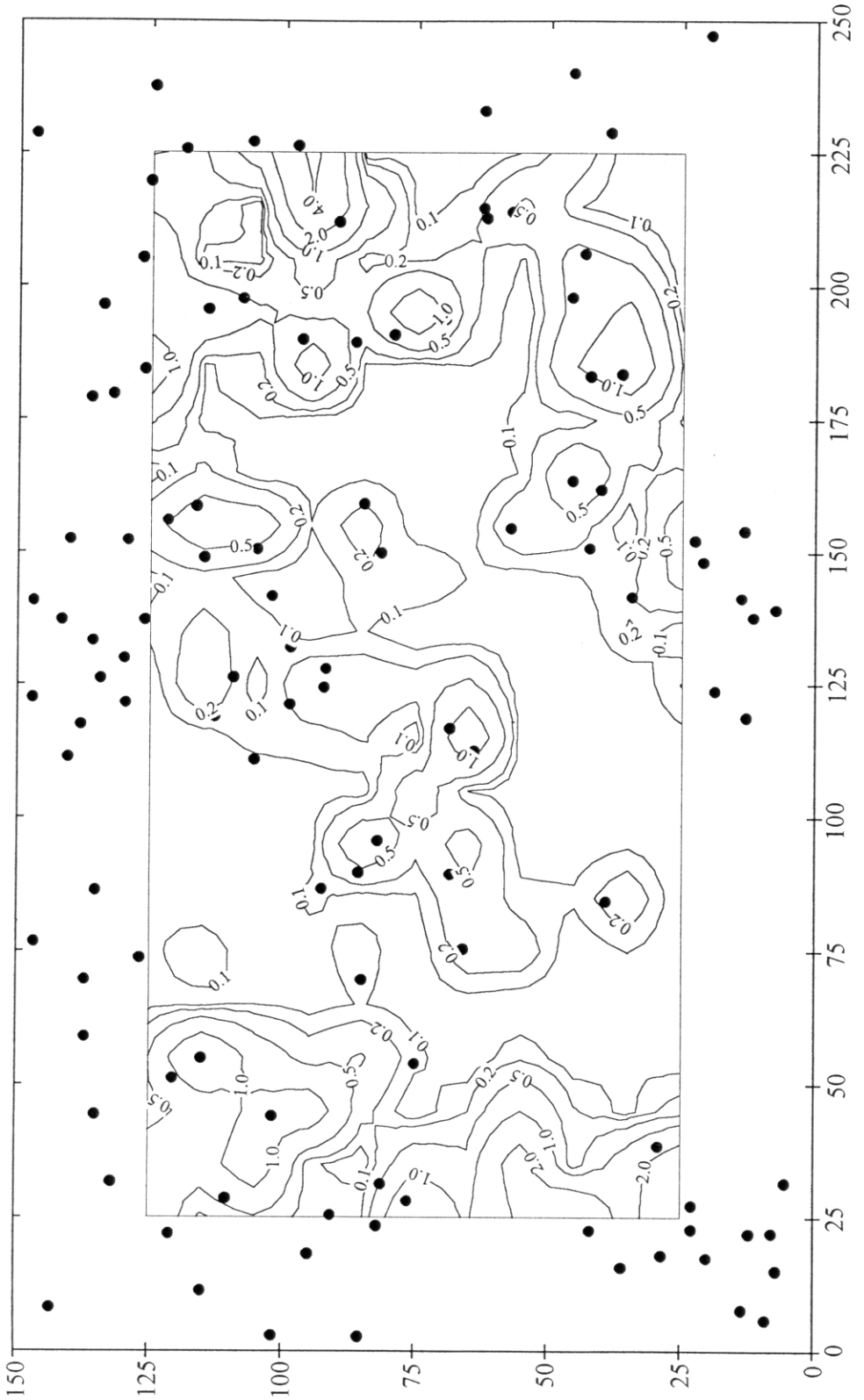
DISCUSSION

Litterfall as a canopy signal

The close relationship between litterfall biomass and standing crop of epiphytic lichens in Douglas-fir forests (i.e., late summer litterfall represents about 1 % of total biomass in the forest canopy, McCune 1994b) allowed us to rapidly survey canopy lichen biomass across 2 hectares of heterogeneous forest without directly sampling from tree crowns. The litterfall method was originally intended for use in among-stand comparisons of lichen biomass because it yields accurate estimates of stand-level biomass for many species

Figure 5.5. Contour plot of *Lobaria oregana* litterfall biomass (g/m^2) in the Eagle Rock RS, western Oregon. Contour intervals represent a doubling series of litterfall biomass: 0.125, 0.25, 0.5, 1.0, 2.0, and 4.0 g/m^2. Locations of remnant Douglas-fir crown centers are indicated by solid circles.

