Stephen C. Sillett and **Peter N. Neitlich,** Department of Botany and Plant Pathology, Oregon State University, Corvallis, OR 97331

Emerging Themes in Epiphyte Research in Westside Forests with Special Reference to Cyanolichens

Abstract

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.

Introduction

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), 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).

A considerable amount of canopy epiphyte research has occurred in westside forests during the last two decades. Early studies 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, the evidence is growing, especially for cyanolichens.

Our purpose in this article is to highlight three major patterns which have emerged from recent studies of epiphytes in westside forests: the slow development of epiphyte communities during forest succession, the apparent upward migration of epiphyte functional groups over time, and the riparian influence on epiphyte distribution. McCune's similar gradient hypothesis provides a framework for the discussion. This paper focuses on several key studies of epiphytes in forests of the Coast and western Cascade Ranges, drawing on both personal observations and preliminary results from ongoing studies. We conclude with a brief discussion of research approaches and some suggestions for future research that will have implications for forest management.

Slow Development of Epiphyte Communities

Studies in Europe (Rose 1992), Montana (Lesica et al. 1991), and Oregon (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 is in cyanolichens, which dominate the old-growth canopy (Pike et al. 1975) but are scarce or absent in younger forests (Figure 1). Several epiphytic cyanolichen species are seldom found in forests less than a century old (Table 1, Holthausen et al. 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/or unsuitable canopy microclimates in younger forests.

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 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 dipersal 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 bewteen old and young forests comes from a recent study in Glacier Bay, Alaska (Neitlich & Campbell, unpublished). 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 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

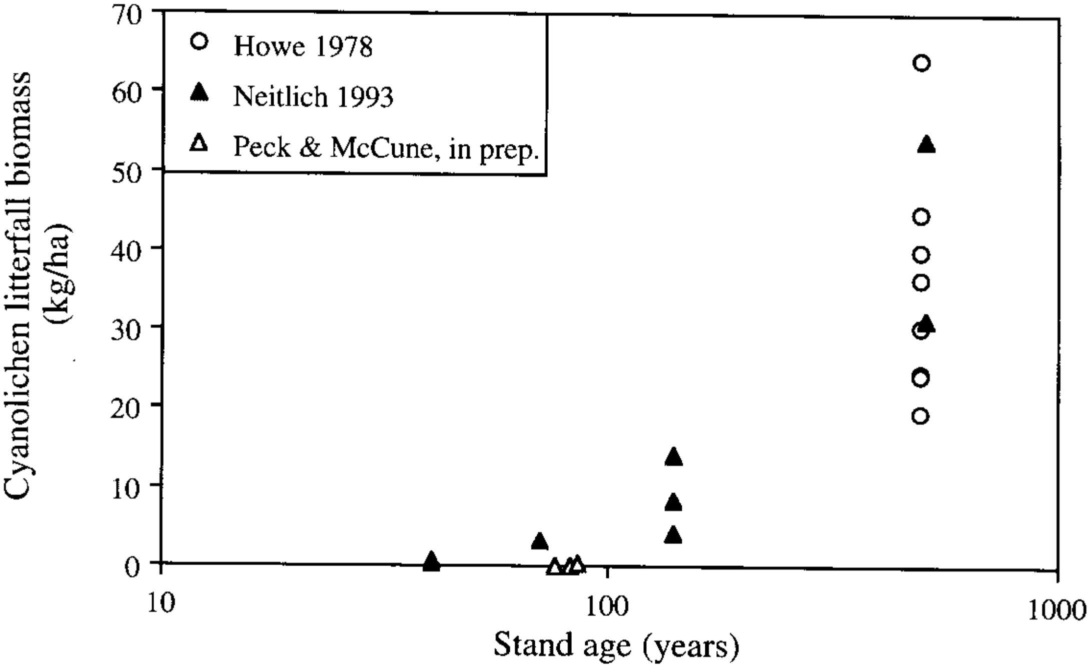

Figure 1. The relationship between epiphytic cyanolichen biomass and stand age for 19 forest stands in the central western Oregon Cascades. All stands were below 900 m elevation, less than 100 m above a major stream, and dominated by Douglas-fir. The x-axis is on a log scale. Data from Howe (1978), Neitlich (1993), and Peck & McCune, in prep.

TABLE 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 OR and WA; occurs lower in canopy in BC and AK
Nephroma silvae-veteris†	3, 4, 16	middle canopy
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

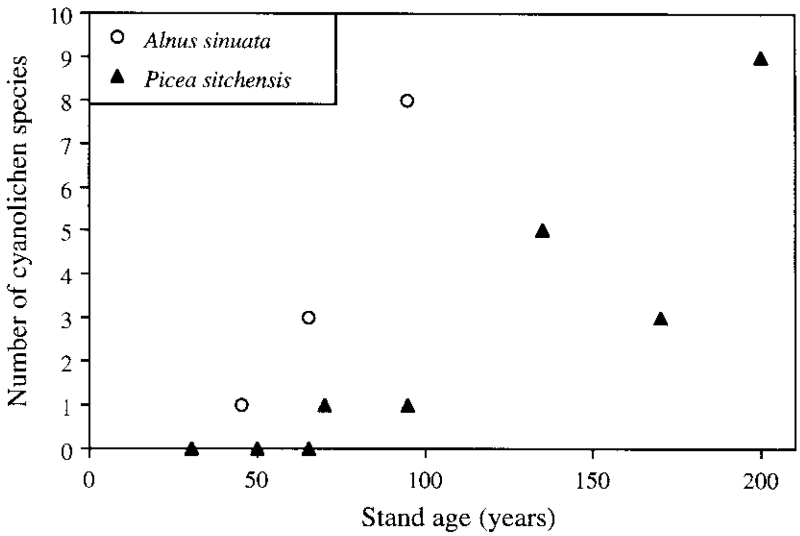

Figure 2. The effect of forest age on cyanolichen species richness on two tree species in spruce forests of Glacier Bay, Alaska. Total number of cyanolichen species are presented for each tree species in each site where they were found in the chronosequence. Tree species in each site were surveyed until four trees were climbed with no additional lichen species encountered. Data from Neitlich & Campbell, unpublished.

