Floristic Survey of Epiphytic Lichens and Bryophytes Growing on Old-Growth Conifers in Western Oregon

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Floristic Survey of Epiphytic Lichens and Bryophytes Growing on Old-Growth Conifers in Western Oregon[1]

Lawrence H. Pike,[2] William C. Denison,[3] Diane M. Tracy,[4]
Martha A. Sherwood[5] and Frederick M. Rhoades[6]

Abstract. *Using direct-aid climbing techniques for sampling trunks and branch systems, we found 74 species of lichens and 32 species of bryophytes growing as epiphytes in a 450-year-old Douglas fir forest in western Oregon. Six epiphyte zones are described: base, moist side of trunk, dry side of trunk, upper trunk, axes of branch systems and branchlets of branch systems. The flora of each zone is compared with that of the rest of the tree and with that found on understory vegetation.*

We employed direct-aid mountain-climbing techniques to climb and sample living trees in a Douglas fir forest in western Oregon. Previous descriptions of Douglas fir epiphytes (Szczawinski, 1953; Coleman, Muenscher & Charles, 1956; Hoffman & Kazmierski, 1969) were based on samples from the lower trunk or felled trees. We relate epiphyte distribution to differences in bark and exposure of major subdivisions of the trunk and canopy.

This paper is based on sampling designed to provide estimates of epiphyte biomass per hectare of forest to be used in ecosystem modeling undertaken by the Western Coniferous Biome, U.S. International Biological Program. Qualitative results only are presented here; our sampling methods are outlined to illustrate intensity of sampling.

Methods

The study area consists of a series of small watersheds in the H. J. Andrews Experimental Forest 75 km east of Eugene, Oregon, in the Cascade Mountain Range. These watersheds

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[2] Department of Biology, George Mason University, Fairfax, Virginia 22030.
[3] Department of Botany, Oregon State University, Corvallis, Oregon 97331.
[4] Department of Biology, University of Alaska, Fairbanks, Alaska 99701.
[5] Department of Plant Pathology, Cornell University, Ithaca, New York 14850.
[6] Department of Biology, University of Oregon, Eugene, Oregon 97403.

have stream outlets at about 450 m and are bounded by ridges of about 650 m elevation. Vegetation consists of old-growth Douglas fir, *Pseudotsuga menziesii* (Mirb.) Franco, with an understory of smaller trees and shrubs. These old-growth Douglas firs are 450–500 years in age (based on annual ring counts); they range from 1–1.5 m in diameter at breast height and from 60–80 m in height.

An old-growth Douglas fir usually consists of one central trunk to which are attached roughly 100 branch systems; each typically includes one or more axes (stems more than 4 cm in diameter) arising from the same area on the trunk. Systems of stems less than 4 cm in diameter together with attached needles are defined as branchlets. Branchlets may arise directly from the trunk or laterally from axes; these may represent the continuation of axes beyond the 4 cm "cutoff" point. Trunk, axis and branchlet epiphytes were sampled separately by the procedures outlined below.

During the initial ascent of the trunk the diameter and inclination of the trunk were measured at 5 m intervals and the location of each branch system was recorded. Rectangular quadrats, 10 × 25 cm, placed at height intervals of 5 m and at locations 45° and 135° around the trunk on either side of the climbing path, were used in estimating epiphyte cover on the trunk. All of the epiphytes, except crustose lichens, were harvested from a subset of these quadrats, then sorted and weighed.

Biomass of epiphytes on branch systems was initially estimated from information gathered by the climbers, relating to surface area (diameter, length of axes, branch system area, etc.) and cover of epiphytes on each branch system (Denison et al., 1972; Pike et al., 1972). A detailed examination of 5 or 6 branch systems chosen by an unequal probability sampling scheme (Hartley, 1966), favoring sampling branch systems with abundant epiphytes and resulting in a sample distributed vertically through the canopy, enabled us to correct these initial estimates. Both living and dead branch systems were eligible for sampling. Within each sample branch system the axes were divided into 0.5 m lengths out to the furthest point where they were still 4 cm in diameter. One cylindrat (a sampling unit including the cylindrical surface of a 1 dm long axis section) was sampled within each 0.5 m length. Thus the surface area included in a cylindrat varied depending on the diameter of the axis. For each cylindrat the noncrustose species were removed, sorted and weighed. Branchlets were described (e.g., diameter measured and total area and epiphyte cover estimated); one-fifth of them were taken to the laboratory where epiphytes were removed and subsamples were examined for microepiphytes.

Eleven large trees ranging in height from 25–80 m and nine smaller, understory trees were climbed. During the summer of 1970 we sampled the trunk epiphytes of two large Douglas firs. In 1971 three more were climbed and one was examined by the procedure outlined above. In 1972 six large trees, four *Pseudotsuga menziesii*, one *Tsuga heterophylla* (Raf.) Sarg. (western hemlock), and one *Pinus lambertiana* Dougl. (sugar pine), were studied. The nine understory trees, *Tsuga heterophylla*, *Taxus brevifolia* Nutt. (western yew) and *Acer circinatum* Pursh (vine maple), were sampled in 1971 and 1972; each was treated as if it were a large branch system.

Access to the canopy of the study trees was provided by techniques modified from direct-aid rock climbing (Denison et al., 1972; Denison, 1973). A climbing rope, hauled up the trunk and secured in position through carabiners attached to hangers, was anchored at its upper end in the crown while the lower end remained free. A belay rope was positioned over a pulley secured near the upper end of the climbing rope. Subsequent ascents were made on the climbing rope using jumars (Swiss climbing aids).

