

ECOLOGY AND CONSERVATION OF *PSEUDOCYPHELLARIA RAINIERENSIS*,  
A PACIFIC NORTHWEST ENDEMIC LICHEN

Stephen C. Sillett, Department of Biological Sciences, Humboldt State University,  
Arcata, California 95521, USA  
Trevor Goward, Edgewood Blue, Box 131, Clearwater, British Columbia, VOE 1N0,  
Canada

**ABSTRACT**

*Pseudocyphellaria rainierensis* is an epiphytic cyanolichen endemic to humid forests extending from southeastern Alaska to Oregon in the Pacific Northwest of North America. It is extremely rare in both British Columbia and southeastern Alaska, where it is restricted to the understory and lower canopy of coastal old-growth forests. In Oregon and Washington, *P. rainierensis* occurs sporadically in mature forests as young as 140 years, but it can be abundant in humid old-growth forest canopies as long as branches are not overwhelmingly dominated by bryophytes. Its patchy distribution within forest stands may be attributed to dispersal limitations or, in some forests, to localized nutrient enrichment in the drip zone of certain tree species (e.g., *Chamaecyparis nootkatensis*). In the Oregon Cascades, transplant experiments demonstrated that a broad range of forest age classes can provide suitable habitat for *P. rainierensis*. Its absence from young forests could therefore be attributed to slow rates of dispersal and/or environmental instability associated with rapid canopy height growth. Edge effects are a potential threat to old-growth associated lichens, but *P. rainierensis* can acclimate to some forest edge environments and even flourish on large trees adjacent to clearings. Since logging has eliminated most *P. rainierensis* populations globally, short-term conservation of this species must rely on the establishment of old-growth forest reserves. Silvicultural procedures such as reduced size of cutting units, live tree retention, maintenance of understory *Taxus* and deciduous trees, uneven thinnings, and extended rotation ages have potential to promote *P. rainierensis* in managed forests in at least some portions of its range.

**INTRODUCTION**

Lichen conservation has become an important consideration in the ongoing reassessment of forest management in the Pacific Northwest (Swanson and Franklin 1992, Rosentreter 1995). Nitrogen-fixing lichens (cyanolichens) are an ecologically significant component of many forests in this region. In humid old-growth forests, biomass of epiphytic cyanolichens may exceed several tons per hectare (Denison 1979, Rhoades 1981, McCune 1993, Neitlich 1993). The nitrogen fixed by these lichens represents a major nutrient input to the ecosystem and provides a base for complex food webs in the forest canopy (Carroll 1979). Approximately thirty cyanolichen species are associated with late successional and old-growth forests in the Pacific Northwest (Rosentreter 1995, Goward 1994). Several of these species rarely occur outside of old-growth forests (Sillett and Neitlich 1996).

Our purpose in this paper is to summarize current knowledge on the distribution and ecology of one cyanolichen, *Pseudocyphellaria rainierensis* Imsh. (Lobariaceae). This summary is based on results of recent studies as well as hypotheses guiding new research. Finally, we briefly discuss potential implications of current research for conservation of *P. rainierensis* in managed forests. Additional information on this species may be found in Goward (1996) and Sillett (1997). An excellent color photograph was published by McCune and Geiser (1997).

#### GENERAL DESCRIPTION

*Pseudocyphellaria rainierensis* is a large, loosely attached foliose lichen with lobes 5-12 (-20) cm long and 0.5-3 cm wide. The thallus is thin, stiff, and brittle when dry. Characteristically this species grows draped over tree branches. It is pale bluish green when dry (turning creamy brown in the herbarium) and bears scattered white pseudocyphellae over the lower surface. The lower surface is also densely tomentose. This the only species of *Pseudocyphellaria* in the Northern Hemisphere species that contains both a green alga and a cyanobacterium. The green algal photobiont forms a more or less continuous layer, while the cyanobacterial photobiont is confined to internal cephalodia sometimes visible from above as small swellings or eruptive warts. The lobe margins are lobulate to lacerate or occasionally densely isidiate. Elongate or coralloid isidia are also often present over the upper surface, especially along stress cracks. Specialized isidia-bearing platforms (called "isidalia" by Goward 1996) are sometimes present. These peculiar structures arise where the cortex gathers upward in tiny circular pedestals.

