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Epiphyte Communities on Sitka Spruce in an Old-Growth Redwood Forest

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Abstract. *Using rope techniques for access, we surveyed epiphytes on five Sitka spruce trees up to 92 m tall in an old-growth redwood forest. We quantified epiphyte diversity by sampling 5% of each tree's surface area of axes (branches >5 cm diameter) and branchlets (branches <5 cm diameter, including foliage). Epiphyte communities included 57 macrolichen, 15 crustose lichen, 17 bryophyte, and two fern species. The five most abundant species—Isothecium myosuroides, Polypodium scolieri, Polypodium glycyrrhiza, Lobaria pulmonaria, and Frullania nisqualensis—contributed 42.1, 13.3, 8.4, 6.7, and 4.7% of the total epiphyte biomass, respectively. There was an average of 36.2 kg of bryophytes, 9.9 kg of lichens, 12.7 kg of ferns, and 131 kg of associated dead organic matter per tree. Axes supported 83% of the biomass and 98% of the dead organic matter. At the whole-tree level, bryophyte biomass was 11.3 times higher and lichen biomass was 2.5 times lower on axes than branchlets. Ferns were restricted to axes. Ordination analysis revealed one dominant gradient in epiphyte composition that was positively correlated with height and lichen diversity, and negatively correlated with bryophyte diversity. Chlorolichens dominated the exposed portion of the gradient with equivalent amounts of cyanolichens and bryophytes. Mosses dominated the intermediate portion of the gradient with equivalent amounts of liverworts, cyanolichens, and chlorolichens. There was very little lichen cover in the sheltered portion of the gradient, which was dominated by bryophytes. Extensive bryophyte mats with large quantities of dead organic matter promote biological diversity on Sitka spruce in redwood forest canopies by storing water and serving as habitats for desiccation-sensitive organisms.*

The west coast of North America is home to some of the world's tallest and most massive forests, including at least 20 conifer species exceeding 60 m in height (Van Pelt 2001). The vast majority of temperate rain forests that once extended from Alaska to California have now been logged, and a great deal of research has focused upon the few remaining old-growth forests. These studies have consistently revealed a high biomass and diversity of canopy epiphytes, including lichens, bryophytes, and even vascular plants. Epiphyte communities in forests dominated by Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco] have received a disproportionate amount of scientific attention, including floristic surveys of Douglas-fir (Clement & Shaw 1999; McCune 1993; McCune et al. 2000; Pike et al. 1975, 1977; Sillett 1995), western hemlock

[*Tsuga heterophylla* (Raf.) Sarg.; Lyons et al. 2000; Sillett & Rambo 2000], and understory vine maple (*Acer circinatum* Pursh; Ruchty et al. 2001). Epiphyte communities in temperate rain forests dominated by other conifers have scarcely been investigated, except for studies of lower trunks (e.g., Glimme & Hong 2002).

The tallest temperate rain forests contain coast redwood [*Sequoia sempervirens* (D. Don) Endl.], and so far only their vascular epiphyte communities have been surveyed (Sillett 1999). The high shade tolerance of redwood excludes most other trees from these forests, but a few species do co-exist. Sitka spruce [*Picea sitchensis* (Bong.) Carr.] trees, which grow along the alluvial terraces of some redwood forests, appear from the ground to support a greater abundance of lichens and bryophytes than

adjacent redwoods. Indeed, the diversity of Sitka spruce epiphyte communities may rival those of Douglas-fir forests in Oregon and Washington.

Our objective in this study was to quantify the biomass and diversity of epiphytic lichens and bryophytes on Sitka spruce trees in an old-growth redwood forest. We used a sampling design that facilitated comparisons of our results with previous epiphyte studies in Douglas-fir forests. This study thus provides important baseline information on epiphyte communities in redwood rain forest canopies.

STUDY AREA

Five tall Sitka spruce trees were selected for detailed study. The trees were distributed along the James Irvine Trail in Prairie Creek Redwoods State Park, Humboldt County, California. All trees were located along the alluvial terraces of Godwood Creek between 2.5 and 4.5 km from the Pacific Ocean. The basal area of this riparian forest exceeds 400 m²/ha, of which 76% is redwood, 20% is Sitka spruce, 3% is western hemlock, and 1% is Port Orford cedar [*Chamaecyparis lawsoniana* (A. Murr.) Parl.]. Sword fern [*Polystichum munitum* (Kaulf.) C. Presl.] dominates the ground cover and is interspersed with huckleberry (*Vaccinium ovatum* Pursh and *V. parvifolium* Smith), salal (*Gaultheria shallon* Pursh), cascara (*Rhamnus purshiana* DC.), and an assortment of herbs and bryophytes. Mean annual rainfall is 168 cm, and temperatures range from 4 to 24 C in summer and 0 to 13 C in winter (Redwood National and State Parks: <http://parks.ca.gov/north/ncrd/pcrsp.htm>).

METHODS

Tree access.—We initially accessed tall tree crowns by shooting rubber-tipped arrows trailing Fireline® filament over sturdy branches between 70 and 80 m high in the crowns. Nylon cord was attached to the arrow end of the filament, hauled over the branches, and then used to haul a 10 mm static kernmantle rope into position. One end of the rope was anchored at ground level, leaving the other end of the rope free for ascent via single rope technique. A pulley was installed near the top of the tree, and nylon cord was left in the tree between research days to maintain the climbing path.

Movement within the crown was facilitated by the use of an arborist-style, split-tail lanyard system. The lanyard utilized two adjustable loops of rope fastened to the climber's harness that can be used simultaneously or individually to allow the climber to ascend, descend, or traverse among the branches. Each rope loop was adjustable by means of a friction hitch connected to a cambium saver wrapped around a sturdy overhead branch (Jepson 2000). The friction hitch allowed the climber to move up or down via shortening or lengthening the rope loop, and the cambium saver minimized the impact of moving rope on delicate epiphytes and other organisms.

Outer crown access.—In the absence of a canopy crane (e.g., McCune et al. 2000), access to the outer and uppermost portions of tall tree crowns is usually quite limited because thin branches cannot support a climber's weight. We developed a safe and nondestructive rope technique to minimize these restrictions. Two 120 m ropes were fixed near the top of the tree at their midpoints. Each of the 60 m long ends was then threaded through sequen-

tial, vertically aligned Y-shaped branch forks spaced farther out and down in the crown from the central trunk until the rope was supported near the crown edge. Additionally, each rope was spaced by azimuth so that there was a rope on the outer crown in each cardinal direction. These four ropes provided a much-needed fulcrum to safely access epiphytes far from the main trunk near the tips of branches.

We snagged these ropes up to 8 m away with miniature grapnel hooks attached to fly-fishing line loaded on automatic rewind reels mounted to our climbing harnesses. The spring-loaded reel minimized tangling and permitted quick retrieval and storage of the grapnel and line. Once the outer crown rope was pulled in to the climber, an ascending device was attached to the rope from the climber's harness. By lengthening a lanyard loop already anchored to an overhead branch, the climber's weight was transferred to the outer crown rope, allowing safe non-destructive lateral movement. Despite these advancements in access, some of the upper- and outermost twigs remained inaccessible unless destructive sampling was employed.

Tree mapping.—We mapped each tree to establish random plot locations and to quantify branch lengths and foliar masses. A fiberglass tape was stretched from ground level to the treetop. Main trunk diameters were measured at ground level, breast height (1.37 m), and 5 m height intervals. We measured the following variables on each branch: height of origin, basal diameter, total horizontal extension from trunk, and cumulative length of branch segments >5 cm diameter. Branches were individually sketched, and all segments >5 cm diameter were numbered sequentially. We then visually estimated lengths of each segment to the nearest 0.5 m. These data allowed us to estimate total lengths of branch segments >5 cm diameter on each tree.

In a mature tree, foliar units are discrete, repeating clusters of leaves that can be counted to quantify foliage on individual branches. Each tree species has recognizable patterns of branch growth and development (Hallé et al. 1978). The foliar units of Sitka spruce are clusters of twigs and leaves supported by branch segments of approximately one cm basal diameter. Counting foliar units on each branch allowed us to estimate the foliar mass of an entire tree.

We randomly selected approximately 5% of each tree's total branch length and foliar units for epiphyte sampling. About one-fifth of these plots were randomly selected for destructive sampling (Table 1). The tree mapping dataset ensured that all branch surfaces on each tree had an equal probability of being selected for sampling.