Access to the branch systems for sampling was provided by a laminated beam or "spar," anchored to the tree at one end by a hinge. The spar extended horizontally from the trunk and was anchored at the distal end by lines attached to the trunk several meters above the hinge. The sampler sat in a moveable seat which hung from the spar. Two spars 3 m and 4 m long provided access to most parts of the largest branch systems.

Data used to determine the distribution of epiphytes within the forest came from examination of samples taken during systematic sampling as described above and from additional collections and observations made while climbing the trees for this study, as well as other studies. Voucher specimens of epiphyte taxa are deposited in the herbarium at Oregon State University (OSC).

Results

Within our study area we recognize six zones for epiphytic lichens and bryophytes on the overstory Douglas fir. Each of the following sections describes one of these zones and its conspicuous or characteristic epiphytes; understory epiphytes are included for comparison with those of the overstory. A complete list of epiphytes known from each zone is given in Table 1. Species are grouped in the table according to similarities in their distributions among the zones: 3 species were found only in the basal zone; 12 species were found only on the dry side of the lower trunk; 30 species were widespread, occurring commonly high and low in the canopy and on some part of the trunk; 23 species were found only on horizontal stems in the overstory canopy; 17 species were found mainly on horizontal stems, both in the understory and overstory; and 22 species were found only on understory trees and shrubs.

Branchlet needles and twigs present distinct habitats for microepiphytes (fungi, bacteria and algae); these epiphytes are discussed elsewhere (Bernstein, Howard & Carroll, 1973; Sherwood & Carroll, 1974).

Understory.—The understory extends from ground level to a height of 5–20 m. Host species range in form from shrubs to trees and are a mixture of deciduous angiosperms, *Acer circinatum*, *Acer macrophyllum* Pursh and *Cornus nuttallii* Aud.*ex*T.&G.; evergreen angiosperms, *Rhododendron macrophyllum* G. Don and *Castanopsis chrysophylla* (Dougl.) DC.; and gymnosperms, *Taxus brevifolia*, young *Pseudotsuga menziesii* and *Tsuga heterophylla*. There were few stems more than 10 cm in diameter, and these were often bent or branched close to the ground, so that they had no vertical trunk. Older stems were heavily covered with epiphytes, chiefly bryophytes and foliose lichens. Young twigs appeared nearly bare.

Data on the epiphytic flora for the understory came from the nine understory trees sampled intensively; observations were confirmed and extended by additional collecting on all species of understory trees and shrubs. The composition of the epiphytic flora was influenced more by openness of the overstory canopy than by host species. Open situations, which were common on south-facing slopes, received more illumination and were warmer and drier than closed ones. Here conspicuous epiphytes were cyanophilic, foliose lichens (*Pseudocyphellaria anomala*, *P. anthraspis*, *P. rainierensis*, *Lobaria oregana*, *Nephroma laevigatum* and *N. resupinatum*); whereas under a closed canopy the mosses *Isothecium stoloniferum* and *Neckera douglasii* and the liverwort *Porella navicularis* predominated.

Basal Zone.—The basal zone is small; beginning at the ground it extends up the moist side (see below) of the trunks of large trees a maximum of 3 dm and slants down to the ground on either side, seldom reaching more than three-fourths of the way around the trunk. Bryophytes cover the bark in a nearly continuous layer, and there is direct contact with forest floor communities.

There are a few species of mosses which, as epiphytes, were unique to this basal zone; they were *Dicranoweisia cirrata*, *Aulocomnium androgynum* and a species of *Barbula*. Floristically the community inhabiting this zone was intermediate between communities inhabiting the forest floor and those on the moist side of the lower trunk. The most conspicuous species were mosses such as *Dicranum fuscescens* and *Hypnum circinale*, which were of widespread occurrence on all but the driest parts of the tree. The moss *Stokesiella oregana* invaded from the forest floor and did not occur elsewhere on the trunk.

TABLE 1. Catalog of epiphytes of an old-growth Douglas fir forest (Watershed 10, H. J. Andrews Experimental Forest, Blue River, Oregon). Species are divided into six groups based on similarity of habitats occupied.

		Lower Trunk				Branch Systems		
Species	Form[a]	Base	Dry Side	Moist Side	Upper Trunk	Axes	Branch-lets	Un-der-story
Aulocomnium androgynum (Hedw.) Schwaegr.	M	X						
Barbula sp.	M	X						
Dicranoweisia cirrata (Hedw.) Milde	M	X						
Calicium pusillum Flörke	Lc		X					
Calicium viride Pers.	Lc		X					
Chaenotheca ferruginea Turn.	Lc		X					
Chaenothecopsis sp.	Lc		X					
Coniocybe furfuracea (L.) Ach.	Lc		X					
Cyphelium inquinans (Sm.) Trev.	Lc		X					
Lecanora phaeobola (Stitzenb.) Magn.	Lc		X					
Lecidea friesii Ach.	Lsq		X					
Lecidea scalaris (Ach.) Ach.	Lsq		X					
Alectoria lata Tayl.	Lfr		X					
Alectoria imshaugii Brodo&Hawksw. ined.	Lfr		X					
Letharia columbiana (Nutt.) Thoms.	Lfr		X					
Lecidea tornoensis Nyl.	Lc				X	X	X	X
Lepraria membranacea (Dicks.) Vain.	Lc	X	X	X	X	X		X
Mycoblastus sanguinarius (L.) Norm.	Lc		X		X	X		X
Ochrolechia oregonensis Magn.	Lc		X	X	X	X	X	X
Pertusaria subambigens Dibb. ined.	Lc				X	X	X	X
Cladonia macilenta Hoffm.	Lsq	X	X	X	X	X		X
Cladonia subsquamosa (Nyl.) Vain.	Lsq	X				X		
Parmeliella saubinetii Zahlbr.	Lsq				X	X	X	X
Cetraria idahoensis Essl.	Lfo				X	X		X
Hypogymnia enteromorpha (Ach.) Nyl.	Lfo				X	X	X	X
Hypogymnia imshaugii Krog	Lfo				X	X	X	X
Lobaria oregana (Tuck.) Müll. Arg.	Lfo				X	X	X	X
Nephroma bellum (Spreng.) Tuck.	Lfo				X	X	X	X
Parmeliopsis hyperopta (Ach.) Arn.	Lfo		X	X		X		X
Parmelia pseudosulcata Gyeln.	Lfo		X	X	X	X	X	X
Peltigera aphthosa (L.) Willd.	Lfo				X	X		X
Platismatia glauca (L.) W.Culb.& C.Culb	Lfo		X	X	X	X	X	X
Platismatia herrei (Imsh.) W.Culb. &C.Culb.	Lfo		X	X	X	X	X	X
Platismatia stenophylla (Tuck.) W. Culb.&C.Culb.	Lfo				X	X	X	X