Apothecia are seldom found in this species, though specimens from two Oregon populations possessed orangish red apothecia 1-2 mm across over the upper surface (Sillett 1997, unpubl.). The ascospores were hyaline, fusiform (30-60  $\mu\text{m}$  x 5-7  $\mu\text{m}$ ), and 1- to 3-septate. Ascospore size, shape, number per ascus were highly variable, and ascus density was low (0-5 per apothecium). Asexual spores are also produced in tiny black pycnidia.

The chemistry of *P. rainierensis* is poorly known. The thallus yields the following spot tests: cortex K+ yellow, C-, KC-, PD-, I-, UV-; medulla K-, C-, KC-, PD-, I+ blue, UV+ white to blue or UV-.

#### GEOGRAPHIC DISTRIBUTION

*Pseudocyphellaria rainierensis* is endemic to western North America and appears to be phylogenetically unrelated to other members of its genus in the Northern Hemisphere (Goward 1996). It was described by Imshaug (1950) based on collections made from Mount Rainier National Park, Washington. Since that time it has been collected from 47 sites ranging from 43°N to 58°N latitude (Figure 1).

Thirty-seven of these sites are located in Washington and Oregon. In western Washington, *P. rainierensis* has been found at sixteen sites: three on the Olympic Peninsula, three in the northern Cascades, two in the Alpine Lakes Wilderness, five in Mount Rainier National Park, and three in the southern Cascades (Neitlich et al. 1994, R. Leshner pers. comm.). In Oregon, it is known from twenty-one sites. Only one of these sites is located in the Oregon Coast Range. The rest, including the only known fertile populations, are located in the Cascade Mountains (Sillett 1997). Throughout this portion of its range, *P. rainierensis* is associated with humid old-growth forests in the *Abies amabilis*, *Picea sitchensis* or *Tsuga heterophylla* Zones (Franklin and