Epiphyte sampling.—This study focused on branch-dwelling epiphytes. Trunks were not sampled. Epiphyte sampling occurred on two substrate types: *axes* (i.e., branches >5 cm diameter) and *branchlets* (i.e., *branches* <5 cm diameter, including foliage). We measured % cover of epiphytes on axes via the spiral transect method (Sillett 1995). Axis plots occupied 0.5 m of branch length and consisted of five wraps of a metric diameter-tape spaced 10 cm apart. Percent cover of epiphytes was estimated by recording the presence of species beneath tick marks on the tape that are π -cm apart (Fig. 1). We used the diameter side of the tape for point intercept sampling to allow for a more reasonable number of tick marks than centimeter spacing would allow. Each time a species was found beneath a tick mark, we recorded a hit for that species. Cover for each species in a plot was calculated as the number of hits divided by the total number of possible hits in the plot (i.e., transect length in cm divided by π). We mea-

TABLE 1. Summary of tree size and epiphyte sampling intensities on axes and branchlets for five Sitka spruce trees in an old-growth redwood forest. Sampling intensities are expressed as percent of tree totals. Numbers in parentheses are sampling intensities for removed samples only. DBH is diameter of main trunk at breast height (1.37 m).

Tree	Height (m)	DBH (m)	Trunk volume (m ³)	Axis length (m)	Foliar mass (kg)	Sampling intensity	
						Axes	Branchlets
1	89.5	1.9	80	449	79	5.8 (1.6)	6.5 (2.0)
2	87.2	2.0	75	337	98	5.0 (0.9)	4.8 (0.9)
3	82.5	2.4	101	367	101	6.0 (1.0)	4.8 (1.3)
4	92.2	2.6	153	652	212	5.8 (1.0)	5.1 (1.1)
5	87.0	2.0	83	424	147	5.8 (1.1)	6.0 (1.4)

sured the following additional variables in each axis plot: height above ground, distance from center of trunk to plot, and % sky. Percent sky was a visual estimate of canopy openness above each plot.

We estimated % cover of epiphytes on branchlets within 0.5 by 0.5 m quadrats. Approximately three foliar units fit in a single quadrat (mean = 3.2, standard error = 0.1). The cover of each epiphyte species within a quadrat was visually estimated to the nearest percent. We measured the following additional variables for each quadrat: height above ground, distance from trunk to plot, and % sky.

All epiphytes were removed from approximately one-fifth of the plots and placed in paper bags. For axis plots, we used a pruning saw to carefully cut through thick bryophyte mats and minimize the impact of collecting on epiphytes outside plot boundaries. The bark and cambium were not disturbed. For branchlet plots, we used pruning clippers and a saw to remove tree components and their epiphytes. All destructive samples were transported to the laboratory for processing.

In the laboratory, we sorted samples by epiphyte species. We also separated dead organic matter and tree foliage from epiphytes. Sorted samples were individually placed in paper bags, oven dried for 24 hours at 60 C, and weighed to the nearest 0.001 g.

Whole-tree masses of epiphytes, dead organic matter, and tree foliage were calculated by dividing total masses of samples removed from a tree by the sampling intensity (i.e., approximately 0.01) for that tree. Masses were determined separately for axes and branchlets. Mass estimates for the fern *Polypodium scolieri* were obtained from Sillett and Bailey (2003).

Identifying many chlorolichens in the field to species was challenging, because some species required chemical testing for confirmation, while others had subtle morphological distinctions that were best viewed under a microscope. The genus *Usnea* was particularly challenging. *Us-*

nea rubicunda, *longissima*, and *ceratina* were easy to identify, but other species were partitioned into the *Usnea cornuta* group that has tufted thalli, and the *U. filipendula* group that has pendulous thalli with a blackening main axis. For similar reasons, *Bryoria*, *Cladonia*, and crustose lichens were not identified to species in the field, and cover estimates were recorded for genera only. In general, inconspicuous crustose lichens were not carefully examined during field sampling. Removed plots, however, were thoroughly searched for crusts in the laboratory.

Nomenclature of macrolichens, microlichens, mosses, and liverworts followed McCune and Geiser 1997; Brodo et al. 2001; Anderson et al. 1990; and Stotler and Crandall-Stotler 1977, respectively. Voucher specimens are deposited in the Humboldt State University Cryptogamic Herbarium (HSC) as well as in the herbarium of Redwood National and State Parks.

Data analyses.—In order to reduce noise from infrequent species, epiphytes occurring in fewer than 5% of the plots were removed from the data matrix prior to all multivariate analyses. Bray-Curtis ordination was performed on the resulting primary matrix of 430 plots \times 31 species using the variance–regression method of endpoint selection and the Sørensen coefficient as the distance measure (McCune & Mefford 1999). Presence/absence species data were transformed by the Beals smoothing function prior to ordination analysis. This transformation smoothed patterns of joint occurrences of species and facilitated extraction of the dominant epiphyte compositional gradient (McCune 1994). Variance extracted by an ordination axis was expressed by the coefficient of determination between Euclidean distances in ordination space and Sørensen distances in the original species space. A secondary matrix of 430 plots \times 6 additional variables (i.e., height above ground, % sky, number of lichen species, number of bryophyte species, lichen cover, and bryophyte cover) was also constructed. Correlations among these variables and plot ordination scores were used to aid interpretation of the dominant compositional gradient.

We performed cluster analysis on the transposed primary matrix in order to delimit groups of epiphytes that shared similar habitats or substrate preferences (McCune & Mefford 1999). Following the rationale of McCune et al. 2000, log-transformed cover values were relativized by species sums of squares prior to this analysis, which used Ward's method of clustering and a Euclidean distance matrix, and the resulting dendrogram was scaled by Wishart's objective function converted to a percentage of information remaining.

We performed association analysis to test whether individual epiphyte species pairs co-occurred more or less often than expected by chance. A 2×2 contingency table was generated for each pair of the 31 species used in the

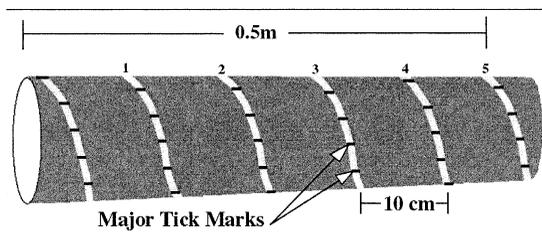


FIGURE 1. Spiral transect sampling involves wrapping a diameter tape five times around a 0.5 m section of branch such that each wrap is 10 cm apart. Species of epiphytes are recorded beneath tick marks that are π -cm apart.

TABLE 2. Epiphytes encountered on five Sitka spruce trees in an old-growth redwood forest. Cover of each taxon was calculated separately for the sheltered, intermediate, and exposed portions of the epiphyte compositional gradient, which represented 98.5% of the information in an ordination analysis of 430 plots containing 31 species. Frequencies were calculated separately for axes (branches >5 cm diameter) and branchlets (branches <5 cm diameter, including foliage). Frequency values for all *Bryoria* and *Usnea* species were derived from removed samples only. Each species' proportion of the total estimated biomass of epiphytes on the five trees (i.e., 294.3 kg) is also indicated. An asterisk (*) indicates species groups that were identified in the field by genus only. ** *Usnea cornuta* cover values include *U. chaetophora*, *U. cornuta*, *U. esperantiana*, *U. fragilesceus* var. *mollis*, *U. scabrata*, and *U. wirthii*. *** *Usnea filipendula* cover values include *U. filipendula* and *U. madeirensis*. *Orthotrichum papillosum*, = *O. lyellii* (Anderson et al. 1990). A dagger (†) indicates species found in study trees but outside plot boundaries.