[a] Lc, crustose lichen; Lsq, squamulose lichen; Lfo, foliose lichen; Lfr, fruticose lichen; M, moss; H, liverwort.

TABLE 1. Continued.

		Lower Trunk				Branch Systems		
Species	Form[a]	Base	Dry Side	Moist Side	Upper Trunk	Axes	Branch-lets	Un-der-story
Alectoria glabra Mot.	Lfr				X	X	X	X
Alectoria sarmentosa (Ach.) Ach.	Lfr		X	X	X	X	X	X
Sphaerophorus globosus (Huds.) Vain.	Lfr	X		X	X	X	X	X
Usnea sp.	Lfr				X	X	X	X
Dicranum fuscescens Turn.	M	X	X	X	X	X		X
Dicranum tauricum Sapeh.	M	X		X		X		
Hypnum circinale Hook.	M	X		X	X	X	X	X
Stokesiella oregana (Sull.) Robins.	M	X				X	X	X
Cephaloziella cf. rubella (Nees) Douin	H			X		X		
Diplophyllum taxifolium (Wahlenb.) Dumort	H	X		X		X		
Scapania bolanderi Aust.	H	X		X	X	X	X	X
Bacidia herrei Zahlbr.	Lc					X[b]		
Bacidia naegelii (Hepp) Zahlbr.	Lc					X	X	
Lecidea cinnabarina Somm.	Lc					X	X	
Lecidea cf. erratica Korb.	Lc						X	
Lopadium pezizoideum (Ach.) Körb.	Lc					X	X	
Ochrolechia pallescens (L.) Mass.	Lc						X	
Stenocybe major Nyl.	Lc					X	X	
Cladonia fimbriata (L.) Fr.	Lsq					X		
Normandina pulchella (Borr.) Nyl.	Lsq					X		
Psoroma hypnorum (Vahl) S. Gray	Lsq					X		
Cetraria chlorophylla (Willd.) Vain.	Lfo					X	X	
Cetraria pallidula Tuck.	Lfo						X	
Cetraria platyphylla Tuck.	Lfo					X		
Hypogymnia tubulosa (Schaer.) Hav.	Lfo						X	
Lobaria scrobiculata (Scop.) DC.	Lfo					X		
Nephroma parile (Ach.) Ach.	Lfo					X		
Pseudocyphellaria crocata (L.) Vain.	Lfo					X	X	
Sticta fuliginosa (Dicks.) Ach.	Lfo					X		
Sticta weigelii (Ach.) Vain.	Lfo					X		
Alectoria fremontii Tuck.	Lfr						X	
Alectoria oregana Tuck.	Lfr					X	X	
Bryum capillare Hedw.	M					X		
Isothecium cristatum (Hampe) Robins.	M					X		
Buellia penichra (Tuck.) Hasse	Lc					X	X	X
Ochrolechia androgyna (Hoffm.) Arn.	Lc					X		X
Cetraria orbata (Nyl.) Fink	Lfo					X		X
Hypogymnia inactiva (Krog) Ohlsson	Lfo						X	X
Hypogymnia physodes (L.) Nyl.	Lfo					X	X	X
Lobaria pulmonaria (L.) Hoffm.	Lfo					X		X
Pseudocyphellaria anomala Magn.	Lfo					X	X	X

[a] Lc, crustose lichen; Lsq, squamulose lichen; Lfo, foliose lichen; Lfr, fruticose lichen; M, moss; H, liverwort.

[b] Occurs only on decorticated wood.

TABLE 1. Continued.