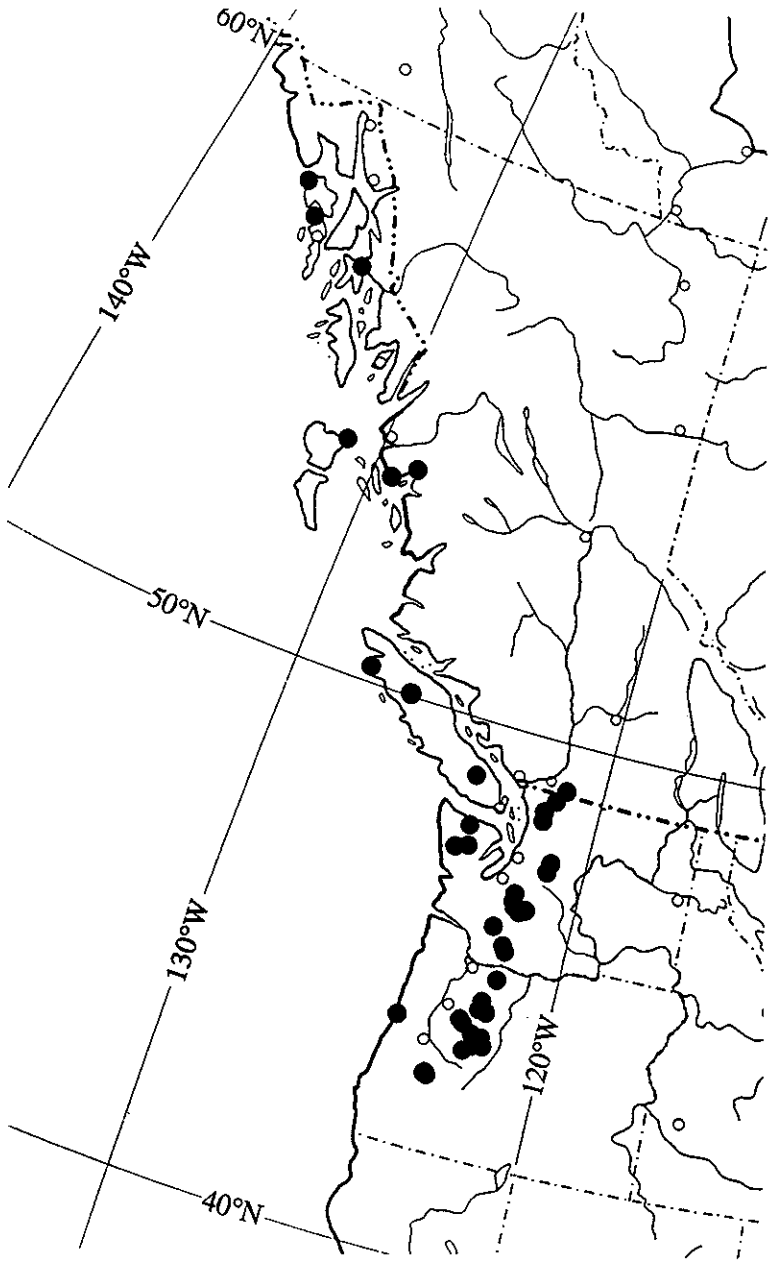


Figure 1. Global distribution of *Pseudocypbellaria rainierensis*. Large, shaded circles represent known populations. Small, unshaded circles represent cities.

Dyrness 1973). Here it colonizes a wide variety of conifers (e.g., *Abies amabilis*, *Pseudotsuga menziesii*, *Taxus brevifolia*, *Thuja plicata*, and *Tsuga heterophylla*), hardwoods (e.g., *Alnus rubra* and *Castanopsis chrysophylla*), and shrubs (e.g., *Rhododendron macrophyllum*). One anomalous population has been reported from a 150-year-old *Abies lasiocarpa* stand on a lava flow on Mt. Baker (Rhoades 1981), but *P. rainierensis* has disappeared from this locality following defoliation associated with an outbreak of the Balsam Woolly Aphid, *Adelges piceae* (Rhoades pers. comm.). Another population was probably destroyed by the eruption of Mount Saint Helens in May 1980.

*Pseudocyphellaria rainierensis* is much rarer in British Columbia and southeastern Alaska, where it is known from only seven and three localities, respectively (Goward 1996, Geiser et al. 1994), all in the Coastal Western Hemlock Zone (Meidinger and Pojar 1991). We emphasize that its rarity in this portion of its range is not merely an artifact of undercollecting. One recent survey of 145 old forests in British Columbia, for example, turned up only a single specimen (Goward 1996), whereas in southeastern Alaska it was found to occur at only three of the 257 sites surveyed by Geiser et al. (1994). At least one of the British Columbia localities, moreover, appears to have been destroyed by logging (Goward 1996).

Throughout its range, *P. rainierensis* is restricted to the immediate coast, valley bottoms in the mountains, or lower slopes. In Oregon, it occurs to about 1200 m, though an altitudinal range of between roughly 500 and 1000 m is more typical (Sillett 1997). Farther north, in British Columbia, most localities are at or near sea level (Goward 1996). Thus, *P. rainierensis* has an essentially coastal distribution in the northern portion of its range but is more common in inland sites farther south (Figure 1).

The near absence of *P. rainierensis* from the Oregon Coast Range may be attributed to the almost complete destruction of low elevation old-growth forests in Oregon (Harris 1984). Careful lichenological surveys of mid-elevation old-growth forests on public lands in southwestern Oregon may discover additional populations.

#### VERTICAL DISTRIBUTION WITHIN THE CANOPY

Vertical distribution of epiphytes in humid forests of the Pacific Northwest changes dramatically during the canopy development that accompanies forest succession. Many lichens possessing only a green algal photobiont rapidly colonize young forests. As tree height increases, many of these chlorolichens remain abundant only in the upper and outer crown, perhaps because of unsuitable microclimates and/or competition from other epiphytes in the lower and inner crowns of large trees (Sillett 1995). Eventually, cyanolichens followed by bryophytes dominate branches in the lower canopy, gradually migrating upwards in response to increasing moisture availability or other factors (McCune 1993). Epiphytic mosses form thick mats on branches in humid old-growth forests. Canopy soil accumulates beneath moss mats, and this soil is exploited by a variety of organisms. Ultimately, large branches in the oldest, wettest forests support plant communities dominated by terrestrial species, including mosses, ferns, shrubs, and even trees (Sillett and Neitlich 1996, Sillett unpubl.).