Taxon	Code	Cover (%)			Frequency (%)		Biomass (% Total)
		Sheltered	Inter- mediate	Exposed	Axes	Branch- lets	
ALL EPIPHYTES		77.1	48.5	32.0			
CYANOLICHENS		0.2	5.8	7.0	25.2	71.0	
<i>Erioderma soreliatum</i>	ERSO					0.9	<0.1
<i>Lobaria oregana</i>	LOOR		0.3	0.5	3.4	11.2	0.8
<i>Lobaria pulmonaria</i>	LOPU	0.1	3.9	4.2	18.9	57.6	6.7
<i>Lobaria scrobiculata</i>	LOSC		0.3	0.6	8.7	32.6	0.4
<i>Nephroma bellum</i>	NEBE	<0.1	0.1	<0.1	1.0	12.9	0.1
<i>Nephroma helveticum</i>	NEHE			<0.1		0.4	<0.1
<i>Nephroma laevigatum</i>	NELA		<0.1			1.3	<0.1
<i>Pseudocyphellaria anomala</i>	PSAN		0.2	0.9	5.3	40.6	0.5
<i>Pseudocyphellaria anthraspis</i>	PSAP	<0.1	0.6	0.2	2.9	12.9	0.3
<i>Pseudocyphellaria crocata</i>	PSCR	<0.1	0.2	0.4	4.4	12.9	0.2
<i>Stictia limbata</i>	STLI	<0.1	<0.1	0.1	1.9	29.0	0.2
CHLOROLICHENS		3.5	8.0	11.8	82.0	87.1	
FRUTICOSE CHLOROLICHENS		0.2	3.3	6.4	42.2	79.9	
<i>Alectoria imshaugii</i>	ALIM					0.5	<0.1
<i>Alectoria vancouverensis</i>	ALVA	0.1	1.0	2.7	19.9	47.8	2.0
<i>Bryoria</i> spp.*	BRspp.	<0.1	<0.1	<0.1		2.4	5.8
<i>Bryoria capillaris</i>	BRCA					1.5	<0.1
<i>Bryoria fremontii</i>	BRFR					0.4	<0.1
<i>Bryoria furcellata</i>	BRFU					0.4	<0.1
<i>Bryoria trichodes</i> ssp. <i>americana</i>	BRTR					1.3	<0.1
<i>Cladonia</i> spp.*	CLspp.	1.4	0.4	<0.1	38.3	2.2	
<i>Cladonia chlorophaea</i>	CLCH					0.5	<0.1
<i>Cladonia furcata</i>	CLFU					0.5	<0.1
<i>Cladonia squamosa</i>	CLSQ					1.0	<0.1
<i>Cladonia subulate</i>	CLSU					0.5	<0.1
<i>Cladonia sulphurina</i>	CLSF					0.5	<0.1
<i>Cladonia transcendens</i>	CLTR				35.4	2.2	0.2
<i>Ramalina farinacea</i>	RAFA			<0.1		0.4	<0.1
<i>Ramalina roesleri</i>	RARO		<0.1	<0.1	1.0	1.8	<0.1
<i>Sphaerophorous globosus</i>	SPGL	0.1	0.4	0.1	19.4	14.3	0.1
<i>Usnea ceratina</i>	USCE					0.4	<0.1
<i>Usnea chaetophora</i>	USCH				2.0	7.8	<0.1
<i>Usnea cornuta</i> **	USCO	<0.1	1.3	2.3	26.5	66.7	0.9
<i>Usnea esperantiana</i>	USES				2.0	13.7	0.1
<i>Usnea filipendula</i> ***	USFI	<0.1	0.3	0.6	16.3	45.1	0.7
<i>Usnea fragilesceus</i> var. <i>mollis</i>	USFR				6.1	19.6	0.1
<i>Usnea longissima</i>	USLO	<0.1	0.1	0.2	6.1	7.8	0.3
<i>Usnea madeirensis</i>	USMA				8.2	11.8	0.1
<i>Usnea rubicunda</i>	USRU		<0.1	<0.1	2.0	19.6	<0.1
<i>Usnea scabrata</i>	USSC				2.0		<0.1
<i>Usnea wirthii</i>	USWI				6.1	45.1	0.1
FOLIOSE CHLOROLICHENS		<0.1	3.6	5.2	34.0	79.0	
<i>Cavernularia hultenii</i>	CAHU		<0.1	0.1	1.5	23.2	<0.1
<i>Cavernularia lophyrea</i>	CALO			<0.1		0.9	<0.1
<i>Cetrelia cetrarioides</i>	CECE			<0.1		0.4	<0.1
<i>Cetraria chlorophylla</i>	CECH		<0.1	<0.1	1.9	3.1	<0.1
<i>Heterodermia leucomelos</i>	HELE	<0.1	<0.1	0.1	2.9	40.2	0.1
<i>Hypogymnia apinnata</i>	HYAP	<0.1	2.4	3.3	25.7	59.8	1.8
<i>Hypogymnia enteromorpha</i>	HYEN					0.5	<0.1
<i>Hypogymnia imshaugii</i>	HYIM					0.5	<0.1
<i>Hypogymnia physodes</i>	HYPH					0.5	<0.1
<i>Menegazzia terebrata</i>	METE		<0.1	<0.1	0.5	1.3	<0.1

TABLE 2. Continued.

Taxon	Code	Cover (%)			Frequency (%)		Biomass (% Total)
		Sheltered	Inter- mediate	Exposed	Axes	Branch- lets	
<i>Parmelia hygrophila</i>	PAHY					0.4	<0.1
<i>Parmelia saxatilis</i>	PASA		<0.1	<0.1	0.5	0.9	<0.1
<i>Parmelia squarrosa</i>	PASQ	<0.1	0.2	0.4	10.2	25.0	0.1
<i>Parmelia sulcata</i>	PASU		<0.1	0.1	4.9	7.1	<0.1
<i>Parmotrema arnoldii</i>	PTAR		<0.1		1.0		<0.1
<i>Parmotrema chinense</i>	PTCH		<0.1	0.2	1.5	12.5	0.1
<i>Parmotrema crinitum</i>	PTCR	<0.1	0.8	1.0	14.6	57.1	0.8
<i>Platismatia glauca</i>	PLGL		<0.1	<0.1	0.5	1.8	<0.1
<i>Platismatia herrei</i>	PLHE		0.1	<0.1	3.4	0.4	<0.1
<i>Platismatia norvegica</i>	PLNO		<0.1		0.5		<0.1
CRUSTOSE CHLOROLICHENS		1.9	0.7	0.2	49.0	6.3	
<i>Calicium viride</i>	CAVI	0.1			0.5	0.4	<0.1
<i>Caloplaca</i> sp.	CAsp.				0.5		<0.1
<i>Graphis</i> sp.	GRsp.	<0.1			0.5		<0.1
<i>Lecanora</i> sp.	LEsp.					0.5	<0.1
<i>Lecanora pulicaris</i>	LEPU					0.5	<0.1
<i>Lecanora subfusca</i>	LESU					0.5	<0.1
<i>Lepraria</i> sp.	LEsp.	1.8	0.2	<0.1	37.4	0.9	<0.1
<i>Loxosporopsis corallifera</i>	LOCO	<0.1	<0.1		1.5		<0.1
<i>Mycoblastus sanguinarius</i>	MYSA		0.1		1.0		<0.1
<i>Ochrolechia</i> spp.*	OCspp.	<0.1	0.4	0.1	8.7	2.2	
<i>Ochrolechia juvenalis</i>	OCJU				7.8	2.2	<0.1
<i>Ochrolechia szatalaensis</i>	OCSZ				0.5		<0.1
<i>Ochrolechia trochophora</i>	OCTR				0.5		<0.1
<i>Pertusaria ophthalmiza</i>	PEOP		0.1	0.1	2.9	5.4	<0.1
<i>Thelotrema lepadinum</i>	THLE					0.4	<0.1
<i>Xylographa</i> sp.	XYsp.				0.5		<0.1
BRYOPHYTES		71.0	28.5	6.2	99.0	100.0	
MOSESSES		56.9	20.2	2.4	94.2	80.8	
<i>Antitrichia curtispindula</i>	ANCU	3.8	0.7	<0.1	16.5	10.3	5.8
<i>Aulacomnium androgynum</i> †	AUAN						<0.1
<i>Bryum capillare</i>	BMCA	0.2			1.5		<0.1
<i>Dicranum fuscescens</i>	DIFU	0.5	<0.1	<0.1	14.6	0.9	0.1
<i>Eurhynchium oreganum</i>	EUOR	0.6			0.5		0.6
<i>Hypnum circinale</i>	HYCI	<0.1			0.5		<0.1
<i>Isothecium cristatum</i> †	ISCR						<0.1
<i>Isothecium myosuroides</i>	ISMV	42.8	16.0	1.6	92.2	63.8	41.2
<i>Neckera douglasii</i>	NEDO	9.0	3.3	0.6	64.6	62.9	5.6
<i>Orthotrichum papillosum</i>	ORPA	0.1	0.3	0.2	9.2	17.4	0.1
<i>Plagiothecium undulatum</i>	PLUN	<0.1			0.5		<0.1
LIVERWORTS		14.1	8.3	3.8	96.1	98.2	
<i>Cephaloziella rubella</i>	CERU				0.5		<0.1
<i>Douinia ovata</i> †	DOOV						<0.1
<i>Frullania nisquallensis</i>	FRNI	6.8	6.4	3.7	93.2	97.8	4.7
<i>Porella navicularis</i>	PONA	7.3	1.7	0.1	65.0	27.2	3.3
<i>Radula bolanderi</i>	RABO	<0.1	0.2		3.4	0.4	<0.1
<i>Scapania bolanderi</i>	SCBO	<0.1			1.0		<0.1
FERNS		2.2	0.3		43.7	3.1	
<i>Polypodium glycyrrhiza</i>	POGL	1.9	0.2		39.8	2.7	8.4
<i>Polypodium scolieri</i>	POSC	0.3	0.1		4.4	0.4	13.3

Multivariate analyses. The likelihood ratio (G, Sokal & Rohlf 1995) was used as a test statistic.