Species	Form[a]	Lower Trunk Base	Lower Trunk Dry side	Lower Trunk Moist side	Upper Trunk	Branch Systems Axes	Branch Systems Branch-lets	Branch Systems Un-der-story
Pseudocyphellaria anthraspis (Ach.) Magn.	Lfo					X	X	X
Antitrichia californica Lesq.	M					X		X
Antitrichia curtipendula (Hedw.) Brid.	M					X		X
Isothecium stoloniferum Brid.	M					X		X
Neckera douglasii Hook.	M					X		X
Orthotrichum consimile Mitt.	M					X	X	X
Frullania nisquallensis Sull.	H					X	X	X
Porella navicularis (Lehm.& Lindenb.) Lindb.	H					X	X	X
Radula bolanderi Gottsche	H					X	X	X
Polypodium glycyrrhiza D.C.Eaton	Fern					X		X
Lecidea berengeriana (Mass.) Nyl.	Lc							X
Rinodina archaea (Ach.) Arn.	Lc							X
Leptogium palmatum (Huds.) Mont.	Lfo							X
Leptogium sinuatum (Huds.) Mass.	Lfo							X
Nephroma helveticum Ach.	Lfo							X
Nephroma laevigatum Ach.	Lfo							X
Nephroma resupinatum (L.) Ach.	Lfo							X
Peltigera canina (L.) Willd.	Lfo							X
Peltigera collina (Ach.) Ach.	Lfo							X
Pseudocyphellaria rainierensis Imsh.	Lfo							X
Claopodium bolanderi Best	M							X
Dendroalsia abietina (Hook.) Britt.	M							X
Dicranum howellii Ren.&Card.	M							X
Homalothecium fulgescens (C. Muell.) Lawt.	M							X
Homalothecium nuttallii (Wils.) Jaeg.&Sauerb.	M							X
Hylocomium splendens (Hedw.) B.S.G.	M							X
Hypnum subimponens Lesq.	M							X
Leucolepis menziesii (Hook.) L.Koch	M							X
Metaneckera menziesii (Drumm.) Steere	M							X
Plagiomnium venustum (Mitt.) Koponen	M							X
Rhytidiadelphus triquetrus (Hedw.) Warnst.	M							X
Frullania bolanderi Aust.	H							X

[a] Lc, crustose lichen; Lsq, squamulose lichen; Lfo, foliose lichen; Lfr, fruticose lichen; M, moss; H, liverwort.

Lower Trunk.—The lower trunk extends to a height of 40–60 m, depending upon the density of the canopy and the height of the tree. The bottom 20–30 m is devoid of branch systems; branch systems in the upper 20–30 m of the lower trunk are often large and may be several meters apart.