Rates of change in vertical distributions of epiphytes appear to be highly variable, depending on factors such as rainfall, topography, and elevation (McCune 1993, Goward 1995, Sillett and Neitlich 1996). Relatively dry, upland old-growth forests typically support only chlorolichens; cyanolichens and bryophytes are scarce or absent except on the forest floor or near streams (Sillett and Neitlich 1996). Epiphytic cyanolichens

dominate canopies of old-growth forests with intermediate moisture regimes, such as those surveyed at the H. J. Andrews Experimental Forest in Oregon (Pike et al. 1975, McCune 1993, Sillett and McCune in press), but they are relatively sparse in very wet, bryophyte-dominated forest canopies. For example, *P. rainierensis* is present in the canopy of very wet old-growth forests along the Carbon River (Mount Rainier National Park, WA) and the South Santiam River (Willamette National Forest, OR; Figure 2E), but its abundance is strikingly low compared to somewhat drier old-growth forests at similar elevations (Figure 2). Epiphytic bryophytes, including terrestrial mosses, dominate the canopies at both sites (Sillett unpubl.). Intense competition from bryophytes and/or unsuitable microclimates (e.g., too consistently wet) may limit the distribution of *P. rainierensis* and other epiphytic cyanolichens in very wet old-growth forest canopies.

Vertical shifts in epiphyte distributions within the canopy are likely to vary in amplitude as well as in rate. Field observations in British Columbia, for example, suggest that the upper limit of *Nephroma occultum*, an epiphytic cyanolichen, varies markedly from region to region, presumably in response to differences in macroclimate (Goward 1995). This observation led Goward to propose three "range classes" within the total geographic distribution of epiphytic macrolichens inhabiting forest canopies. In its "primary range," a species extends into the upper canopy and is clearly well adapted to regional macroclimate. In its "secondary range," the same species is less adapted and, therefore, absent from the upper canopy, perhaps reflecting an intolerance of summer droughts and/or winter freezes. Finally, in its "tertiary range," the species may require particular microclimatic conditions found only in the understory and lower canopy of old-growth forests, which are relatively sheltered from macroclimatic extremes compared to upper and middle canopies (Geiger 1965).

The few existing surveys of *P. rainierensis* are insufficient to fully evaluate the dynamics of its vertical distribution, but a few tentative conclusions are warranted for some regions. British Columbia and southeast Alaska are within the tertiary range of *P. rainierensis* because of its restriction to the understory and lower canopy of old-growth forests (Goward 1996, L. Geiser, pers. comm.). In the Oregon Cascades, *P. rainierensis* attains its highest known vertical distribution (i.e., 50 m in the crown of a 70 m tall tree, Figure 2) and has been found in forests as young as 140 years. In this region, *P. rainierensis* is most abundant in the lower canopy and understory. Since *P. rainierensis* is rarely found in the upper canopy, it may lack a primary range at this time, and the Oregon Cascades may be part of its secondary range. Alternatively, its absence from the upper canopy in Oregon may indicate an inability to keep pace with vertical canopy growth because of poor dispersal. Vertical shifts in epiphyte distribution, however, are a stand-level phenomenon; epiphyte colonization does not necessarily proceed from the bottom up in all trees. For example, *P. rainierensis* occurred in the mid-crown of a 140-year-old Douglas-fir tree but was absent from the understory beneath this tree (Figure 2A).