RESULTS

The Sitka spruce trees surveyed in this study were between 82.5 to 92.2 m tall and 1.9 to 2.6 m diameter at breast height. The largest Sitka spruce, tree four, had twice as much axis length and trunk volume and almost three times as much foliar mass

as the other trees (Table 1). The proportion of axis length to foliar mass was similar among four of the trees (i.e., 2.9 to 3.6 m/kg), but tree one had a much higher ratio (i.e., 5.7 m/kg), because it was impacted by a disturbance event that left a number of broken branches in the middle of its crown. This declining tree also had numerous conks of the heart-rot fungus, *Phellinus pini* [(Thore.:Fr.) A. Ames.].

TABLE 3. Epiphyte species diversity associated with various sample groupings on five Sitka spruce trees in an old-growth redwood forest. Species richness was expressed as the mean number of species per plot \pm one standard deviation. Beta diversity was calculated by dividing the total number of species within a group by the mean number of species per plot within a group. Samples sizes are indicated in parentheses.

Sample delineation	Species richness	Beta diversity	Total number of species
By epiphyte group (430)			
Bryophytes	3.2 \pm 1.3	4.7	17
Lichens	5.5 \pm 4.2	13.3	72
Cyanolichens	1.3 \pm 1.7	8.3	11
Chlorolichens	4.1 \pm 3.1	15.0	61
Ferns	0.2 \pm 0.4	8.8	2
By substrate			
Axes (206)	7.0 \pm 2.6	8.5	60
Branchlets (224)	9.2 \pm 3.9	5.7	52
By ordination stratum			
Sheltered (143)	5.8 \pm 2.0	6.9	40
Intermediate (144)	8.1 \pm 3.3	7.1	57
Exposed (143)	10.8 \pm 3.4	4.9	53

The epiphyte flora of Sitka spruce in a redwood forest.—We encountered a total of 91 epiphyte species on the five trees, including 57 macrolichens, 15 crustose lichens, 11 mosses, six liverworts, and two ferns (Table 2). Ten species contributed more than 1% of total epiphyte biomass, including three mosses (*Isoetecium myosuroides*, *Antitrichia curtipendula*, and *Neckera douglasii*), two liverworts (*Frullania nisquallensis* and *Porella navicularis*), one cyanolichen (*Lobaria pulmonaria*), two chlorolichens (*Alectoria vancouverensis* and *Hypogymnia apinnata*), and both *Polypodium* ferns (Table 2). Beta diversity was nearly three times higher for lichens than for bryophytes, but plot-level species richness was similar for lichens and bryophytes (Table 3). Branchlet plots supported more epiphyte species and had a more consistent species composition (i.e., lower beta diversity) than axis plots even though we encountered more species on axes than branchlets overall (Table 3).

Epiphyte biomass and proportions of epiphyte groups were very different on axes and branchlets (Table 4). Axes supported 83% of the epiphyte biomass and 98% of the mass of dead organic matter

on a tree's branch systems. Overall, the mass of dead organic matter was higher than epiphyte biomass (69 vs. 31% of total mass). Bryophytes accounted for 62% of the total epiphyte biomass and were much more abundant on axes than branchlets (92 vs. 8% of bryophyte biomass). Lichens, on the other hand, were less abundant on axes than branchlets (27 vs. 73% of lichen biomass). Ferns contributed the remainder of epiphyte biomass (22%) and were nearly restricted to axes.

Bryophytes clearly dominated epiphyte communities on Sitka spruce, forming thick mats that consistently covered branch surfaces in the lower two-thirds of the crowns. Relatively high cover of both mosses and liverworts occurred throughout tree crowns on axes, but bryophyte cover was quite low on branchlets (Fig. 2). The moss *Isoetecium myosuroides* was the most abundant species, contributing over 41% of total epiphyte biomass. The liverwort *Frullania nisquallensis* occupied the broadest range of epiphytic habitats, occurring in 96% of all plots sampled (Table 2).

Polypodium ferns were most abundant between 40 and 50 m above the ground, although small amounts of ferns occurred nearly to the treetops (Fig. 2). Despite contributing over 13% of total epiphyte biomass, *P. scouleri* occurred in less than 5% of the plots and was not among the 31 species considered in multivariate analyses. Biomass estimates for *P. scouleri* were derived from Sillett and Bailey (2003), who sampled every fern mat on the five trees ($n = 89$). According to these estimates, over 60% of fern biomass was attributable to *P. scouleri*. We probably underestimated biomass of *P. glycyrrhiza*, because some of our sampling occurred during the early fall when this deciduous species has no leaves.

Cyanolichens contributed less to overall epiphyte biomass than bryophytes and ferns, but they were slightly more abundant than chlorolichens (Table 4). *Lobaria pulmonaria* was by far the most abundant cyanolichen with nearly three times as much biomass as all other cyanolichens combined. Cyanolichens were scarce in the lower crowns, but they were less restricted in their vertical range than most chlorolichens (Fig. 2). This broader distribution is also reflected by the lower beta diversity for cyanolichens than chlorolichens (Table 3).

TABLE 4. Estimated masses of epiphytes and associated dead organic matter (DOM) on axes (branches >5 cm diameter) and branchlets (branches <5 cm diameter) of five Sitka spruce trees in an old-growth redwood forest. Values are mean dry masses (kg) per tree \pm one standard error.

	Bryophytes	Cyanolichens	Chlorolichens	Ferns	Biomass	DOM
Axes	33.3 \pm 8.3	1.6 \pm 0.5	1.1 \pm 0.4	12.7 \pm 2.1	48.7 \pm 8.0	128.1 \pm 19.5
Branchlets	2.9 \pm 0.8	3.9 \pm 1.5	3.4 \pm 1.2	0.0 \pm 0.0	10.2 \pm 1.5	2.8 \pm 0.6

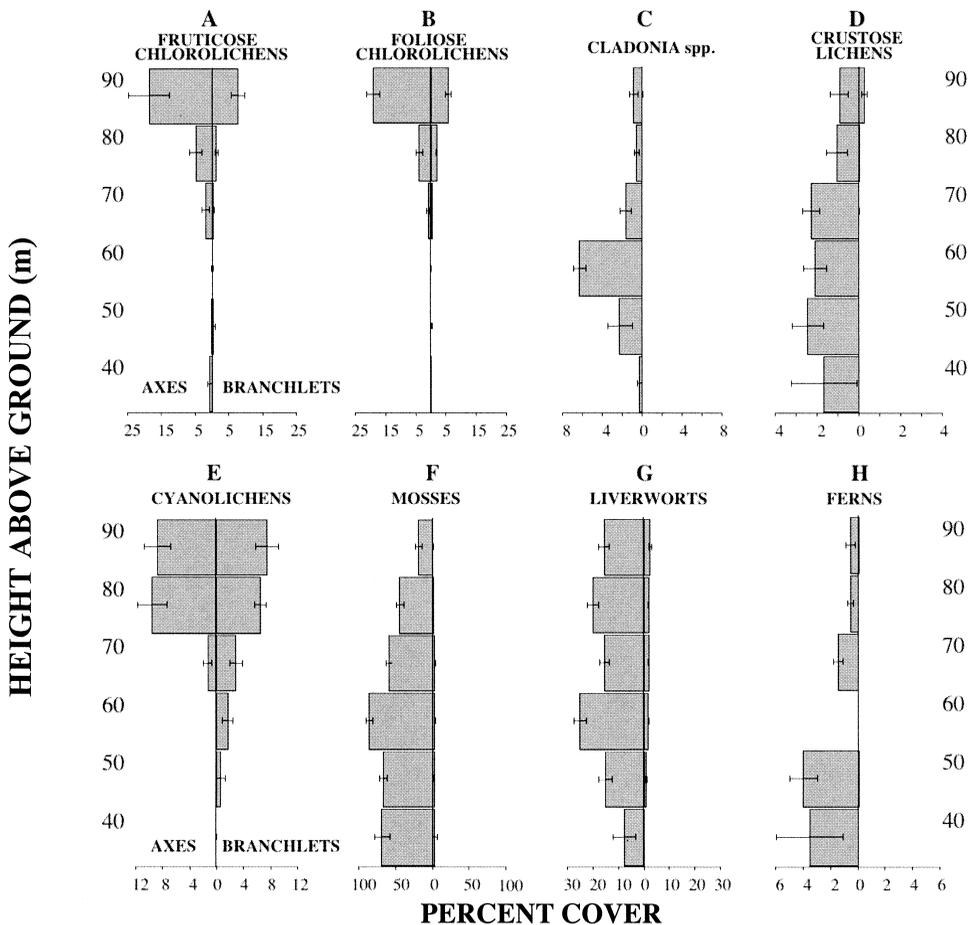


FIGURE 2. Epiphyte cover in 10 m height strata for axes and branchlets on Sitka spruce in an old-growth redwood forest. Values are means \pm one standard error ($n = 5$ trees).