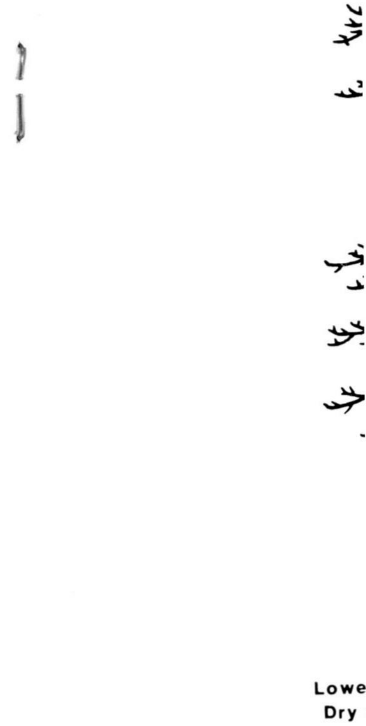

FIGURE 1. Dia
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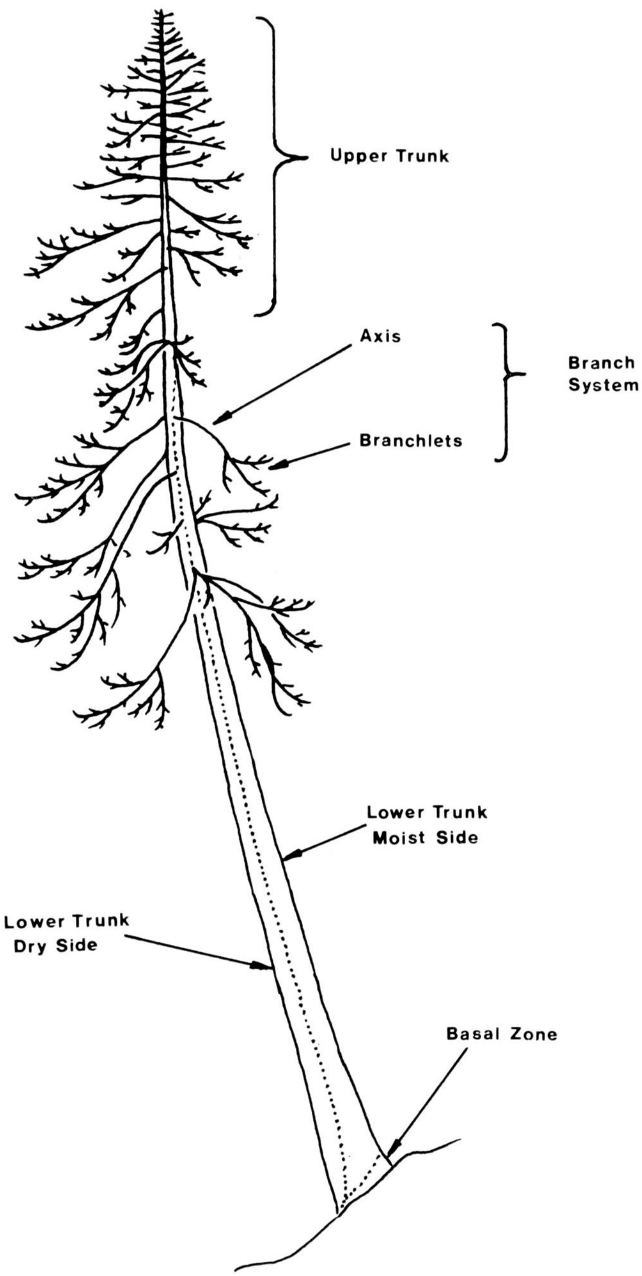
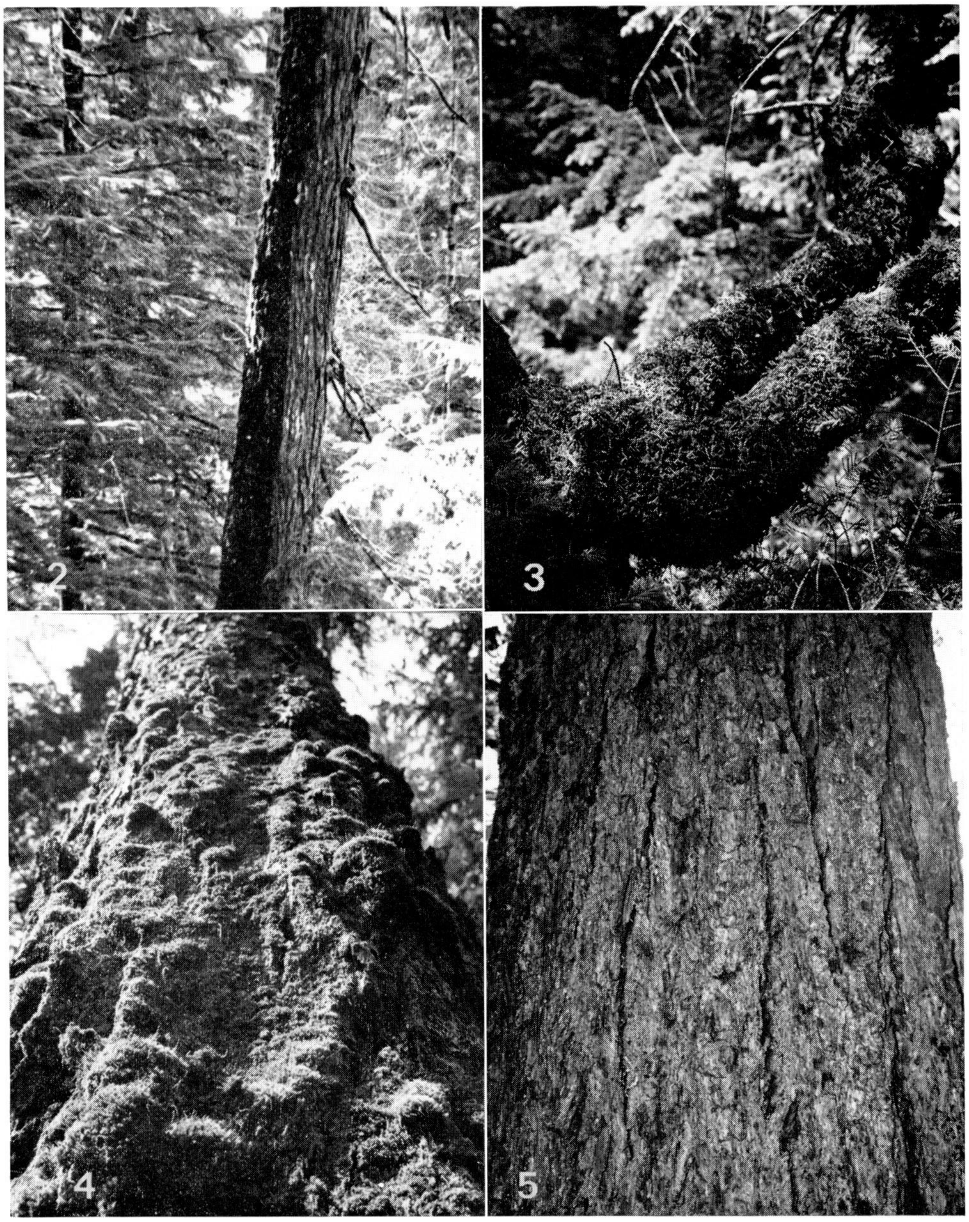


FIGURE 1. Diagram of old-growth Douglas fir, showing position and extent of major zones. Not drawn to scale.



FIGURES 2–5. Old-growth Douglas fir, H. J. Andrews Experimental Forest, Blue River, Oregon. — 2. Lower trunk showing sharp distinction between moist and dry sides. Tree is on a north-facing slope and leans toward the north, which is to the right in the picture. — 3. View of two axes in the canopy showing mosses and accumulation of trapped needles. — 4. Moist side of the lower trunk as viewed from the ground. — 5. Dry side of lower trunk of the same tree shown in Figure 4.

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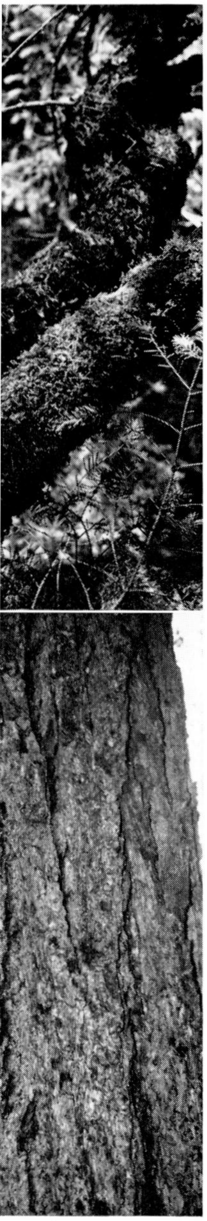

Forest, Blue River,
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side of lower trunk

Few trunks are perfectly vertical. The upper side of the trunk receives most of the limited moisture which falls through the canopy or runs down the trunk; thus the lower trunk is often sharply divided between a moist side and a dry side, which we distinguished as separate zones (Fig. 1–2).

Moist Side.—The moist side of the lower trunk is roughly triangular. It is broadest near the ground, where it extends roughly two-thirds of the way around the trunk immediately above the basal zone, and decreases in width as it extends upward until it is a narrow strip on the upper side of the trunk.

Bryophytes covered most of the bark in the lower part of this zone (Fig. 4) and were found as scattered clumps in the middle and upper parts. The common bryophytes were *Scapania bolanderi*, *Hypnum circinale* and *Dicranum fuscescens*.