#### PATCHY DISTRIBUTION WITHIN FOREST STANDS

When it is present in a forest, *P. rainierensis* typically occurs in small, isolated "pockets" (e.g., understory trees and shrubs in well illuminated habitats, Pike et al. 1975) but is absent from intervening areas. Recent canopy-level surveys in the Oregon Cascades found it on fewer than twenty percent of the large trees climbed (Sillett unpubl.). In a ground-level study of a mixed-age stand, *P. rainierensis* was found in

only three of 231 two-meter-radius litterfall plots systematically distributed over a two hectare area (Sillett and Goslin in prep.). We offer two hypotheses to explain this patchiness: 1) *P. rainierensis* accumulates slowly in forests because of poor dispersal abilities and/or 2) its occurrence is favored by nutrient enrichment and thus reflects the localized nature of nutrient loading in forests.

According to the first hypothesis, slow dispersal prevents *P. rainierensis* from extending over its full ecological range (i.e., occupying all or most of the suitable habitat) within a forest stand. The fact that the highest abundance of *P. rainierensis* ever recorded occurs in the oldest forest ever surveyed in Oregon, a 700-year-old mid-elevation forest near the bottom of the Middle Santiam River valley, is consistent with this hypothesis. In this forest, *P. rainierensis* was the sixth most abundant lichen species, it covered up to fifty percent of branch surfaces in the lower canopy, it was found in seventeen of twenty litterfall plots, and it occurred in each of the seven large trees climbed (Sillett 1995). Thus, several centuries may be required for *P. rainierensis* to become abundant in a forest stand even under optimal conditions (Figure 2).

Recent observations in British Columbia (Goward in prep.) support the nutrient enrichment hypothesis. In a low elevation old-growth forest on nutrient-rich soils, *P. rainierensis* was only found within the drip zone of old *Chamaecyparis nootkatensis* trees, where it grew intermingled with twenty-five other cyanolichen species on understory *Abies amabilis* trees. This "drip zone effect" was not observed in similar forests on nutrient-poor soils, suggesting that foliage of overstory *C. nootkatensis* trees leaches surplus nutrients, providing enriched throughfall to understory epiphytes. Nutrient concentrations, especially calcium, beneath *C. nootkatensis* trees are indeed higher than those beneath other conifers (Kiilsgaard et al. 1987). Limited support for this hypothesis also comes from the lichenological literature. Small-scale variation in the availability of soil calcium was partially responsible for major differences in epiphyte communities inhabiting different *Quercus* trees within a Norwegian forest; trees growing on calcium-enriched soils supported epiphyte communities with more cyanolichens (Gauslaa 1985). Similar correlations were found in study of epiphytes on *Quercus* and *Fraxinus* trees in Scotland, although a causal link between soil nutrients and epiphyte community structure can only be established with manipulative experiments (Bates 1992). Clearly, additional research is required to evaluate the merit of this hypothesis for *P. rainierensis*.

#### ASSOCIATION WITH OLD GROWTH

We are using manipulative experiments to determine potential causes for strong positive associations between some epiphytic lichens and old growth in the Pacific Northwest. Three experiments were designed to test the following alternative but not mutually exclusive hypotheses: 1) particular conditions found only in old growth are necessary for lichen survival and growth, 2) slow dispersal limits lichen colonization of young forests, and 3) environmental instability associated with rapid height growth makes young forests unsuitable habitat for lichens. This research, which is summarized briefly below, could be used to develop conservation strategies for *P. rainierensis* and other endemic lichens in managed forests.

In the first experiment, mature thalli of *P. rainierensis* and *Lobaria oregana* were transplanted into forests of different ages in the Oregon Cascades to determine if either species required particular conditions found only in old forests (Sillett and McCune 1997). After one year, *P. rainierensis* thalli transplanted into young forests performed at

