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Vertical Distribution of Dominant Epiphytes in Douglas-Fir Forests of the Central Oregon Cascades

Abstract

The canopies of old-growth Douglas-fir forests support a diversity of epiphytic lichens and bryophytes. We quantified the vertical distributions of six dominant epiphytes throughout the crowns of large *Tsuga heterophylla* (46–57 m tall) and *Pseudotsuga menziesii* (60–78 m tall) trees in five forest stands of the central Oregon Cascades. There were no major differences in epiphyte distribution between the two tree species, but epiphytes on *T. heterophylla* generally peaked in abundance at heights 10–20 m below those on *P. menziesii*. Alectorioid lichens were most abundant in the upper crowns but scarce in the lower crowns. The fruticose green algal lichen *Sphaerophorus globosus* was evenly distributed throughout the crowns. The cyanolichen *Lobaria oregana* and the moss *Antitrichia curtispindula* were most abundant in middle crowns. *Lobaria pulmonaria* was most abundant in the lower–middle crowns. It was scarce or absent in the upper crowns. The moss *Isoetecium myosuroides* was also scarce or absent in the upper crowns. It was most abundant in the lower crowns. The vertical patterns described in this study are not representative of all old-growth Douglas-fir forests. In wetter forests, bryophytes are dominant throughout the canopy. In drier forests, alectorioid and other green algal lichens extend farther down in the canopy, and bryophytes and cyanolichens are restricted to the lower canopy.

Epiphytes are a conspicuous and ecologically significant component of forests in the Pacific Northwest, where they have been studied for over 25 years. A great deal is known about their floristics (Pike et al. 1975), community dynamics (Sillett 1995, Sillett and McCune 1998, Sillett et al. 2000a), population dynamics (Rhoades 1983), tree-level biomass (Pike et al. 1977, Sillett 1995), stand-level biomass (McCune 1993, Neitlich 1993), distribution by functional groups (Lyons 1998, McCune 1993, McCune et al. 1997, Sillett and Neitlich 1996), roles in nutrient cycling (Carroll 1979, Denison 1973, 1979, McCune and Daly 1994, Pike 1978), growth rates (Denison 1988, Rhoades 1977, Sillett 1994, Sillett and McCune 1998, Sillett et al. 2000b), dispersal limitations (Sillett et al. 2000b), vulnerability to edge effects (Sillett 1994, 1995), and susceptibility to forest management practices in old-growth Douglas-fir forests (Goward 1995, Peck and McCune 1997, Sillett and Goslin 1999, Sillett and Goward 1998, Sillett et al. 2000b). However, little quantitative information on vertical distributions of epiphytes on different tree species in these forests is currently available. The purpose of this study is to describe the vertical distributions of dominant epiphytes on two tree species, *Tsuga heterophylla*

(Raf.) Sarg. and *Pseudotsuga menziesii* (Mirb.) Franco. We estimated the abundance of six epiphytes throughout the crowns of ten tall trees.

Study Area

We sampled epiphytes in five old-growth forest stands within the Willamette National Forest in the Cascade Range of western Oregon: three in the H. J. Andrews Experimental Forest, one along the South Santiam River near House Rock Forest Camp, and one along the South Fork McKenzie River near Cougar Reservoir (see Sillett et al. 2000b for more specific information). The stands were 450 to 600 years of age, 470 to 790 m elevation, 0 to 120° aspect, and 60 to 85 m tall. They were dominated by *Pseudotsuga menziesii* with smaller amounts of *Tsuga heterophylla*, *Thuja plicata* Donn., *Taxus brevifolia* Nutt., *Acer macrophyllum* Pursh., and *Alnus rubra* Bong. Basal areas ranged from 91 to 199 m²ha⁻¹ for conifers and 0.2 to 6.4 m²ha⁻¹ for hardwoods. Average annual precipitation in the stands ranged from 1.5 to 2.4 m (Oregon Climate Service). These stands have been utilized in previous epiphyte studies (Sillett et al. 2000ab).

TABLE 1. Dimensions of ten study trees in the Willamette National Forest in western Oregon. The five forest stands are listed from north to south. All measurements are in meters.