Bark on the moist side was 3–6 cm thick. Outer layers were soft and sloughed off easily under climbing boots or other abrasion. Sometimes the bark had a plate-like structure, but more commonly it had ridges 5–8 cm wide running up the trunk, with fissures between the ridges 1–5 cm wide and 1–3 cm deep. These ridges (often several meters long) curved and anastomosed.

Sphaerophorus globosus was the most conspicuous lichen on the moist side. *Lepraria membranacea* occurred as whitish patches on bark and clumps of moss. *Cladonia* squamules, mostly sterile, were commonly encountered on both the moist side and the dry side of the lower trunk.

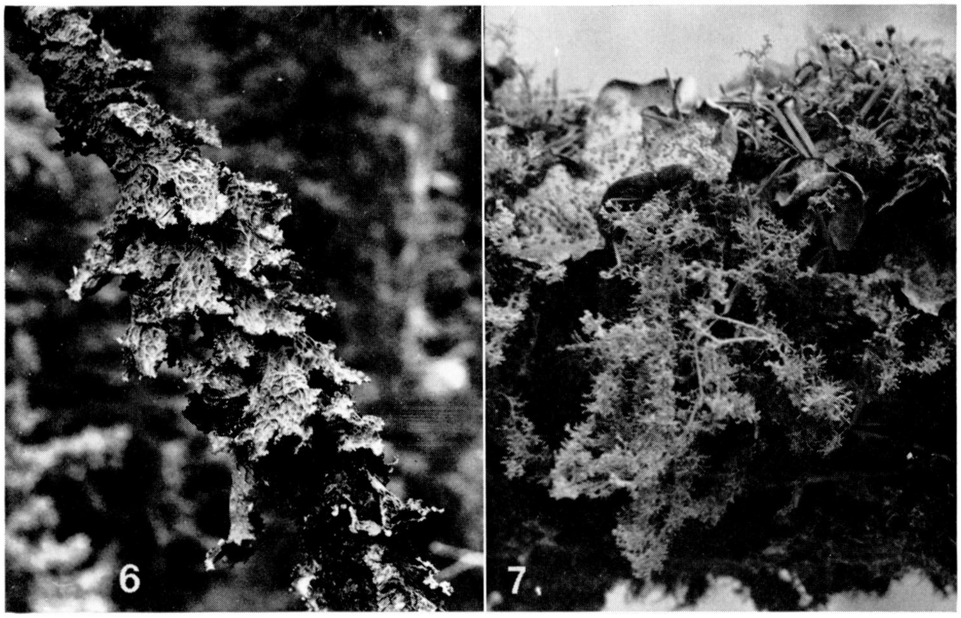
Dry Side.—The dry side is relatively narrow at ground level, but near the top of the lower trunk it encircles most of the trunk. Bark on the dry side was harder and less easily dislodged than on the moist side; vertical fissures were as much as 20 cm deep.

Much of the dry side appeared bare (Fig. 5). Crustose and squamulose lichens were the predominant epiphytes. Mosses and large foliose or fruticose lichens occurred primarily where surface irregularities at the bases of branch systems or stubs created conditions resembling those on the moist side. *Cladonia macilenta*, *Ochrolechia oregonensis* and *Lepraria membranacea* were common. Members of the order Caliciales were characteristic of this zone. These included: *Coniocybe furfuracea* (near the base of the tree), *Chaenotheca ferruginea*, *Cyphelium inquinans*, *Calicium viride* and *Calicium pusillum*. *Lecanora phaeobola*, *Lecidea friesii* and *Lecidea scalaris* were also characteristic of the dry side. Three fruticose lichens, *Alectoria imshaugii*, *A. lata* and *Letharia columbiana*, occurred in narrow, vertical transition zones between the moist and dry sides.

Upper Trunk.—The upper trunk includes 10–20 m of trunk between the lower trunk and the region where the trunk becomes only a few centimeters in diameter. Above that region the epiphytes on the trunk were essentially the same as on the branch systems.

Orientation of the upper trunk was often more nearly vertical than that of the lower trunk. Individual branch systems arising from the upper trunk were smaller, more closely spaced and more evenly distributed around the trunk than those below. Whereas branch systems originating on the lower trunk generally sloped downward, those on the upper trunk usually slanted upward or were horizontal. Bark on the upper trunk was relatively stable and not easily dislodged; bark thickness and depth of fissures were both about 1–2 cm.

Light intensities were higher at the surface of the upper trunk than on the lower trunk, and temperatures presumably were more extreme. Wind penetrated



FIGURES 6–7. Lichens on axes in the canopy. — 6. Large thalli of *Lobaria oregana*. — 7. *Peltigera aphthosa* and *Sphaerophorus globosus*.

the canopy in this zone, resulting in accelerated drying, wind erosion of epiphytes and lateral sway of the trunk. Whereas precipitation reached the lower trunk only after falling through the canopy or running down the trunk, wind-driven precipitation struck the upper trunk directly. Both light and humidity were more evenly distributed around the trunk than they were below; consequently the epiphyte communities were not sharply divided between a moist and a dry side.

Mosses occurred mainly at the base of branch systems. *Dicranum fuscescens* and *Hypnum circinale* were the common species.

Foliose and fruticose lichens were much more conspicuous on the upper trunk than on the lower trunk. There were more species covering a greater proportion of the trunk surface and individual thalli were larger. *Alectoria sarmentosa*, *Platismatia glauca*, *Hypogymnia enteromorpha*, *Sphaerophorus globosus*, and *Lobaria oregana* were the most abundant species. Crustose lichens, especially *Mycoblastus sanguinarius* and *Ochrolechia oregonensis*, were an important element of the epiphyte cover.