Two-thirds of all epiphyte species encountered on the five trees were chlorolichens. These species were divided into four morphological groups that varied in abundance and distribution. Foliose and fruticose chlorolichens were mostly restricted to the upper crowns and represented the bulk of chlorolichen biomass. Together, these groups covered nearly 40% of the tree surfaces in the top 10 m of the crowns (Fig. 2). Crustose lichens and *Cladonia* were more widely distributed, reaching peak abundances on axes between 50 and 70 m above the ground (Fig. 2).

Associations among epiphytes.—There were many positive and negative associations among the 31 epiphyte species investigated in the multivariate analyses (Fig. 3). It is precisely because of these numerous associations that multivariate data reductions via ordination and cluster analyses were so successful (see below). Most bryophyte species co-occurred in mats except for *Orthotrichum papillosum*, which often intermingled with lichens, especially *Parmotrema crinitum*, on branchlets. Asso-

ciations among lichens were both positive and negative and did not clearly relate either to type of photobiont or to thallus morphology. The only lichens positively associated with bryophytes were *Cladonia* and *Lepraria*. These lichens were, in turn, negatively associated with many other lichen species. *Lepraria* was typically found on the undersides of large branches supporting thick overlying bryophyte mats. The fern *P. glycyrrhiza* always occurred amidst bryophyte mats. Multivariate analyses provided further insights on species-habitat relationships.

Dominant compositional gradient.—The Bray-Curtis ordination performed on Beals-smoothed presence-absence data extracted one axis explaining 98.5% of the total variation in the species data. Height ($r = 0.63$), % sky ($r = 0.66$), lichen species richness ($r = 0.76$), and lichen cover ($r = 0.35$) were positively correlated, while bryophyte species richness ($r = -0.60$) and bryophyte cover ($r = -0.72$) were negatively correlated with ordination scores along this gradient. Ranking all 430 plots by

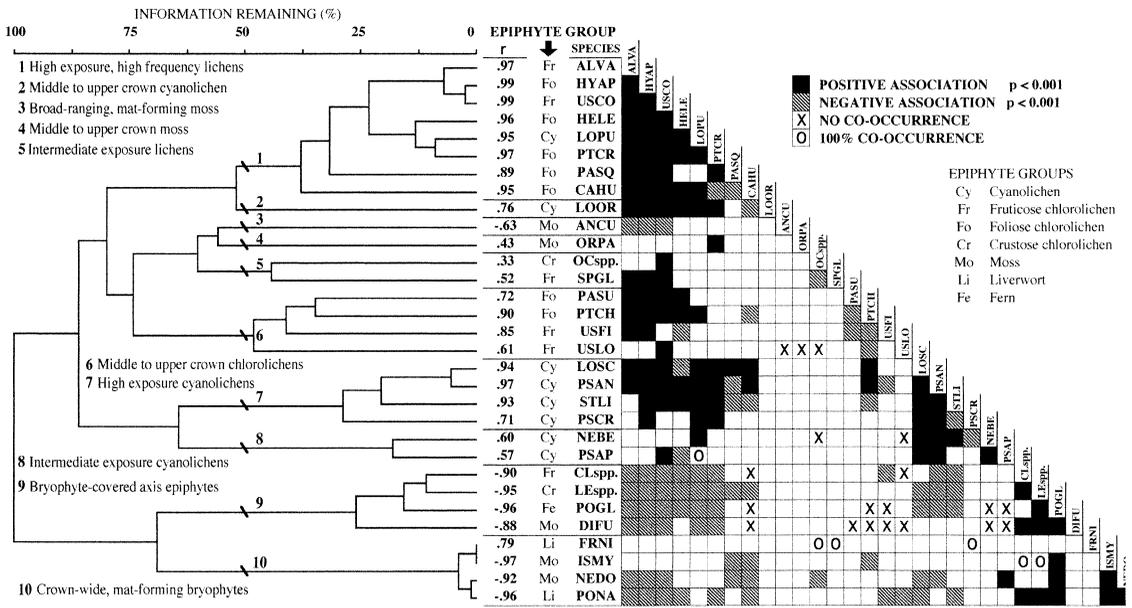


FIGURE 3. Dendrogram (left) and associations analyses (right) for epiphytes on Sitka spruce trees in an old-growth redwood forest. Each square in the associations grid represents the result of a 2 by 2 contingency table for a species pair. Only species occurring in 5% or more of the sampled plots are included. Shaded squares indicate statistically significant positive or negative associations. An X indicates that the species pair did not co-occur in any sampled plot. An O indicates 100% co-occurrence for the less frequent species of the pair. Order of species was determined by the dendrogram. Ten species groups are indicated at the level of 50% information remaining on the dendrogram. Correlations of species along the dominant compositional gradient are also listed. Refer to Table 2 for full names of species codes.

ordination scores and dividing the ranked list into thirds assisted with the interpretation of the gradient. The resulting three sets of plots were classified as exposed, intermediate, and sheltered (see Discussion). Exposed plots occurred predominately on branchlets in outer and upper crowns, intermediate plots were on axes in middle to upper crowns and on branchlets in middle to lower crowns, and sheltered plots were mostly restricted to axes in middle to lower crowns (Fig. 4).

Epiphyte composition among the three groups of plots varied dramatically (Fig. 5). Exposed plots were dominated by chlorolichens with roughly equivalent amounts of co-occurring cyanolichens and bryophytes. Liverworts dominated the bryophyte component in exposed plots. Sheltered plots were overwhelmingly dominated by bryophytes with very little lichen cover. In sheltered plots, crustose lichens (93% *Lepraria*) and *Cladonia* dominated the lichen component, and mosses dominated the bryophyte component. Intermediate plots were dominated by mosses with roughly equivalent amounts of co-occurring liverworts, cyanolichens, and chlorolichens. Exposed plots had the lowest beta diversity (Table 3), indicating the relatively homogenous distribution of macrolichens in this portion of the gradient.

Species groups.—Cluster analysis revealed dis-

tinct groups of species that had similar distribution patterns within the crowns. The dendrogram was trimmed at the level of 50% information remaining, and the resulting ten groups were interpreted by graphically combining the dendrogram with results from ordination and association analyses (Fig. 3) and by examining scatterplot distributions of individual species (Fig. 6). Species within a group tended to be positively associated with each other, have similar associations with other species, and have similar distributions within the crowns.

Vertical distribution patterns as well as affinities for axes versus branchlets varied considerably among the ten groups of species. Some groups contained species that occurred throughout the crowns, while others contained species with more limited distributions. Each group of species is described below.

1. High exposure, high frequency lichens: *Alectoria vancouverensis*, *Hypogymnia apinnata*, *Usnea cornuta*, *Heterodermia leucomelos*, *Lobaria pulmonaria*, *Parmotrema crinitum*, *Parmelia squarrosa*, and *Cavernularia hultenii*. These species were most frequent and abundant in upper crowns, but they also occurred in middle and sometimes lower crowns. *Heterodermia* and *Cavernularia* were both nearly restricted to branchlets (Fig. 6 [1A–H]).

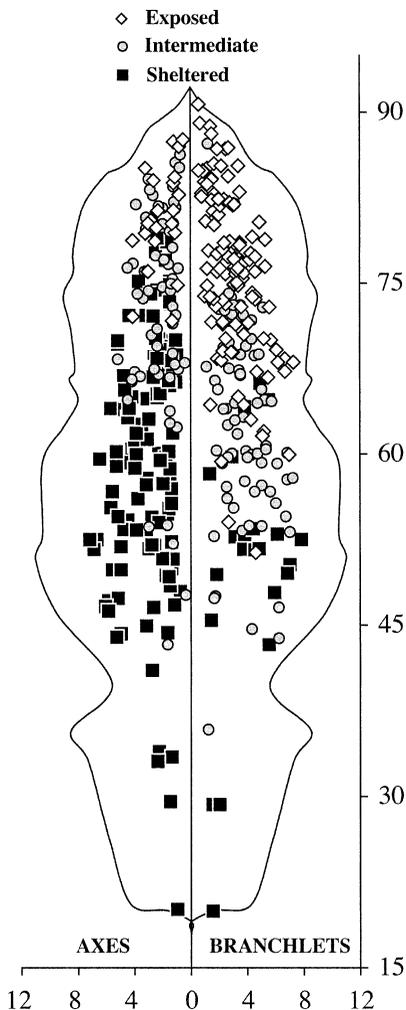


FIGURE 4. Spatial distribution of 430 sample plots on axes and branchlets of five Sitka spruce trees in an old-growth redwood forest. Classifications of the plots as exposed, intermediate, and sheltered were based upon ordination analysis of sample plots in species space.