Figure 5.5



(McCune 1994b). Our data demonstrate that the method can also be used to assess within-stand distribution patterns of abundant species. The signal to noise ratio for litterfall deposition beneath a tree crown is probably too low to permit accurate estimates of lichen biomass for individual trees, but the bulk of lichen thalli falling from a tree crown are probably deposited within the projected area of that crown. Proximity variables accounting for crown asymmetry (e.g., DCENTER and DEDGE) yielded substantially higher correlations with lichen biomass than those relating only to locations of tree trunks (e.g., DTRUNK). The signal to noise ratio of litterfall is probably highest for lichens with large, foliose thalli (e.g., *Lobaria*) and lowest for lichens with long, pendant thalli easily borne by wind and ensnared by tree branches (e.g., *Alectoria*).

Remnant tree effects

Remnant Douglas-fir trees influenced the composition of lichen litterfall more than any other kind of tree in the Eagle Rock RS. Our analyses revealed two independent spatial scales of remnant tree effects on biomass of *L. oregana* and *S. globosus* (i.e., the nearest remnants effect and the grove effect). The nearest remnants effect is clearly visible in the contour plot of *L. oregana* litterfall where lichen biomass diminishes rapidly with increasing distance from individual crowns (see Figure 5.5). The simplest explanation for this effect is that both species are most abundant on remnant trees and that litterfall deposition beneath source trees accounts for much of this pattern. However, limited dispersal of both species from remnant trees into the regenerating canopy has also occurred because we found some thalli growing on trunks and branches of young conifers and hardwoods. *S. globosus* occurred primarily on the trunks and inner branches of remnant trees while *L. oregana* was more widespread, occurring abundantly on branchlets in the outer crown (pers. obs.). For both species, correlations with multiple tree variables

diminished with increasing search radii, but this decline was more drastic for *S. globosus*. This suggests that *S. globosus* litterfall is deposited closer to the source tree than *L. oregana* litterfall (see Table 5.2). Again, *L. oregana* and *S. globosus* have dispersed into and successfully colonized the surrounding canopy to a limited extent.

If some lichens are largely restricted to remnant trees, these populations may be relicts from the intact forest canopy that existed prior to the fires. Alternatively, these species may have colonized remnant trees since the fires. We suspect the former possibility for two reasons. First, epiphyte assemblages in large trees appear to be somewhat resistant to moderate levels of disturbance (Chapter 2), and some cyanolichens can acclimate to changing environments in tree crowns (Chapter 3). Second, we found substantial populations of three old growth-associated cyanolichens possessing very limited dispersal capabilities (*Nephroma occultum*, *Pseudocyphellaria rainierensis*, and *Sticta weigelii*) while climbing in several remnant trees scattered throughout the stand. These species are scarce or absent in even-aged Douglas-fir forests less than a century old (Neitlich 1993). They would probably not have been able to recolonize the Eagle Rock RS if their populations were completely destroyed by the last fire.

The grove effect on biomass of *L. oregana* and *S. globosus* may be attributable to edge effects. Recall that litterfall biomass of both species was slightly higher within groves of remnant trees than on the edges of groves or near isolated trees. Sillett (1995) found few differences in lichen biomass between the forest interior and clearcut edge of a relatively wet old-growth Douglas-fir stand, but the drier environment of the Eagle Rock RS might lead to more pronounced edge effects in the canopy, especially in the absence of thick moss mats (Chapter 2). Exposed trees may provide fewer suitable habitats for *L. oregana* and *S. globosus* than more sheltered trees within groves. It is important to remember that the nearest remnants effect was much stronger than the grove effect for *L. oregana*.

Hardwood effects

Factors that affect epiphytic lichen habitat (e.g., crown architecture, microclimate, bark chemistry, and bark texture) overlap broadly between tree species. Consequently, few (if any) lichens are truly restricted to a single kind of tree in temperate forests (Schmitt and Slack 1990). Many of the most abundant lichens in the Eagle Rock RS (e.g., *Alectoria sarmentosa*, *Hypogymnia enteromorpha*, *H. imshaugii*, *H. inactiva*, *Platismatia glauca*, *P. herrei*) were not associated with particular kinds of trees. They occurred on a wide variety of substrates throughout the stand. Associations between several cyanolichens (e.g., *Lobaria pulmonaria*, *Peltigera* spp., and *Pseudocyphellaria* spp.) and hardwoods probably reflect preferences of these epiphytes for habitat conditions more prevalent on hardwoods than on conifers (Bates 1992, Kuusinen 1994). Epiphytic cyanolichens tend to colonize hardwoods more quickly than conifers (Chapter 1), and cyanolichen diversity in young conifer forests can be quite high in canopy gaps containing hardwoods (Neitlich and McCune 1996).