Stand	<i>Tsuga heterophylla</i>		<i>Pseudotsuga menziesii</i>		notes
	tree height	tree dbh	tree height	tree dbh	
1	57.0	0.81	64.0	2.64	main trunk snapped at 61 m
2	52.0	0.97	60.5	1.86	main trunk snapped at 57 m
3	46.0	0.81	73.5	1.99	—
4	54.5	1.02	66.5	1.46	—
5	48.5	0.97	77.5	1.89	—

Methods

Tree Selection and Access

In each stand, we selected one large *P. menziesii* and the largest healthy *T. heterophylla* for detailed study. More specific information about each tree is summarized in Table 1. Tree crowns were accessed by shooting a monofilament over sturdy 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 other end using vertical rope technique. We used 20-m long arborist's rope lanyards to access progressively higher branches and move laterally through tree crowns. Tree heights were measured by lowering a graduated fiberglass tape from the topmost foliage to the forest floor. Numbered aluminum tags were then attached to the main trunks at 10 m intervals. These tags were used as benchmarks for epiphyte sampling.

Epiphyte Sampling

We visually estimated epiphyte abundances within each 10 m stratum. Epiphyte abundance was recorded on a 0–6 scale: 0) absent, 1) 1–3 individual thalli, 2) up to 5% cover, 3) 5–10% cover, 4) 10–25% cover, 5) 25–50% cover, and 6) greater than 50% cover. We considered only six prominent branch-dwelling epiphytes that were easily recognized from the climbing path on each tree: 1) alectorioid lichens (i.e., mostly *Alectoria sarmentosa* with smaller amounts of *A. vancouverensis*, *Bryoria* spp., and *Usnea* spp.), 2) the green algal fruticose lichen *Sphaerophorus globosus*, 3) the cyanolichen *Lobaria oregana*, 4) the cyanolichen *Lobaria pulmonaria*, 5) the moss *Antitrichia curtispindula*, and 6) the moss

Isotheicum myosuroides. Finally, we visually estimated the average crown radius within each 10 m stratum to the nearest 0.5 m.

Results and Discussion

All of the epiphytes sampled in this study have similar distribution patterns on both tree species. The few discrepancies are attributable to differences in tree stature alone. Epiphytes on *T. heterophylla*, whose average height is 52 m, peak in abundance at heights 10–20 m below those on *P. menziesii*, whose average height is 68 m. Epiphytes are absent above 60 m on *T. heterophylla* simply because the tallest tree is only 57 m.

Vertical distributions of the six epiphytes differ greatly (Figure 1). Abundance of alectorioid lichens steadily increases from the lower to upper tree crowns. They cover over 25% of substrates above 50 m on *P. menziesii* and above 40 m on *T. heterophylla*. Old-growth Douglas-fir forests can support over 500 kg ha⁻¹ of these lichens (Neitlich 1993, Sillett and Goslin 1999). *Sphaerophorus globosus* is more evenly distributed than any other epiphyte in this study, covering 5–10% of substrates throughout crowns of both tree species. This lichen is prevalent on trunks and branches in the inner crown, but it is scarce on branchlets and twigs in the outer crown (Lyons 1998, Sillett and Goslin 1999). *Lobaria oregana* is most abundant between 40 and 60 m on *P. menziesii* and between 30 and 50 m on *T. heterophylla*, where it covers over 25% of substrates. This is the dominant epiphyte in humid old-growth Douglas-fir forests with a biomass of 900–2600 kg ha⁻¹, which is 60–80% of the total lichen biomass (McCune 1994, Neitlich 1993, Pike 1978). A closely related species, *L. pulmonaria*