2. Middle to upper crown cyanolichen: *Lobaria oregana*. Although similar in crown distribution to *Lobaria pulmonaria*, *L. oregana* was much less frequent and abundant. Both *Lobaria* species contrasted with other cyanolichens by occupying axes nearly as often as branchlets. *Lobaria oregana* was the only cyanolichen not encountered below 65 m (Fig. 6 [2]).

3. Broad-ranging, mat-forming moss: *Antitrichia curtispindula*. This relatively infrequent moss was abundant when found on axes within the lower two-thirds of the crowns, but it also occurred on branchlets in middle to lower crowns and occasionally even on axes in upper crowns (Fig. 6 [3]).

4. Middle to upper crown moss: *Orthotrichum papillosum*. This moss was the only bryophyte more abundant in exposed and intermediate plots

than in sheltered plots. It was more frequent on branchlets than axes (Fig. 6 [4]).

5. Intermediate exposure lichens: *Ochrolechia* and *Sphaerophorus globosus*. These taxa had their greatest abundance on intermediate exposure plots (Table 2), but they were negatively associated with each other. *Ochrolechia* typically covered bare bark on axes, whereas *Sphaerophorus* often occurred amidst bryophyte mats or on branchlets (Fig. 6 [5A,B]).

6. Middle to upper crown chlorolichens: *Parmelia sulcata*, *Parmotrema chinense*, *Usnea filipendula*, and *Usnea longissima*. These chlorolichens did not extend into uppermost crowns and were less frequent than chlorolichens of group 1. *Parmelia sulcata* and *Usnea filipendula* were nearly as frequent on axes as branchlets, while the other two species were much more frequent on branchlets (Fig. 6 [6A–D]).

7. High exposure cyanolichens: *Lobaria scrobiculata*, *Pseudocyphellaria anomola*, *Sticta limbata*, and *Pseudocyphellaria crocata*. These cyanolichens occurred nearly to the treetops, and they were much more frequent on branchlets than axes, especially *Sticta* (Fig. 6 [7A–D]).

8. Intermediate exposure cyanolichens: *Nephroma bellum* and *Pseudocyphellaria anthraspis*. Unlike all other cyanolichens, these species were most abundant on intermediate exposure plots (Fig. 6 [8A,B]).

9. Bryophyte-covered axis epiphytes: *Cladonia*, *Lepraria*, *Polypodium glycyrrhiza*, and *Dicranum fuscescens*. These species were found almost exclusively on axes covered with bryophyte mats. *Cladonia*, *Lepraria*, and *P. glycyrrhiza* exhibited broad vertical distributions, whereas *Dicranum* was nearly absent from upper crowns (Fig. 6 [9A–D]).

10. Crown-wide, mat-forming bryophytes: *Frullania nisquallensis*, *Isoetecium myosuroides*, *Neckera douglasii*, and *Porella navicularis*. These bryophytes were distributed throughout the crowns on both axes and branchlets, but their cover was consistently higher on axes. *Frullania* was the only member of the group that was more frequent on branchlets than axes (Table 2), thus explaining its positive correlation along the dominant compositional gradient (Fig. 6 [10A–D]).

DISCUSSION

Epiphytes on Sitka spruce vs. Douglas-fir.—Quantitative comparisons between epiphyte communities on Sitka spruce and Douglas-fir are possible because of the extensive research on Douglas-fir epiphytes (e.g., Clement & Shaw 1999; McCune 1993; McCune et al. 2000; Pike et al. 1975; Sillett 1995). Douglas-fir and Sitka spruce are the second

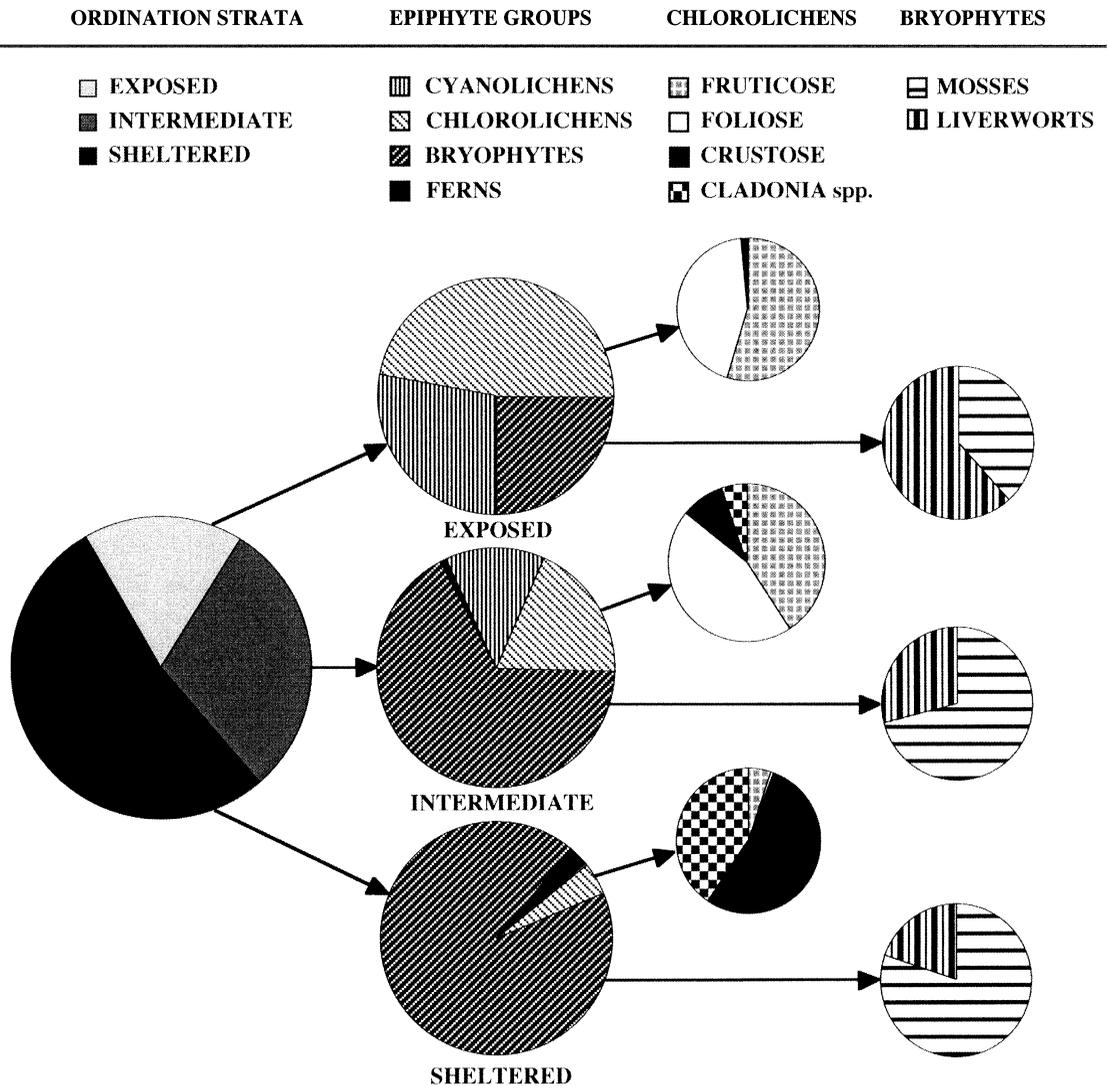


FIGURE 5. Relative proportions of tree total epiphyte cover for exposed, intermediate, and sheltered portions of the dominant compositional gradient on five Sitka spruce trees in an old-growth redwood forest. Classifications as exposed, intermediate, and sheltered were based upon ordination analysis of sample plots in species space. Ferns in this diagram include only *P. glycyrrhiza*.

and third tallest tree species on Earth, respectively; only coast redwood is taller. Both species, which are members of Pinaceae, also have a high affinity for epiphytes, and their geographic ranges overlap. Differences include shade tolerance (Sitka spruce > Douglas-fir) and habitat preference (i.e., Sitka spruce is restricted to moist, low elevation coastal forests, while Douglas-fir extends into higher elevations in drier, more continental climates; Burns & Honkala 1990). Sitka spruce also differs from Douglas-fir in having persistent leaf bases on its twigs.