Branch Systems.—On old-growth Douglas fir, branch systems are easily distinguished from the main trunk: stems are smaller in diameter (rarely more than 15 cm) and are nearly horizontal. Branch systems vary in length, but seldom extend more than 5 m from the trunk. An axis will occasionally change its growth pattern and grow upward, paralleling the trunk; its epiphytic flora then resembles that of the lower trunk or that of the upper trunk, depending on the age of the branch system and its position within the canopy.

Older branch systems bore evidence of repeated damage presumably due to wind or ice. Younger axes arising from the stubs of older broken ones frequently formed a fan-shaped array surrounding the stub.

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Axes.—The bark on axes (stems > 4 cm diameter) varied in thickness from 5–15 mm; it was rough, with irregularly-shaped scales; it was relatively soft and absorbent; and it flaked and crumbled easily.

As with the trunk, the upper side of an axis is moist when there is water available; the under side is drier. Precipitation reaches the upper side directly or via through-fall; the under side receives relatively little moisture from either of these sources. In the winter axes catch and hold snow on their upper sides.

The upper sides of axes had the richest epiphyte flora found on the trees, both in numbers of species and in amount of epiphyte biomass per unit of tree surface area. The most conspicuous species were foliose lichens; *Lobaria oregana*, in particular, formed large lettuce-like wads 20 cm or more across (Fig. 6). *Platismatia glauca*, *P. herrei*, *Hypogymnia enteromorpha* and *H. imshaugii* were also common. *Lobaria pulmonaria*, *L. scrobiculata*, *Peltigera aphthosa* and *Pseudocyphellaria crocata* were found on the upper sides of axes and rarely, if ever, elsewhere on the trees. The most conspicuous fruticose species was *Sphaerophorus globosus*. Common crustose species included: *Mycoblastus sanguinarius*, *Parmeliella saubinetii*, *Ochrolechia oregonensis* and *Pertusaria subambigens*.

Mosses, especially *Dicranum fuscescens*, formed thick mats on the upper sides of axes within 1–2 m of the trunk (Fig. 3). Further away from the trunk *Hypnum circinale* was the most abundant moss. *Antitrichia californica* and *A. curtipendula* were occasionally found on axes but nowhere else on the trees.

The dry under sides of axes were dominated by the liverworts *Radula bolanderi*, *Porella navicularis*, *Diplophyllum taxifolium* and *Frullania nisquallensis*. Liverworts were minor elements of the epiphyte flora elsewhere on the large trees. *Lepraria membranacea* was the only lichen commonly found on the under sides of axes.

Branchlets.—As we define them, branchlets are systems of stems less than 4 cm in diameter at the base. Since living branchlets have needles attached, we use the term twig to refer to the stems of branchlets only. Branchlets varied up to 4 m in length: the proximal end might be 50 years old or more; the distal end of a living branchlet was bounded by the current year's growth and the terminal buds. Douglas fir twigs on our study site retained most of their needles for about eight years. The bark of twigs was smooth and firm, compared with that of the trunk and axes, and had a thickness from 1–4 mm.

Since branchlets are at the edge of a tree's canopy, these receive higher levels of light than most of the remaining surface of the tree. Rainfall strikes foliage and twigs directly, and these receive additional water which drips from higher branch systems. Because of the exposure, and the low water-holding-capacity of the bark, twigs dry out quickly after a rainfall. Twigs can, however, hold a considerable load of snow during and after a wet snowfall.

A well-defined successional sequence of epiphytes was evident on branchlets where stems less than 2 cm in diameter (about the last 20 years of growth) could be aged easily by observing terminal bud scars and branching pattern. Fruticose lichens (which fall from above and become lodged in the foliage) and small, sterile, crustose lichens were apparent before the tenth year. An inconspicuous *Lecidea* (tentatively identified as *L. erratica*) was particularly prevalent on very young twigs. Older needles may also support a substantial cover of sterile crustose lichens. Cover of such crustose lichens as *Bacidia naegelii*, *Pertusaria subambigens*, *Lecidea tornoensis*, *Ochrolechia oregonensis* and *Lecidea cinnabarina* increased rapidly on twigs after their needles had been shed, and in the upper canopy might reach 60% by the fifteenth year. In the lower canopy, succession appeared to be slower.

Fruticose lichens were more evident on branchlets than elsewhere. Included were *Alectoria sarmentosa*, *A. oregana*, *A. glabra*, *Sphaerophorus globosus* and *Usnea* sp. On older twigs young thalli were found of those foliose lichens which mature on axes, including *Lobaria oregana*, *Platismatia glauca*, *P. stenophylla*, *Hypogymnia enteromorpha*, *H. imshaugii* and *Pseudocyphellaria anomala*. Thalli of *Lobaria oregana* on twigs were commonly much larger than would be expected from the age of the substrate; these represented parts of thalli which fell from above in the canopy, became lodged and subsequently became attached and continued growing.

Only one moss, *Orthotrichum consimile*, was found regularly on branchlets. Three liverworts, *Frullania nisquallensis*, *Porella navicularis* and *Radula bolanderi*, were widespread but inconspicuous.

Discussion

Our sampling provided detailed information on the entire surface of 20 trees in a single area. Previous investigators of Douglas fir epiphytes (Szczawinski, 1953; Coleman et al., 1956; Hoffman & Kazmierski, 1969) examined more trees which were distributed over several sites but were limited by the inaccessibility of the canopy to examination of the lower trunk and samples taken from felled trees. Initially we employed a professional logger to cut three large trees, but found that the epiphytes were dislodged and the branch systems fragmented when the trees hit the ground. We decided instead to climb living trees.