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. 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 (*e.g.*, Sillett 1994, 1995a) are a reasonable alternative in which growth rates provide a relative measure of epiphyte habitat suitablity 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? A recent study of a 700-year-old Douglas-fir forest suggests it does. In this stand (described in Sillett 1995b), cyanolichens and bryophytes, especially *Antitrichia curtipendula,* were abundant throughout the forest profile. Several cyanolichen species normally found in the understory of 450-year-old Douglas-fir forests (*e.g., Pseudocyphellaria rainierensis,* Pike et al. 1975) were widely distributed in the lower to middle crowns of the large Douglas-fir trees in this stand. Similarly, 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 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.

TABLE 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

The Riparian Influence on Epiphyte Distribution

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 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 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 3). The effects of streams on canopy microclimate may be less pronounced at higher elevations

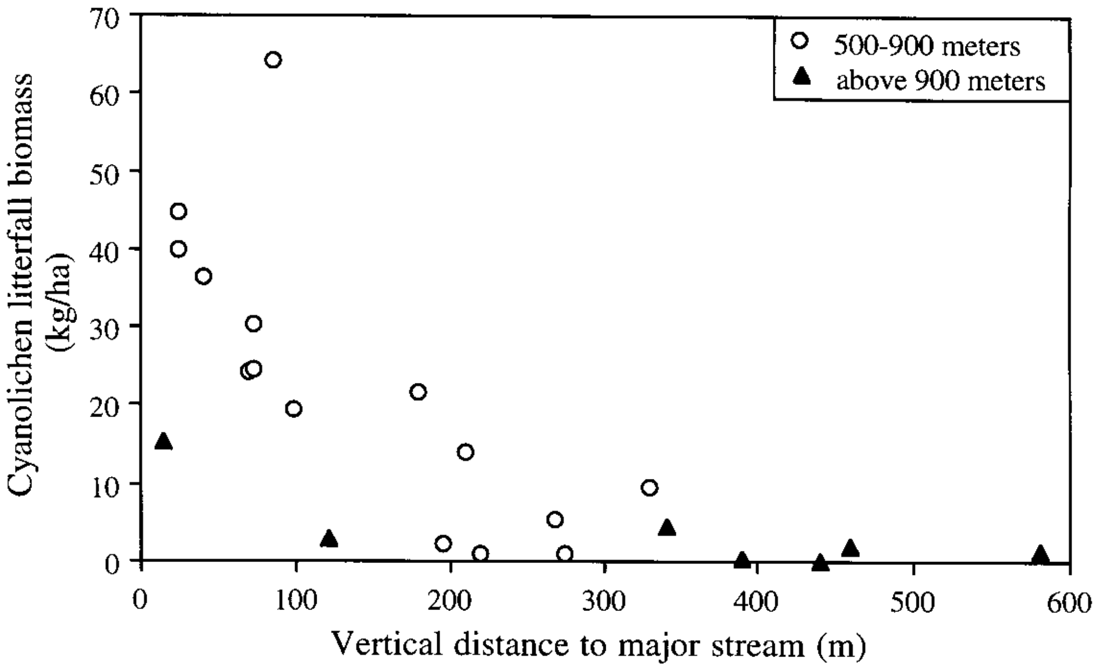

Figure 3. The relationship between epiphytic cyanolichen biomass and proximity to major streams for 22 stands of old-growth Douglas-fir forest in the H.J. Andrews Experimental Forest in the western Oregon Cascades. Open circles represent stands below 900 m elevation. Shaded triangles represent stands above 900 m in elevation. Data from Howe (1978).

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 (see below).

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. 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 1994) provides a ground-based alternative to more extensive 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, green 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 dilemna. Furthermore, the extent to which late-successional epiphyte species can withstand the microclimatic changes following logging is currently unknown, although some of these species are capable of adjusting to the new microclimate in partially exposed trees (Sillett 1994, 1996).

The potential of uneven-aged management to facilitate recovery of epiphytes in managed forests can be explored in two ways. First, we might retrospectively study natural stands whose structure presumably resembles the intended outcome of a modern silvicultural treatment at rotation age. The effects of retained trees on epiphyte distributions in these stands can be determined by both litterfall and canopy sampling (e.g., Peck and McCune, in prep., Sillett 1995a). Second, survival of epiphytes after silvicultural as well as natural disturbances should be monitored from within the canopy.

Viability ratings for epiphytes in the FEMAT report (FEMAT 1993) suggest that persistence of many epiphyte species will require creation of old-growth characteristics in managed stands. Existing data are insufficient to evaluate the capacity of westside forests to support epiphytes, however, given the high spatial and temporal variability in epiphyte distributions. We recommend an epiphyte litterfall survey of unmanaged stands throughout the Pacific Northwest. These data could be used to develop a model that would help agencies set realistic targets for epiphyte recovery in managed forests.

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