There is substantial overlap in epiphyte species composition between Sitka spruce and Douglas-fir, but there are some important floristic differences.

The high diversity of *Usnea* (11 spp.) on Sitka spruce in this study contrasts with the low diversity (3 spp.) observed on Douglas-fir by McCune et al. (2000). *Hypogymnia* diversity is surprisingly low on Sitka spruce with all but three of 185 occurrences being *H. apinnata* in this study. Eight and seven species of this genus were reported on Douglas-fir by McCune et al. (2000) and Sillett (1995), respectively. Several cyanolichens reported on Douglas-fir did not occur on the Sitka spruce we studied, including *Nephroma occultum*, *Pseudocyphellaria rainierensis*, and *Sticta weigeli*. These old-growth associated species (see Rosentreter 1995; Sillett & Neitlich 1996) apparently reach the southern limits of their geographic ranges in

Oregon. Finally, the chlorolichens *Heterodermia leucomelos*, *Parmelia squarrosa*, *Parmotrema crinitum*, *Ramalina roesleri*, *Usnea rubicunda*, and *U. wirthii* and the cyanolichen *Erioderma soledatum* have not yet been reported on Douglas-fir.

Several bryophytes reported on both Douglas-fir and Sitka spruce differed markedly in their abundance on the two tree species. *Antitrichia curtipendula* was the most abundant moss in a 700-year-old Douglas-fir forest (Sillett 1995), while *Isothecium myosuroides* was seven times more abundant than *A. curtipendula* on Sitka spruce in this study. *Douinia ovata* can be abundant on Douglas-fir, covering the lower surfaces of large, moss-laden branches (Sillett 1995). We found *D. ovata* only twice on Sitka spruce, and both times it was outside plot boundaries. *Frullania nisquallensis* was the most abundant liverwort in this study, but it was much more sparsely distributed in the 450-year-old and 700-year-old Douglas-fir forests studied by Pike et al. (1975) and Sillett (1995), respectively. This tenacious liverwort occurred on nearly every available substrate throughout Sitka spruce crowns, including bark, foliage, and even other epiphytes.

Cyanolichen abundance also differed between this study and previous studies of Douglas-fir. *Lobaria oregana* is consistently reported as the dominant epiphytic lichen in old-growth Douglas-fir forests, but *L. pulmonaria* was far more abundant than *L. oregana* on the five Sitka spruce trees surveyed in this study. However, we did observe an incredibly high quantity of *L. oregana* on a 97-m-tall Sitka spruce tree in Prairie Creek Redwoods State Park (Sillett & Ellyson, unpubl.). Such tree-to-tree variation in *L. oregana* abundance may be a consequence of this species' very limited dispersal capabilities (Sillett et al. 2000a,b). The paucity of epiphytic bryophytes and cyanolichens on redwoods suggests that this tree species may not provide suitable habitats for many species, including *L. oregana*. The overwhelming dominance of redwoods in these forests may present a problem for slowly dispersing epiphytes; suitable trees may be spatially distant in a forest composed mostly of inhospitable redwoods. Dispersal limitations may also be invoked to explain the otherwise puzzling absence of *Peltigera britannica* on Sitka spruce. This cyanolichen, which does occur in northern California, is associated with bryophyte mats in old-growth Douglas-fir forest canopies (Sillett 1995). Suitable substrates for *P. britannica* are thus plentiful on Sitka spruce.

Tree-to-tree variation.—Of the 91 species of epiphytes encountered in this study, 32 of these were found on a single tree, while only 30 species were found on all five trees. High tree-to-tree variation in epiphyte communities is also indicated by the

reduction in beta diversity when calculated for individual trees (mean = 6.3) compared to all five trees together (10.1). Dispersal limitations of epiphytes probably contributed to this heterogeneity, but variation in canopy structure may also be important.

While the five study trees varied somewhat in size, site-to-site variation in canopy structure appears to be more important to epiphytes than tree size itself. Only tree three had a non-emergent upper crown and was closely surrounded by tall, neighboring trees. On average, plots in this tree were less exposed to sunlight than plots in the other trees (38% vs. 49% sky, one-way ANOVA, $F = 3.8$, $p < 0.005$). Ten species were found only on this tree, including two normally terrestrial mosses (i.e., *Eurhynchium oreganum* and *Plagiothecium undulatum*). Aboveground adventitious roots were also found amidst bryophyte mats on several of its branches. These roots had well-developed ectomycorrhizal associations with *Leucopaxillus amarus* [(Alb. & Schw.:Fr.) Kühn.], whose mushrooms were found on the branches. Dense shading, terrestrial mosses, and the presence of canopy roots suggest that epiphytes on tree three were subject to a more humid, sheltered environment than epiphytes on the other four trees.

Whole-tree epiphyte mass estimates.—Excluding large redwoods, which can support hundreds of kg of ferns alone (Sillett & Bailey 2003), our mass estimates indicate that Sitka spruce in redwood forests can support more epiphytic material (i.e., 59 kg biomass and 131 kg dead organic matter per tree) than any conifer previously studied. For comparison, Pike et al. (1977) found 17.8 kg of epiphytes per tree on Douglas-fir in Oregon, Clement and Shaw (1999) found 27.1 kg of epiphytes per tree on Douglas-fir in Washington, and Rhoades (1981) found 12.8 kg of epiphytes per tree on subalpine fir [*Abies lasiocarpa* (Hook.) Nutt.].

Biomass ratios of bryophytes, cyanolichens, and chlorolichens vary greatly among the coniferous forests for which whole-tree estimates of epiphyte biomass are available (i.e., 8:1:1 in this study, 1:5:1 in Pike et al. 1977, 1:1:11 in Clement & Shaw 1999, and 1:3:2 in Rhoades 1981). Sitka spruce is the only tall conifer surveyed to date with a higher bryophyte than lichen biomass. The relatively small proportions of chlorolichen and cyanolichen biomass on Sitka spruce are likely due to the vertical displacement of lichens by bryophytes in very wet forests (Sillett & Goward 1998; Sillett & Neitlich 1996). In merely moist forests, bryophytes are restricted to the lower and middle canopy, cyanolichens dominate the middle canopy, and chlorolichens are most abundant in the upper canopy (McCune 1993; Sillett & Rambo 2000). In relatively dry for-