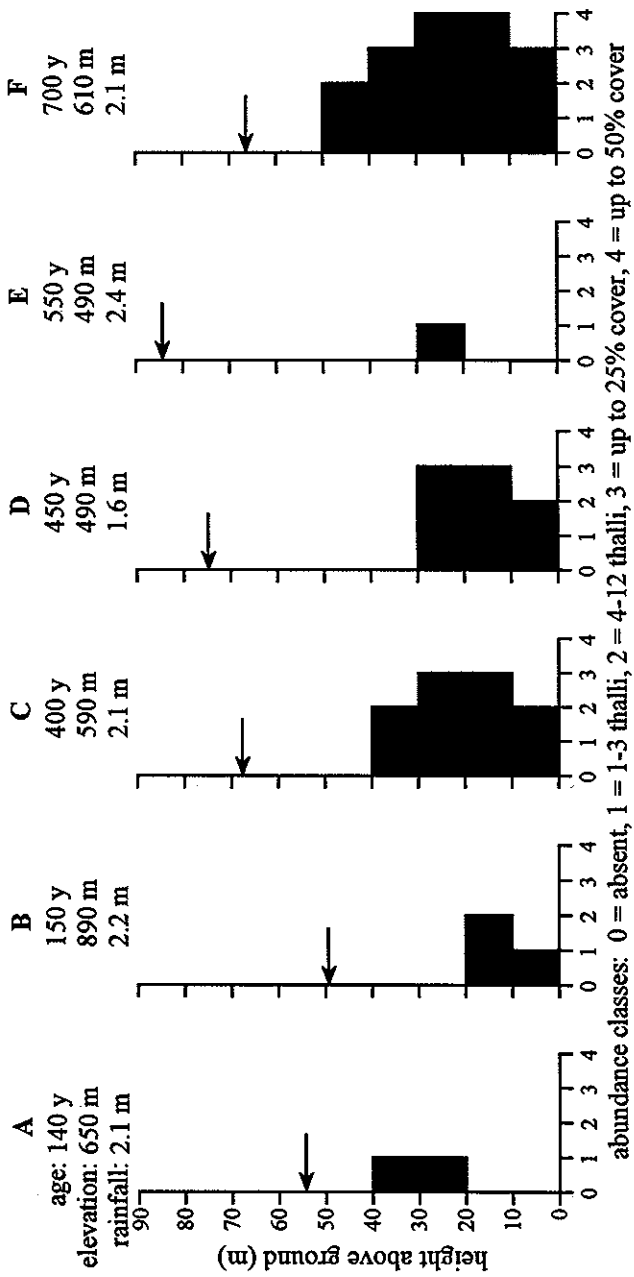


Figure 2. Vertical distribution of resident *Pseudocypbellaria raimierensis* populations along vertical transects in six forests from the Oregon Cascades. Approximate age, elevation, and annual rainfall are indicated for each forest. Each transect extended to the top of an individual *Pseudotsuga* tree, whose height is indicated by the horizontal arrow. Abundance was estimated visually at ten meter height intervals along the transect. Note that abundance is measured along a logarithmic scale.

least as well as those transplanted into old growth. Thalli in young forests actually remained more vigorous than thalli in old growth. They grew quite rapidly in each forest (Figure 3), and rates of mortality were uniformly low. These results indicate that in the Oregon Cascades, a broad range of forest age classes could provide suitable canopy habitats for *P. rainierensis*. Its failure to colonize young forests under natural conditions suggests that factors other than microclimate (e.g., dispersal) may be limiting in this portion of its geographic range.

Although it is possible to nondestructively collect propagules from lichen thalli for transplantation (Scheidtger 1995), the large quantities of propagules needed in the second experiment precluded the use of a rare species like *P. rainierensis*. In the first experiment, however, *L. oregana* also grew at least as well in young forests as it did in old growth. And like *P. rainierensis*, this large, old-growth associated foliose lichen has both a green alga and a cyanobacterium as photobionts. It also produces symbiotic propagules (lobules) as its primary means of dispersal (Rhoades 1983). Moreover, *L. oregana* was abundant enough to provide sufficient material for the second experiment without compromising existing populations.