Most of the *L. oregana* biomass in the stand occurred near remnant trees, but this species was also locally abundant on hardwoods. Perhaps *L. oregana* is limited by low light availability beneath dense conifer canopies. However, the low biomass of this species in the upper crowns of young conifers suggests that factors other than light availability must also be important. Rates of establishment may restrict the distribution of *L. oregana* and other lichens in Douglas-fir forests. The bark of young conifers may be less likely to retain epiphyte propagules than the rougher bark of older trees or hardwoods (Armstrong 1990). Alternatively, bark chemistry and/or crown architecture may account for differential establishment of lichens on hardwoods versus conifers (Hyvärninen et al. 1992). Studies explicitly addressing the issues of bark texture, dispersal, and their potential effects on cyanolichen establishment in Douglas-fir forests are currently underway.

Topographic effects

The highest biomass of *L. oregana* in the Eagle Rock RS occurred in two areas of the stand possessing distinctive topography. We noted the sparse overstory and well-illuminated understory of the lower ridge in our initial survey of the stand. This was also the only area of the stand where cyanolichens, including *L. oregana*, were abundant on the lower trunks and branches of young conifers. Our regression analyses could not determine the exact cause of *L. oregana* abundance in the lower ridge, although its distinctive environment accounted for a substantial portion of the variation in litterfall biomass of this species. We suspect a combination of factors, including a more favorable light environment and proximity to two major propagule sources: a dense grove of remnant trees located in the southwestern corner of the stand (in the direction of the prevailing winds) and several hardwoods scattered across the lower ridge (see Figure 5.5).

The other area of the stand with very high *L. oregana* litterfall biomass (> 2 g/m^2) was located within an east-facing trough along the riparian slope (compare Figures 5.1 and 5.5). High *L. oregana* litterfall biomass here may merely reflect random deposition of unusually large pieces of litterfall from two nearby remnant trees, but we suspect that *L. oregana* is abundant here for other reasons. The two nearest remnant trees are located on the edge of an area that burned in 1871 but was unaffected by the 1892 fire (Goslin 1996). Furthermore, canopy humidity in this area may be higher than elsewhere in the stand because of the proximity of a year-round stream located just beyond the eastern boundary of the mapped area (Figure 5.1). Elevated humidity combined with longer environmental continuity may have led to unusually high *L. oregana* biomass in these tree crowns. We found large populations of *L. oregana* and other cyanolichens (e.g., *Sticta weigelii*) in the crowns of these trees.

Management implications

The cyanolichen *L. oregana* is an important nitrogen source in old-growth Douglas-fir forests, contributing up to 4 kg $N \cdot ha^{-1} \cdot yr^{-1}$ (Denison 1979). Maintenance of this species and other cyanolichens in managed forests will increase the productivity and biodiversity of these ecosystems. Cyanolichen colonization of regenerating forests, however, appears to be a rather slow process. After a century following the last major fire (1892), *L. oregana* is still most abundant in the vicinity of remnant trees. However, the effect of remnant trees on *L. oregana* appears to extend well beyond remnant tree crown edges (see Figure 5.2). This pattern suggests that *L. oregana* is slowly invading the regenerating forest by dispersal from remnant trees. Since *L. oregana* grows just as well in the canopy of young forests as it does in old growth (Chapter 4), its abundance in the regenerating forest must be limited by rates of dispersal and/or establishment. The long-term persistence of cyanolichens on remnant trees after fire indicates that these populations will continue to serve as a source of propagules for inoculation of the regenerating forest.

Our results suggest that cyanolichen conservation in managed forests will be facilitated by recently implemented silvicultural practices in the Pacific Northwest. Two stand-level components of silviculture being reconsidered are rotation age and retention level of live trees in harvest units (Gillis 1990). We expect large, retained trees to mimic remnant trees in terms of resident epiphyte diversity and abundance. Like remnant trees, retained trees will continue to harbor epiphyte populations that can then inoculate younger trees. Retaining groves of live trees rather than scattered, isolated trees may improve the chances for cyanolichen persistence in retained tree crowns because of more favorable canopy microclimates within groves. However, our data indicate that the nearest remnants effect is much stronger than the grove effect for *L. oregana.* Therefore, retaining scattered, isolated trees may lead to more effective dispersal of this species over a broader area. Lengthening rotation ages from 60-100 years to over 100 years will improve chances of

successful dispersal and establishment of cyanolichens in the regenerating forest. Douglas-fir forests 140 to 150 years old often have considerable cyanolichen biomass in the canopy (Neitlich 1993, Chapter 4). Cyanolichen recruitment is likely to be patchy in the regenerating forest, but some areas will probably develop a high cyanolichen biomass relatively quickly, much like the lower ridge. Maintaining hardwoods in the regenerating forest may also facilitate cyanolichen recovery in managed forests because cyanolichen biomass and diversity appear to develop more quickly on hardwoods than on conifers (Neitlich and McCune 1996, Chapter 1). These populations will also serve as sources of propagules for the inoculation of young conifers.