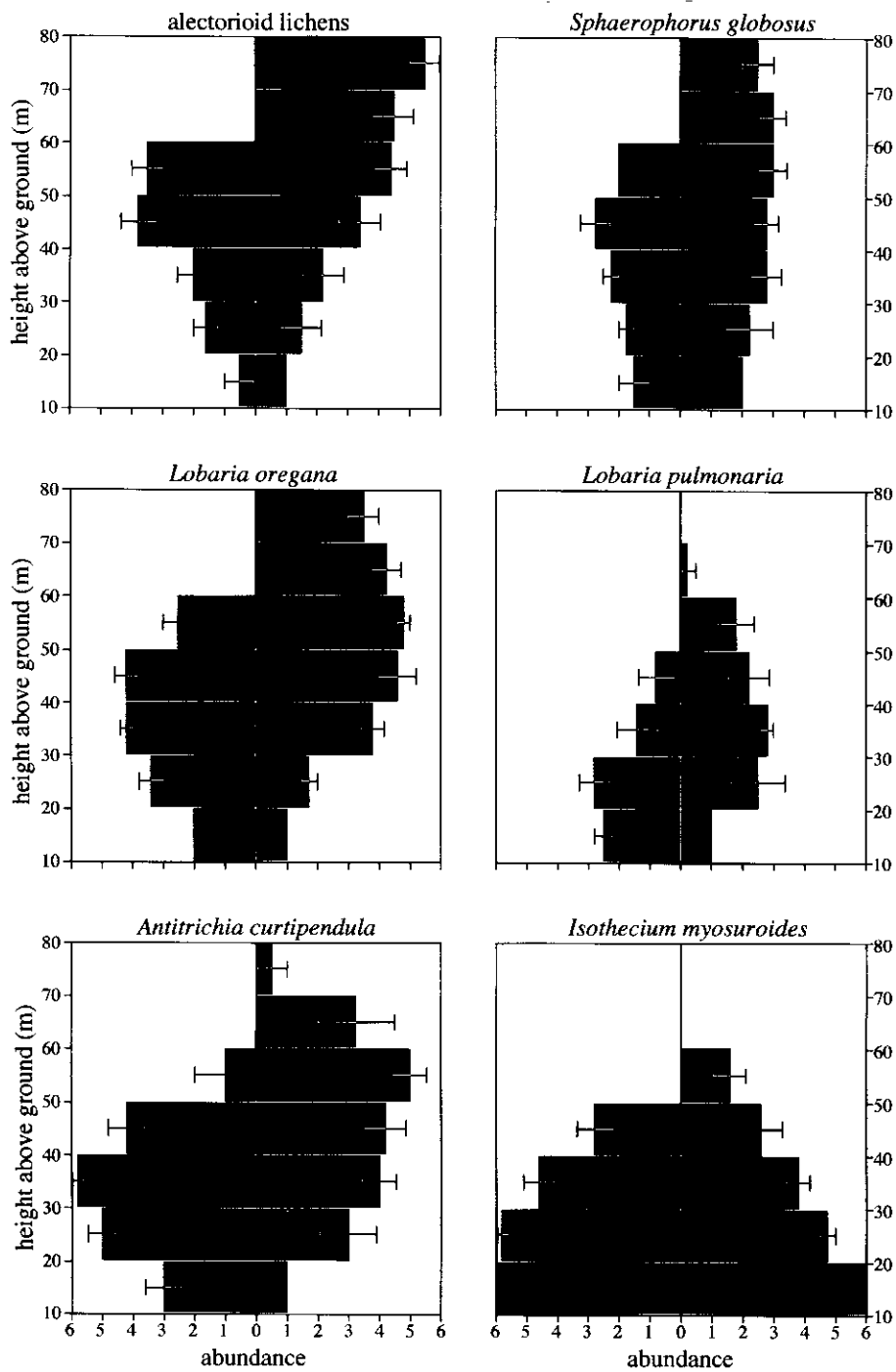


Figure 1. Vertical distribution of six epiphytes in humid old-growth Douglas-fir forests of the central Oregon Cascades. For each epiphyte, the distribution on *Tsuga heterophylla* is shown on the left, and the distribution on *Pseudotsuga menziesii* is shown on the right. Abundance is on a 6-point, logarithmic scale (see Methods). Values are means and standard errors ($n = 5$ trees per tree species). Note that *T. heterophylla* trees were considerably shorter than *P. menziesii* trees (see Table 1 and Figure 2).

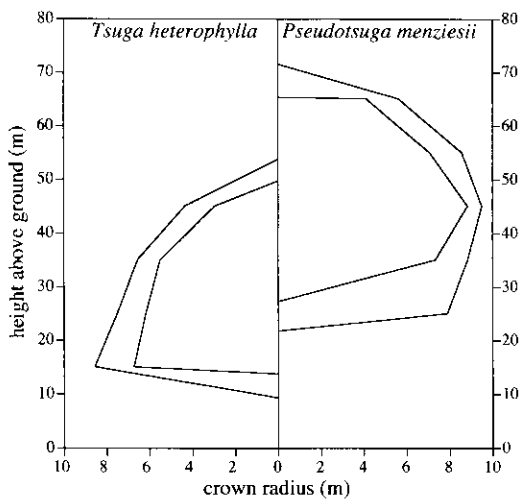


Figure 2. Crown profiles of *Tsuga heterophylla* and *Pseudotsuga menziesii* trees surveyed in this study. Inner and outer boundaries represent one standard error below and above the mean radii of the live crowns ($n = 5$ trees per tree species).