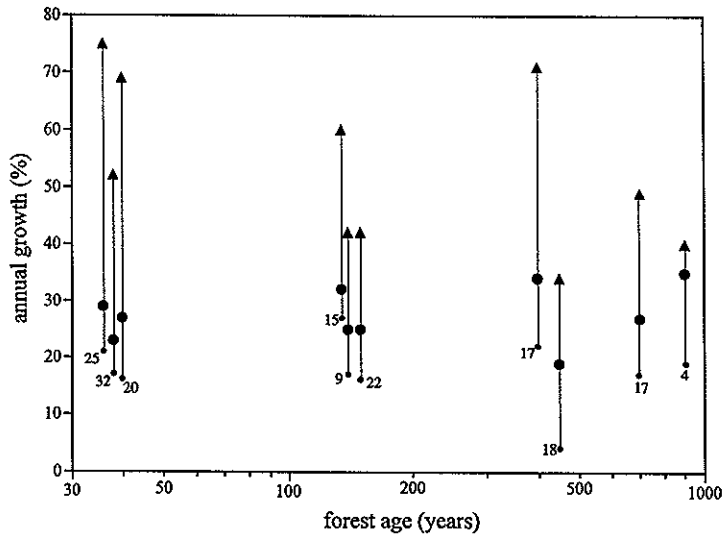
In the second experiment, branches in forests of different ages were inoculated with *L. oregana* lobules to determine if dispersal limits epiphyte colonization of forest canopies. Branches were removed from trees, stripped of resident epiphytes, surface-sterilized, and lashed to tree crowns in young forests and in old growth (Sillett et al. in prep.). Half of these branches were manually covered with lobules each season for one year. Rates of establishment on all branches will be measured two years later. A significant inoculation effect would implicate dispersal as a limiting factor. The extent to which these results could apply to *P. rainierensis* and other lichens can be evaluated with a long-term experiment that required much less living material.

Rapid height growth quickly alters canopy microclimates in young forests; well-illuminated branches soon become shaded by expanding crowns. If dispersal of epiphytic cyanolichens can not keep pace with changing conditions, they may be unable to persist in young forests after successful colonization. More stable environmental conditions associated with older forests, which have only moderate height growth, would thus tend to promote the accumulation of slowly dispersing species. In the third experiment, thalli and symbiotic propagules of *P. rainierensis* were transplanted from old growth into young tree crowns to determine if they can persist within rapidly growing forests. The fate of introduced populations will be monitored over the coming decades to evaluate the long-term potential of these forests as habitats for epiphytic cyanolichens.

#### EDGE EFFECTS

Much of the old growth remaining in the Pacific Northwest is impacted by edge effects (Norse 1990). Edges of old-growth forests bordering clearings are warmer, brighter, windier, and less humid than the forest interior (Chen et al. 1995), and epiphytic lichens on forest edges dry out much faster after rain than those in the forest interior (Renhorn et al. 1997). Intriguingly, *P. rainierensis* is able to persist on trees growing at the edges of clearings in some areas. In the Oregon Cascades, for example, luxuriant populations of this species have been found growing on a 55 m *Pseudotsuga* tree adjacent to a 20-year-old clearing, as well as on a 25 m *Tsuga* tree adjacent to a 40-year-old clearing. Immediately after logging, populations of *P. rainierensis* on edge trees probably suffer as exposed thalli sicken and die. Dieback, however, is apparently incomplete, and some thalli survive, ultimately acclimating to microclimatic conditions





**Figure 3.** Annual growth rates for transplanted thalli of *Pseudocyphellaria rainierensis* in ten forests of different ages in the Oregon Cascades. Forty thalli were weighed and transplanted into tree crowns in each forest. After one year they were collected and reweighed. Data from the same forests are connected by thin, vertical lines. Three estimates of annual growth are presented for each forest. Average growth of all living, unfragmented thalli (small, shaded circles), average growth of healthy, unfragmented thalli (large, shaded circles), and maximum growth of a single thallus (shaded triangles). Many thalli died, disappeared, and/or fragmented during the experiment. The number of unfragmented, living thalli recovered from each forest is indicated at the base each vertical line.

near the forest edge. For example, *P. rainierensis* has persisted for more than a century on large *Pseudotsuga* trees that were isolated from each other by fire and subsequently surrounded by dense, regenerating forest (Sillett and Goslin in prep.). Likewise, reciprocal transplants of *P. rainierensis* among tree crowns in a 700-year-old forest revealed that thalli transplanted from the forest interior to the edge grew poorly, whereas thalli transplanted from the edge back to the edge grew quite well (Sillett 1994).