Chapter 6. Conclusions

This thesis contributes to a growing body of knowledge on the canopy epiphyte ecology of Douglas-fir forests in the Pacific Northwest. Prior to initiating the studies contained herein, three basic patterns in epiphyte distribution were known: 1) biomass and diversity of epiphytes, especially cyanolichens, slowly increase during forest succession, 2) epiphyte functional groups migrate upwards in the forest canopy during succession, and 3) cyanolichens are abundant in old growth on lower slopes but scarce farther upslope away from streams (Chapter 1). Causes of these patterns were poorly understood, and very little was known about the potential effects of logging activities on epiphytes in Douglas-fir forests. My thesis research has attempted to assess the impact of clearcut logging on epiphytes in adjacent, unlogged forest (Chapters 2 and 3), to unravel some causes of the slow accumulation of epiphytes in young forests (Chapters 4), and to evaluate the potential of live tree retention for maintaining old growth-associated epiphytes in managed forests (Chapter 5).

Clearcut logging creates sharp and microclimatically distinct forest edges. Epiphytes inhabiting trees located on the edge of fresh clearcuts must tolerate major environmental changes or perish. Since extensive fragmentation of old growth Douglas-fir forests has resulted in widespread loss of interior forest conditions in the Pacific Northwest, survival of old growth-associated species in edge habitats is critical for conservation. Well-developed epiphyte assemblages in very old, wet forests appear to be somewhat resistant to edge effects. After 20 years, epiphyte assemblages in tree crowns on the clearcut edge of a 700-year-old forest were not dramatically different from those of the forest interior, and some species had even acclimated to the new environment. Thick, water-holding moss mats may be an important component of these assemblages, facilitating the survival of

desiccation-sensitive species. Epiphyte assemblages in drier forests lacking thick canopy moss mats may be more vulnerable to edge effects. Future studies could address this possibility by sampling litterfall along clearcut edges and in the forest interior of stands from a variety of landscape contexts.

Many epiphyte species are closely associated with old growth and are seldom found in young forests. Potential causes for the low biomass and diversity of epiphytes in young forests include unsuitable habitats, slow rates of dispersal, and slow rates of establishment. Young forest canopies appear to provide suitable habitats for cyanolichens; growth rates of mature thalli are at least as high in young forests as they are in old growth. Thick moss mats are not required for normal growth of cyanolichens, although species closely associated with moss mats do grow slightly better on moss mats than on bare bark. Rates of dispersal and/or establishment probably limit cyanolichen occurrence in young forests. This is encouraging news for epiphyte conservation. If we leave old trees which are sources of epiphyte propagules nearby, these species should eventually be able to colonize regenerating forests. Studies quantifying rates of dispersal and establishment are currently underway. An epiphyte litterfall survey of unmanaged Douglas-fir forests throughout the Pacific Northwest is also needed because existing data are insufficient to evaluate the capacity of these forests to support epiphytes. Such data could be used to develop a model that would help agencies set realistic targets for epiphyte recovery in managed stands.

Retention of large, live trees in harvest units has been proposed as one way to facilitate conservation of old growth-associated species in managed forests. This method may work well for epiphytes. Remnant trees in a natural, multiple-age stand appear to have retained several old growth-associated lichen species since the last major fire. Cyanolichen populations on remnant trees appear to have served as a propagule source for colonization of younger trees, especially hardwoods, in some areas of the stand. Even so, cyanolichen biomass was quite low in much of the regenerating forest. Retention of old trees,

maintenance of regenerating hardwoods, and longer rotation periods have great potential to maintain cyanolichens in managed forests. Additional research on live tree retention, particularly studies that monitor of epiphyte populations in freshly exposed trees, are needed to fully evaluate the conservation potential of this silvicultural tool for epiphytes.

In conclusion, this thesis makes several contributions to our understanding of canopy epiphyte ecology that have implications for management of Douglas-fir forests. I hope this research will facilitate future studies and encourage ecologically sound management practices in the Pacific Northwest.

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