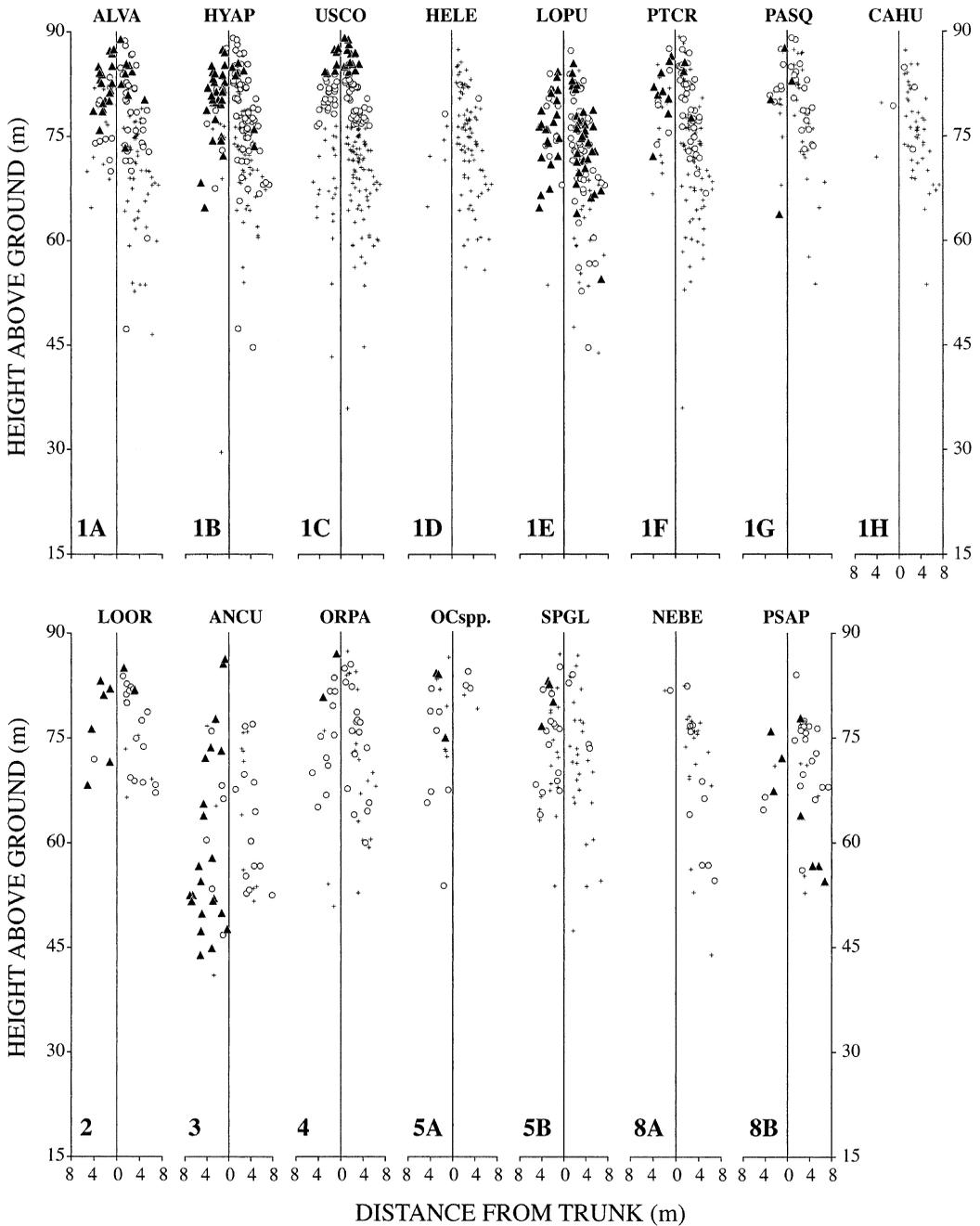


FIGURE 6. Distribution of 31 epiphyte species on five Sitka spruce trees in an old-growth redwood forest. Graphs depict crown locations of each plot containing a given species among the 430 plots sampled on all five trees. Symbols indicate cover of epiphytes. A plus sign (+) indicates less than 1% cover, an open circle indicates 1 to 5% cover, and a black triangle indicates greater than 5% cover. Axis plots are displayed on the right, and branchlet plots are displayed on the left side of each graph. Epiphyte species are presented in ten groups derived from cluster analysis (see dendrogram in Fig. 3).

ests, bryophytes and cyanolichens are scarce, and chlorolichens dominate the canopy (Clement & Shaw 1999).

Epiphyte gradients in tall forests.—The fact that epiphyte composition changes with height has been

well documented in many forests. There are pronounced changes in microclimatic conditions from the top to the bottom of forests that are particularly relevant to poikilohydric epiphytes. Humidity decreases and exposure to desiccating wind increases

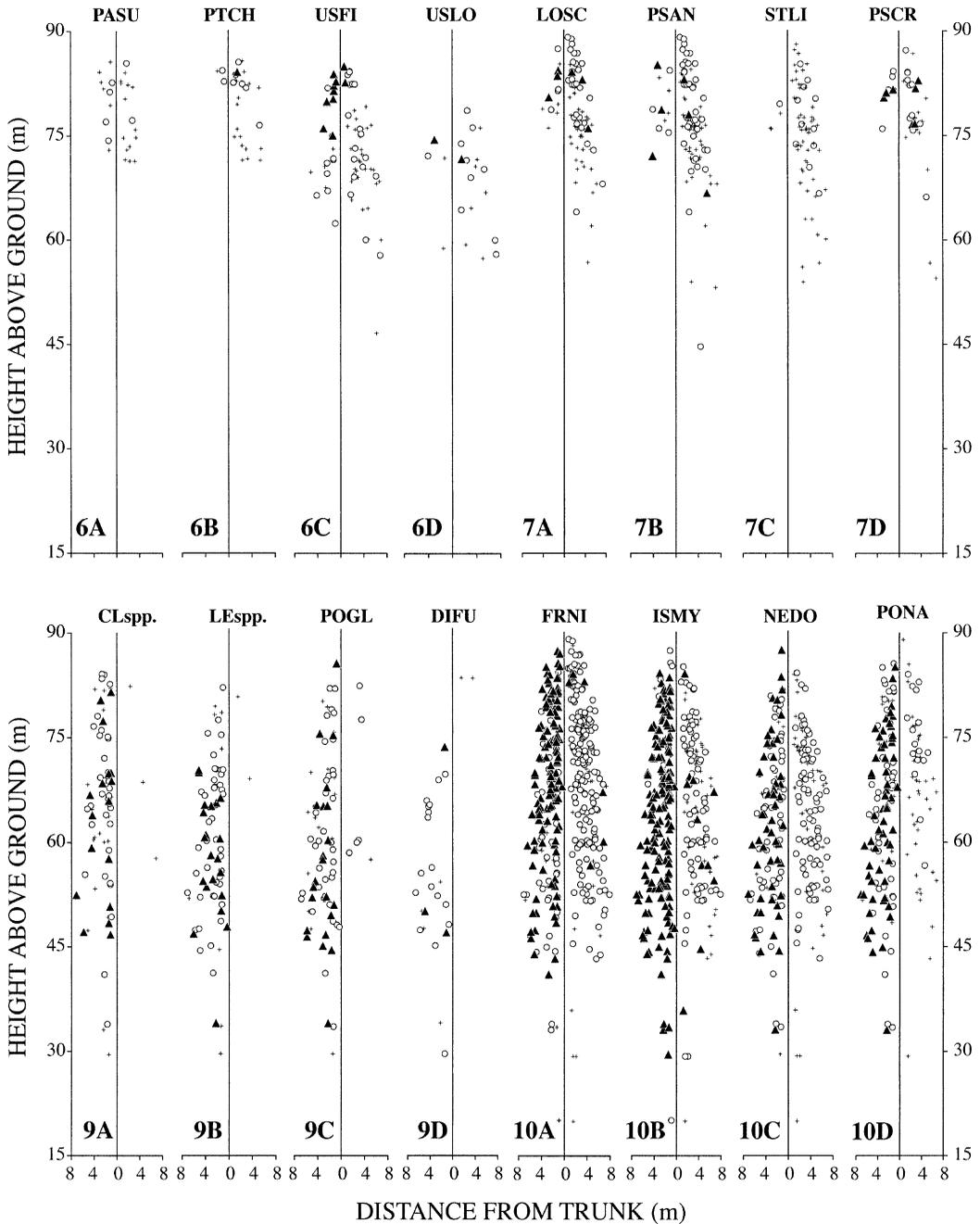


FIGURE 6. Continued.

with height in the canopy (Campbell & Coxson 2001; Parker 1995). Since individual species vary in desiccation tolerance, epiphyte communities are strongly stratified by height, especially in tall, moist forests (McCune 1993; McCune et al. 2000).

We interpreted the dominant compositional gradient in Sitka spruce epiphyte communities as an exposure gradient because of positive correlations between ordination scores and both height and %

sky as well as the predictable, associated changes in epiphyte communities along such a gradient (i.e., increasing lichen and decreasing bryophyte diversity). And while the vertical component of the exposure gradient is particularly pronounced in an old-growth redwood forest, a horizontal component to this gradient also exists. Exposure to desiccation probably increases along branch systems from axes in the inner crown to branchlets in the outer crown.

In this study, exposed plots extended much farther down in the crowns on branchlets than on axes. A downward extension of exposed plots was also observed along the clearcut edge of an old-growth Douglas-fir forest (Sillett 1995). However, community-level differences between axes and branchlets probably represent an interplay between desiccation tolerance and succession. Desiccation sensitive epiphytes (e.g., many bryophytes) may be unable to survive in the xeric environment of exposed sites in upper and outer crowns, while desiccation tolerant epiphytes (e.g., many lichens) may be unable to compete with aggressive, mat-forming bryophytes in the mesic environment of sheltered sites in lower and inner crowns. Manipulative experiments (e.g., Stone 1989) are needed to evaluate the relative importance of these factors for epiphytes on Sitka spruce.

Ecological importance of Sitka spruce epiphytes.—Lichens, bryophytes, and ferns co-exist on Sitka spruce branches, but the overwhelming dominance of bryophytes is indicative of a losing successional battle for most lichens. Relentless bryophytes cover entire axes, often doubling the apparent basal diameters of branches. Only foliated branchlets remain free of these mats. The immense surface areas of sponge-like bryophyte mats promote nutrient capture from leachates and throughfall (Nadkarni 1986), and their high water holding capacity increases moisture availability for associated organisms (Sillett & McCune 1998; Veneklaas et al. 1990).

In addition to *Polypodium* ferns and a few lichens, a wide variety of other organisms flourish amidst bryophytes on Sitka spruce. We regularly observe fungi, mollusks, annelids, and arthropods on thick bryophyte mats during the rainy season. Rodents, marbled murrelets (*Brachyramphus marmoratus*), and wandering salamanders (*Aneides vagrans*) also utilize these mats. These epiphytes may therefore serve a critical role in maintaining the biodiversity of redwood forest canopies.

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