Several factors probably contribute to the apparent resilience of *P. rainierensis* to edge effects. Acclimation may occur most rapidly in humid forests supporting thick moss mats on branches. By retaining water, these mats may help desiccation-sensitive species grow by prolonging hydration periods (see Sillett 1995). Indeed, *P. rainierensis* thalli do grow slightly but significantly better on moss mats than on bare bark (Sillett and McCune in press). The cephalodiate nature of *P. rainierensis* may also contribute to its resilience. The capacity of its green algal photobiont to photosynthesize in humid air allows *P. rainierensis* to grow during conditions when many other cyanolichens, which

have a single cyanobacterial photobiont, are dormant. Unlike green algal photobionts, cyanobacterial photobionts require liquid water for photosynthesis (Lange et al. 1988, 1993). The ability to photosynthesize in humid air could compensate growth losses attributable to shorter hydration periods following rain at forest edges. Finally, thalli from exposed habitats exhibit morphological changes (e.g., a thicker tomentum) that increase water storage capacity and decrease drying rates (Snelgar and Green 1981).

## CONSERVATION

*Pseudocyphellaria rainierensis* is rare throughout most or all of its range. Its patchy distribution, endemic status, strong association with old growth, and potential vulnerability to human disturbance led Goward (1996) to recommend it for endangered status in Canada and led Sillett (1997) to recommend it for threatened status in the United States. While this species is more abundant in Oregon and Washington than in Canada, even here it is essentially restricted to old growth. There can be little doubt that industrial logging has already led to its disappearance at many localities and could contribute to further declines. For this reason, we believe that *P. rainierensis* should be considered a threatened species throughout its range. At the present time, however, it is designated as "vulnerable" in Canada, and it receives no official endangerment status in the United States.

The simplest and certainly most effective strategy for conservation of *P. rainierensis* involves the protection of its remaining old-growth forest habitat. Unfortunately, only one of the six extant Canadian localities is currently situated within a protected area; all of the others are open to logging. In the United States, the situation may be less urgent, at least in the short term, because of the protection *P. rainierensis* is supposed to receive under the FEMAT plan (Rosentreter 1995). According to this plan, all sites with known populations will be protected and surveys will be conducted prior to ground-disturbing activities in potential habitat. Furthermore, many of the known populations in the United States are located within protected areas on public lands (i.e., National Parks, State Parks, Wilderness Areas, or Research Natural Areas).

In addition to protecting existing populations, long-term conservation of *P. rainierensis* will require creation of suitable habitats in managed forests. It may be possible to promote this species and other epiphytic lichens in managed forests by using certain silvicultural procedures. Reducing the size of cutting units, for example, may facilitate propagule dispersal into the regenerating forest from populations remaining in adjacent, older forests. Similarly, retaining large, live trees over the duration of stand rotation may permit inoculation of the regenerating forest canopy from populations persisting in the crowns of retained trees. Maintaining deciduous trees in the understory may speed recovery of *P. rainierensis* in regenerating forests because epiphytic cyanolichens tend to accumulate on deciduous trees more quickly than on conifers (Sillett and Neitlich 1996, Neitlich and McCune 1997). Retaining old *Taxus* trees in the understory will also help because their crowns often provide suitable *P. rainierensis* habitat for *P. rainierensis* in old growth (Sillett 1997). Uneven thinning of dense, regenerating forests should also promote *P. rainierensis* colonization because epiphytic cyanolichens frequently occupy well-illuminated substrates in canopy gaps (Pike et al. 1975, Neitlich and McCune 1997). Finally, extending rotation ages to over 200 years is likely to considerably improve chances of successful dispersal and establishment of *P. rainierensis*; some forests can accumulate considerable cyanolichen biomass in only 150 years (Rhoades 1981, Neitlich 1993, Sillett & McCune 1996). Such silvicultural

procedures are more likely to prove successful in this species' secondary range (i.e., Oregon Cascades) than in its tertiary range (i.e., British Columbia and Alaska), where its level of old-growth dependency is presumably much greater.

#### ACKNOWLEDGMENTS

We are grateful for the constructive comments of Bruce McCune and an anonymous reviewer on the manuscript.

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