accounts for 3–19% of the total lichen biomass in such forests (McCune 1994, Neitlich 1993, Sillett 1995). It is most abundant between 30 and 40 m on *P. menziesii* and between 10 and 30 m on *T. heterophylla*, where it covers over 10% of substrates. Unlike *L. oregana*, which can tolerate exposed sites in the upper canopy (Sillett 1995), *L. pulmonaria* is virtually absent above 60 m on *P. menziesii* and above 50 m on *T. heterophylla*. The moss *Antitrichia curtipendula* is most abundant between 30 and 60 m on *P. menziesii* and between 20 and 50 m on *T. heterophylla*, where it covers over 25% of substrates. It forms extensive mats up to 10 cm thick on large branches, and individual trees can support up to 7 kg dry weight of this species (Sillett 1995). The moss *Isoetecium myosuroides* is most abundant below 30 m, where it covers 25–50% of substrates on *P. menziesii* and over 50% of substrates on *T. heterophylla*. Unlike *A. curtipendula*, it is sparsely distributed in the upper canopy and absent above 60 m on *P. menziesii* and above 50 m on *T. heterophylla*. We did not record any epiphytes below 10 m because the study trees have no branches below this height (Figure 2). However, *I. myosuroides* is prevalent on the lower branches of smaller *T. heterophylla* trees as well as on understory vegetation (Lyons 1998, Pike et al. 1975).

The vertical distribution of an epiphyte species generally reflects its sensitivity to desiccation and ability to attain positive net photosynthesis at low water contents (Hosokawa et al. 1964, Tobiessen et al. 1977). In tall Douglas-fir trees, some species (e.g., alveoloid lichens and other green algal lichens) prefer exposed sites in the upper, outer crowns, while others (e.g., several cyanolichens and many bryophytes) prefer sheltered sites in the lower, inner crowns (Sillett 1995). Such preferences are probably the result of an interplay between desiccation tolerances and competitive abilities. For example, a desiccation-sensitive moss may not be able to survive in the xeric environment of the upper canopy, while a desiccation-tolerant lichen may not be able to compete with aggressive mat-forming mosses in the mesic environment of the lower canopy. Based on the vertical distributions documented in this study, the epiphytes may be tentatively ranked from highest to lowest desiccation tolerance or from lowest to highest competitive ability as follows: 1) alveoloid lichens, 2) *Sphaerophorus globosus*, 3) *Lobaria oregana*, 4) *Antitrichia curtipendula*, 5) *Lobaria pulmonaria*, and 6) *Isoetecium myosuroides*. Ecophysiological and transplant experiments are needed to test this hypothesis.

The patterns documented in this study should not be considered representative of all old-growth Douglas-fir forests, because there is high landscape-level variability in epiphyte distribution depending on moisture regime (McCune 1993). An intermediate moisture regime favors a canopy epiphyte community with high cyanolichen diversity, whereas forests on the wetter or drier ends of the moisture gradient are more dominated by bryophytes or green algal lichens, respectively. In wet forests, bryophytes can dominate the entire vertical profile. For example, bryophytes are super-abundant in the rain forests of Olympic and Mount Rainier National Parks, Washington (pers. obs.), where mosses normally found on the forest floor also flourish as epiphytes (Sillett and Neitlich 1996). These rain forest canopies are so mossy that epiphytic lichens, including cyanolichens, are much less abundant than in the central Oregon Cascades (Sillett and Goward 1998). In dry forests, vertical ranges of alveoloid and other green algal lichens extend farther down in the canopy (Sillett 1995), while bryophytes and cyanolichens become restricted to the lower canopy

(Goward 1995). Such drier forests support a smaller biomass of bryophytes and cyanolichens, but alectoroid and green algal lichens are abundant (Howe 1978, Sillett unpubl.). Even the old-growth Douglas-fir forest at the Wind River Canopy Crane site in the southern Washington Cascades, which experiences slightly drier summer conditions than the forests in this study, supports relatively few

epiphytic bryophytes and cyanolichens, especially above 30 m (McCune et al. 1997). Old-growth associated cyanolichens, including *L. oregana*, *Pseudocyphellaria rainierensis*, and *Sticta weigelii*, appear to reach their greatest accumulations and widest vertical distributions in the humid Douglas-fir forests of the central Oregon Cascades (pers. obs.).

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