Our methods were designed primarily to yield crude biomass estimates rather than community structure or floristic information. Bryophytes and foliose and fruticose lichens were removed and weighed, but crustose lichens were not. Thus we have quantitative data for some, but not all species. The crustose species included in our list (Table 1) were either collected independently or were sorted out from biomass samples while cleaning them for weighing. Although in some instances we recorded epiphyte cover, our categories were usually broader than species (e.g., all mosses) so that we do not have data which can be used to analyse intracommunity structure.

One consequence of the difference in our methodology is that we find it hard to make direct comparisons between our results and those of others. The authors cited above compared epiphyte associations with vascular plant associations on several different stands. On the other hand, we compared the epiphytes found on different parts of individual trees, viewing the surface of the tree itself as a landscape with local variations in topography, climate and vegetation.

For our study area, in small watersheds, the direction in which a tree leans was more important than compass direction in determining the horizontal distribution of epiphytes around a trunk. The side of the lower trunk having an abundance of mosses was not necessarily the north side. On south-facing slopes trees leaned toward the south and mosses grew on the north ("upper") side; but on north-facing slopes, where trees leaned toward the north, mosses grew on the south side. Regardless of the compass direction, the uphill side of the trunk received more moisture and, consequently, supported more mosses.

The boundaries of the zones recognized in this paper were affected by our sampling scheme. For example, although we discuss the difference between epiphytes of stems larger and smaller than 4 cm in diameter, there was no sharp distinction between

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these assemblages. This size was simply a convenient cutoff point between axes and branchlets for our sampling. On the other hand there was probably as sharp a difference between the epiphytes on the upper and lower sides of axes as there was between those on the moist and dry sides of the trunk, but our sampling did not enable us to describe this difference.

The division of the lower trunk into a moist side and a dry side was striking (Fig. 2), but the distribution of epiphytes around the trunk was probably more complex. Several species (e.g., *Alectoria imshaugii*) were most abundant near the line of transition between the dry and moist sides. Also, large branch system stubs caused local variations in surface moisture and were accompanied by islands of epiphytes which differed from those in the immediate vicinity.

The most striking vertical transition in epiphytes was from lower trunk to upper trunk. This occurred high in the canopy, above the lower branch systems and at roughly the point above which the branch systems occurred at regular intervals of a meter or less. The upper trunk had more species of epiphytes than either the dry or moist side of the lower trunk; there was a greater biomass of lichens per unit of bark (commonly > 100 g/m^2) than was found elsewhere on the trunk (where lichen biomass seldom exceeded 50 g/m^2); and there were fewer differences in the epiphyte associations around the trunk.

Our data, in general, supports Szczawinski's hypothesis (1953) that the epiphytes observed on trunks of trees in xeric sites were displaced upward on trunks in more mesic sites. We found, for example, that *Alectoria sarmentosa*, which Szczawinski found characteristic of the "driest corticolous community in the Douglas-fir forest . . .," occurred in abundance on trunks of exposed trees on south-facing slopes or on ridges and was rare on the lower trunk of trees in the mesic sites near the bottom of the watershed. In contrast, *Dicranum fuscescens* was abundant on trunks and branches of trees low in the watershed but was rare on the very exposed trees.

The mass of epiphytes borne by the upper branches was not apparent from the ground. The studies previously cited give little information about this important component of the epiphytic vegetation. On one large Douglas fir (number 286 on a watershed-level stem map, cf. Hawk, 1974; diameter at 1 m = 145 cm, height = 77 m), for example, we estimated that the oven-dry weight of epiphytes on branchlets and axes was 10.9 and 7.5 kg, respectively. This compares with estimates of 3.7 kg of trunk epiphytes and 190 kg of needles on the same tree (Pike & Denison, unpublished data). Several of these lichens, including *Lobaria oregana* which was the most abundant species, fix atmospheric nitrogen. It is probable that lichens growing on branch systems are of importance to the nitrogen economy of the forest as a whole (Pike et al., 1972; Denison, 1973).

Some of the lichens found on the larger axes, e.g., *Peltigera aphthosa* (Fig. 7) and *Psoroma hypnorum*, were species usually found on moss-covered soil or rocks in western Oregon. Most of the branches were nearly horizontal or sloped at angles less than 45°; humus accumulated from weathering bark and decomposing needles trapped by the epiphytes, resulted in the development of a soil-like organic layer on the upper sides of axes. This layer supported growth of species normally found on the ground.

The biomass of twigs on old-growth conifers is small relative to the biomass of axes and trunk, but the surface area is large. For example on tree 286 we estimated that the biomass of trunk, axes and twigs was 27,000, 1500 and 600 kg, respectively;

whereas the respective surface areas were 225, 180 and 410 m^2. In making these surface area computations, stem sections were treated as cylinders with smooth surfaces; we realize that the actual surface area that is available for colonization by epiphytes is somewhat greater than the figures we present, particularly on the trunk where there were deep fissures. Nevertheless, since the quantity of epiphytes on a given tree is related to surface area, it is not surprising that a significant proportion of the epiphytes is found on branchlets.

We have not attempted to separate crustose lichens from bark and to estimate biomass. Since crustose lichens were abundant on young twigs and therefore covered a substantial surface area, this omission may be significant. Even without crustose lichens, the epiphyte biomass, up to 22 kg per tree, is impressive. Unlike tree biomass, most of which is relatively inert wood, all of the epiphyte biomass is physiologically active when wet. Thus in evaluating the ecological contribution of epiphytes it is more realistic to compare their biomass with that of foliage, or of foliage and fine roots, than it is to compare their biomass with the total biomass of the host tree. We found that, in general, epiphyte biomass ranges between 10–20% of that of the foliage of the host tree, suggesting that epiphytes have a significant influence in the functioning of the forest as a whole.

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